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Neuroimaging investigations of cortical specialisation for different types of semantic knowledge

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Declaration

a) This thesis was composed by the student.

b) The work comprising this thesis is the student's own.

c) The work has not been submitted for any other degree or professional qualification.

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Contents

Lay summary

This thesis explores how our understanding of words and concepts is connected to our experiences of the world around us. Some theories suggest that our knowledge is closely tied to our ability to move and sense things. This thesis focused on two main questions: First, are the brain regions responsible for our sensory processing involved in understanding the meaning of words? Second, how does the brain help us to cut the world into pieces, and perceive these pieces together as a whole thing?

For the first question, researchers used brain imaging and studies of brain damage to look at how our brain processes concepts related to actions and senses. Some theories say that our brain recreates these experiences when we understand words, while others say this might not be necessary. The researchers found evidence that brain regions connected to vision and motion play a role in understanding action-related concepts. However, there's still debate about how exactly this works.

In terms of motion concepts, there is a part of the brain known as V5 that's important. The V5 is involved in sensing visual movements (e.g., seeing a cow jumped over a fence). Some studies say that the V5 activity helps with understanding motion-related concepts (e.g., understanding the sentence 'a cow jumped over a fence'). But others disagree. By using different types of brain imaging analyses, my research found that V5 is involved in understanding motion events. This information helps us understand how the brain processes the meaning of motion-related words.

The second question focused on how the brain helps categorizing concepts in the world and understanding associations between different things. Some researchers say that the anterior temporal lobe (ATL) is the main hub for this. However, other researchers claim that ATL is mainly for categorizing and understanding the features of single objects. These researchers also suggest that temporoparietal junction, TPC, is important for understanding information relating to actions and places. This TPC has a region called angular gyrus that is involved in understanding sentences and events. My research tested these ideas by conducting various experiments.

I first looked at how our brain understands two types of relationships: taxonomic relations where things are in the same category (like 'dog' and 'wolf'), and thematic relations where things are connected in events or scenes (like 'dog' and 'bone'). Some studies have claimed that ATL is more involved in processing taxonomic relations, and TPC in. I did a meta-analysis of many studies and found that thematic relations are more related to action and location processing regions in TPC. Then I tested people's speed to make judgements about object words, finding that thinking about actions and places facilitated thematic judgements. However, processing colours and shapes did not facilitate taxonomic judgements. This shows that TPC could be specialised for thematic relations because these involve understanding actions and places.

Finally, I looked at how the brain processes the meanings of objects and events. Previous research has suggested a part of ATL, the vATL, was mainly involved understanding object similarities, while angular gyrus is specialised for understanding events. Through analysing neuroimaging data, I found that both vATL and AG are involved in understanding events, and vATL may be more involved in this than in understanding objects. This supports the idea that AG is important for event comprehension, although the performance of vATL is different from what was thought before.

Overall, research of the thesis helps us reveal when we understand language, how the brain connects our life experiences to the meanings of words. It also sheds light on how different parts of the brain work together to create our understanding of the world around us: how we distinguish concepts from each other and how we connect them together.

Abstract

Embodied theories proposed that semantic knowledge is grounded in motor and perceptual experiences. This leads to two questions: (1) whether the neural underpinnings of perception are also necessary for semantic cognition; (2) how do biases towards different sensorimotor experiences cause brain regions to specialise for particular types of semantic information. This thesis tackles these questions in a series of neuroimaging and behavioural investigations.

Regarding question 1, strong embodiment theory holds that semantic representation is reenactment of corresponding experiences, and brain regions for perception are necessary for comprehending modality-specific concepts. However, the weak embodiment view argues that reenactment may not be necessary, and areas near to perceiving regions may be sufficient to support semantic representation.

In the particular case of motion concepts, lateral occipital temporal cortex (LOTC) has been long identified as an important area, but the roles of its different subregions are still uncertain. Chapter 3 examined how different parts of LOTC reacted to written descriptions of motion and static events, using multiple analysis methods. A series of anterior to posterior sub-regions were analyzed through univariate, multivariate pattern analysis (MVPA), and psychophysical interaction (PPI) analyses. MVPA revealed strongest decoding effects for motion vs. static events in the posterior parts of LOTC, including both visual motion area (V5) and posterior middle temporal gyrus (pMTG). In contrast, only the middle portion of LOTC showed increased activation for motion sentences in univariate analyses. PPI analyses showed increased functional connectivity between posterior LOTC and the multiple demand network for motion events. These findings suggest that posterior LOTC, which overlapped with the motion perception V5 region, is selectively involved in comprehending motion events, while the anterior part of LOTC contributes to general semantic processing.

Regarding question 2, the hub-and-spoke theory suggests that anterior temporal lobe (ATL) acts as a hub, using inputs from modality-specific regions to construct multimodal concepts. However, some researchers propose temporal parietal cortex

(TPC) as an additional hub, specialised in processing and integrating interaction and contextual information (e.g., for actions and locations). These hypotheses are summarized as the "dual-hub theory" and different aspects of this theory were investigated in in Chapters 4 and 5.

Chapter 4 focuses on taxonomic and thematic relations. Taxonomic relations (or categorical relations) occur when two concepts belong to the same category (e.g., 'dog' and 'wolf' are both canines). In contrast, thematic relations (or associative relations) refer to situations that two concepts co-occur in events or scenes (e.g., 'dog' and 'bone'), focusing on the interaction or association between concepts. Some studies have indicated ATL specialization for taxonomic relations and TPC specialization for thematic relations, but others have reported inconsistent or even converse results. Thus Chapter 4 first conducted an activation likelihood estimation (ALE) meta-analysis of neuroimaging studies contrasting taxonomic and thematic relations. This found that thematic relations reliably engage action and location processing regions (left pMTG and SMG), while taxonomic relations only showed consistent effects in the right occipital lobe. A primed semantic judgement task was then used to test the dual-hub theory's prediction that taxonomic relations are heavily reliant on colour and shape knowledge, while thematic relations rely on action and location knowledge. This behavioural experiment revealed that action or location priming facilitated thematic relation processing, but colour and shape did not lead to priming effects for taxonomic relations. This indicates that thematic relations rely more on action and location knowledge, which may explain why the preferentially engage TPC, whereas taxonomic relations are not specifically linked to shape and colour features. This may explain why they did not preferentially engage left ATL.

Chapter 5 concentrates on event and object concepts. Previous studies suggest ATL specialization for coding similarity of objects' semantics, and angular gyrus (AG) specialization for sentence and event structure representation. In addition, in neuroimaging studies, event semantics are usually investigated using complex temporally extended stimuli, unlike than the single-concept stimuli used to investigate object semantics. Thus chapter 5 used representational similarity analysis (RSA), univariate analysis, and PPI analysis to explore neural activation patterns for event and object concepts presented as static images. Bilateral AGs

encoded semantic similarity for event concepts, with the left AG also coding object similarity. Bilateral ATLs encoded semantic similarity for object concepts but also for events. Left ATL exhibited stronger coding for events than objects. PPI analysis revealed stronger connections between left ATL and right pMTG, and between right AG and bilateral inferior temporal gyrus (ITG) and middle occipital gyrus, for event concepts compared to object concepts. Consistent with the meta-analysis in chapter 4, the results in chapter 5 support the idea of partial specialization in AG for event semantics but do not support ATL specialization for object semantics. In fact, both the meta-analysis and chapter 5 findings suggest greater ATL involvement in coding objects' associations compared to their similarity.

To conclude, the thesis provides support for the idea that perceptual brain regions are engaged in conceptual processing, in the case of motion concepts. It also provides evidence for a specialised role for TPC regions in processing thematic relations (pMTG) and event concepts (AG). There was mixed evidence for specialisation within the ATLs and this remains an important target for future research.

Chapter 1: Introduction

This thesis is concerned with how semantic knowledge is represented in the brain and how the representation of different types of semantic information is organised topographically. This chapter reviews different theoretical perspectives on this fundamental question. It begins by reviewing embodied accounts of semantic cognition, then moves onto hub-and-spoke theory, and finally discuss mixed evidence of dual-hub theory. This chapter concludes by identifying the key outstanding research questions that that will be addressed in the remainder of the thesis.

1.1 A brief history of embodied cognition

Beginning in the 1950s, cognitive scientists became inspired by developments in computer science, and started considering human cognition as the representation and manipulation of information, similar to symbolic processing in computers. Theories and paradigms from this research tradition are usually summarized as 'computationalism' (Piccinini, 2009). In the following decades, computationalism had a great impact on the development of cognitive psychology, and governed research in other cognitive sciences, such as artificial intelligence and robotics. In computationalism theories, humans' high-level cognitive functions, such as reasoning, classification, and memory, use amodal symbols as the basic unit for processing (Shapiro, 2007), similar to the calculations over abstract symbols in computing. Although the processing of these amodal mental representations is performed by the brain, human cognition was considered functionally independent of the body and the brain, just as software is independent of hardware (Niedenthal et al., 2005). Early models of semantics were concerned with modelling connections between amodal symbolic concepts (Collins & Quillian, 1969; Quillian, 1967). Modern distributional semantics approaches (e.g., latent semantic analysis) make the same assumption that human semantics can be represented without direct input from perceptual or motor processes (for review, see Meteyard et al., 2012).

But since the 1980s, an alternative perspective claiming that 'body affects (even decides) mind' has become more popular, and is supported by increasing

behavioural and neural evidence (Osbeck, 2009). In the embodied view, cognitive characteristics are closely related to the physical properties of the body; even high-level mental processes are affected by body states and how the body acts in the world. And in some radical embodied theories, disembodied cognition is impossible (Inui, 2006; Shapiro, 2007).

There are different versions of embodied theories, but they all argue against the view that cognition involves pure computation of amodal symbols (Calvo & Gomila, 2008). Generally, studies of embodied cognition made main arguments in three aspects: bodily states affect cognitive processing, mental representations (as basic units of cognition) are grounded in sensory-motor experiences, and representations are situated.

Social psychology studies have observed that people's judgements can be affected by cleanliness, temperature, or colour perceptions. It was found that people are more demanding for cleaning tools after recalling immoral experiences (Zhong & Liljenquist, 2006), and made harsher moral judgments on contested social issues after cleaning themselves (Zhong et al., 2010). In addition, physical temperature is also associated with interpersonal warmth (trust). Evidence suggests that people who hold hot drinks are more likely to believe a target person is more generous, trustworthy or caring, while those holding cold drinks might have opposite thoughts and feel less social proximity (IJzerman & Semin, 2009; Williams & Bargh, 2008). Colour perception might also affect judgements: compared with teams wearing non-black uniforms, those who wearing black uniforms can be considered more aggressive and receive more penalties (Frank & Gilovich, 1988; Webster et al., 2012); and when evaluating if a word is positive or negative, people reacted faster when positive words presented in bright colours, and negative words presented in dark colours (Meier et al., 2004; Sherman & Clore, 2009). These studies indicated that basic perceptual experiences and physical states could influence high-level cognition in a variety of ways.

The embodied cognition perspective has also been highly influential in the field of semantic memory. Studies of semantic knowledge and representation suggest that concept processing can be supported by simulating perceptual and motor experiences associated with different concepts. Lesion studies have found that

damage to certain sensorimotor brain areas can lead to selective deficits in processing knowledge of corresponding modalities or categories (Cree & McRae, 2003; Damasio & Damasio, 1994; Gainotti, 2006; Gainotti et al., 1995; Humphreys & Forde, 2001; Simmons & Barsalou, 2003; Warrington & McCarthy, 1987). For example, damage to colour perception areas can lead to deficits in colour knowledge (e.g., Miceli et al., 2001), and damage to the junction of the temporal, occipital, and parietal cortices was associated with recognition problems for tools (e.g., Damasio et al., 1996; Tranel et al., 1997). Neuroimaging research has also shown that simulation of sensorimotor experiences might be central to conceptual processing (Martin, 2001, 2007). For example, when we represent knowledge about objects, brain areas involved in perceiving shape, colour and motion of objects can be activated. It has been reported when people verify object properties, the corresponding modal areas for those properties are engaged (Goldberg et al., 2006; Kan et al., 2003; Kellenbach et al., 2001; Simmons et al., 2007). In addition, regions necessary for processing categories' dominant features respond preferentially to the categories' concepts. For example, visual areas are especially active when people process animal concepts, but motor areas become more active for artifacts like manipulatable tools (Kiefer, 2005; Martin, 2001, 2007; Thompson-Schill, 2003). Similarly, gustatory areas respond more when processing food concepts, while olfactory areas respond more when processing semantics related to smells (González et al., 2006; Simmons et al., 2005). Furthermore, specialisation within modality-specific regions can be separated by different categories. For example, motions of animals and artifacts are coded by different parts of motor regions (Martin, 2007).

There are also some embodied cognition accounts emphasizing the role of situated action, social interaction, and the environment (Barsalou, 2003; Glenberg, 1997; Prinz, 1997; Smith & Semin, 2004; Yeh & Barsalou, 2006). According to Gibson (2014), human cognition is a system which evolved to support action in specific situations (especially social interactions), and the importance of environment should be emphasized since it shapes cognitive mechanisms. Unlike a computer manipulating amodal symbols, human cognition is considered as a more dynamic structure: fixed representations do not exist in the brain, as instead, multiple systems are involved in implementing perception, action, and cognition, each of which exists

in many continuous states. And in learning, these states are coupled to reflect patterns of interaction with each other and the environment, making the process of achieving goals more effective (Clark, 1998; Prinz, 1997; Steels & Brooks, 2018; Thelen et al., 2001; Thelen & Smith, 1994).

1.2 Semantic knowledge and embodied cognition

Concepts are basic units of semantic knowledge and form the foundation of communication and thoughts. Although concepts were once believed to be stored and manipulated by an amodal system, more recent neural evidence suggests that concepts are grounded in brain areas that process sensory or action-related information. Plenty of studies reported that concept representation or imagery engages regions for perceiving corresponding stimuli. This has been found in studies of multiple modalities' concepts, including sound, colour, action and motion.

Neuroimaging studies have found that posterior superior temporal gyrus (pSTG) and middle temporal gyrus (MTG) process both perception of sounds and knowledge of sounds. Kiefer et al. (2008) used both fMRI and ERP, finding that sound-related words activated pSTG and MTG, regions which were long associated with sound perception (e.g., Binder et al., 2000; Humphries et al., 2014; Leaver & Rauschecker, 2010; Liebenthal et al., 2005; Obleser et al., 2007). This suggests that even visually presented words can rapidly activate auditory brain areas for sound-related concepts. Activation in these regions increased when the acoustic features of words became more relevant. With fMRI, Hoenig et al. (2011) further found that words and pictures of musical instruments activated right pSTG and MTG in musicians. This indicated that the right auditory cortex is involved in representing acoustic features of musical instruments, particularly for individuals with musical experience. And critically, this suggested that these features are automatically activated when the concepts are accessed. This aligns with previous studies showing the importance of these regions in comprehension of music-related semantics (Koelsch et al., 2004; Koelsch & Siebel, 2005).

The causal role of auditory cortex in processing sound concepts was further investigated by Trumpp et al. (2013). By testing a patient with a lesion in left pSTG and MTG, it was found that, damage to the left auditory regions selectively affected

comprehension of sound-related everyday objects' concepts (e.g., "bell"), but did not impair understanding concepts of non-sound-related objects (e.g., "armchair"), animals (both sound-producing like "frog" and non-sound-producing like "tortoise").This study indicated that the engagements of pSTG and MTG might be necessary for processing sound concepts.

More recent fMRI studies of sound imagery used multivariate pattern analysis (MVPA), revealing that STG and MTG were involved in coding semantic information relating to sound representation. Linke and Cusack (2015) grouped sounds by semantic category, and used MVPA to examine if neural activity patterns within a category were more similar than across categories. They found that MTG and broad auditory cortex showed higher neural pattern similarity within sound categories. In another MVPA analysis by Gu et al. (2019), signals in bilateral STGs and sensorimotor regions could be used to decode sound categories, within both mental imagery and perception. These findings implicate sound perceiving regions, STG and MTG, not only in processing sound concepts, but directly in coding semantic categories for sounds. This demonstrates the utility of MVPA to draw conclusions about semantic representations beyond those allowed by univariate fMRI analysis. This is a key theme in the present thesis.

The domain of colour perception has also provided evidence for parallels between perception and semantic representation. To identify colour perception brain regions, usual tasks include passively viewing colourful versus grayscale Mondrian images (Chao & Martin, 1999; Howard et al., 1998), and brightness judgments of visual stimuli (Beauchamp et al., 1999; Simmons et al., 2007). Although there is some variability of the brain regions activated during these different tasks, studies using a variety of techniques indicate that colour perception depends on a network of brain regions including the ventral occipitotemporal cortex and lingual gyrus (Beauchamp et al., 1999; Chao & Martin, 1999; Howard et al., 1998; Simmons et al., 2007).

Similar regions are involved in representing colour knowledge. Lesion studies found that damage to ventral temporal cortex can result in colour agnosia (Farah et al., 1988; Luzzatti & Davidoff, 1994). Neuroimaging studies also reported activations of ventral temporal cortex when people name or verify the colours of objects (Chao & Martin, 1999; Goldberg et al., 2006; Kellenbach et al., 2001; Martin et al., 1995;

Oliver & Thompson-Schill, 2003; Wiggs et al., 1998). In particular, some studies have directly compared colour perception tasks with colour knowledge retrieval tasks, finding that left fusiform gyrus and left lingual gyrus were involved in both perceiving colour and retrieving object colour (Hsu et al., 2012; Hsu et al., 2011; Simmons et al., 2007). For example, Simmons et al. (2007) found colour naming and perception tasks had overlapping activations in the left fusiform gyrus. Hsu et al. (2011) further reported that, in the task of comparing the colours of objects (presented as visual words), left fusiform gyrus was activated more when people had to retrieve more detailed colour knowledge (e.g., more detailed colour information is needed when comparing butter and egg yolk to school bus, but less is needed for comparing paprika and pencil to ladybug). And compared to words presented in spoken form, visual stimuli could elicit more response in left fusiform gyrus.

However, not all studies had consistent results. For example, Chao and Martin (1999) observed that, when generating colour names for achromatic object pictures, activations were more lateral to the occipital regions associated with colour perception. This inconsistency leads to the question: whether retrieving colour knowledge necessarily requires colour perceiving regions, and what factors caused contradictory results from different studies.

Similar findings and arguments can also be found in studies about knowledge of other modalities. For example, the knowledge representation of action and motion.

Action comprehension deficits were associated with motor regions by lesion studies (for review, see Aziz-Zadeh & Damasio, 2008). Bak et al. (2001) found, for example, that, for people with motor neuron disease, verb processing was affected more than nouns in picture naming and comprehension tasks. Studies of people with frontotemporal dementia and progressive supranuclear palsy also support the idea that deficits in verb processing may be associated with damage to frontal and frontostriatal brain areas associated with action processing (Cappa et al., 1998; Daniele et al., 1994). A more systematic investigation was done by Tranel et al. (2003), through testing action concept retrieval in people with lesions of different sites in both hemispheres. In this study, participants were asked to evaluate attributes of pictured actions and chose the pictures meeting certain criteria. It was found that participants with impaired retrieval of action knowledge had highest lesion

overlap in the following regions: left premotor/prefrontal sector, the left parietal region, and the white matter under the left posterior middle temporal lobe. All these regions are involved in planning or observing actions (Culham & Valyear, 2006; Lingnau & Downing, 2015; Tanji & Hoshi, 2001). A similar deficit was also reported in a study of aphasic people: people with damage in premotor or parietal areas had impaired comprehension of action words (Saygin et al., 2004).

Studies using fMRI provided more spatially precise evidence. Many have reported that processing action words could also elicit activation in motor cortex similar to that seen when people make actual actions (for review, see Aziz-Zadeh & Damasio, 2008). This has been supported by studies using a variety of tasks and stimuli in different modalities, including reading words referring to body parts' actions (Hauk 2004), listening to action-related sentences (Tettamanti et al., 2005), and describing imagery of interactions with objects (Esopenko et al., 2012). In addition, semantic information about certain body parts engage parts of motor cortex for corresponding body parts (Esopenko et al., 2012; Hauk et al., 2004; Tettamanti et al., 2005). For example, Hauk et al. (2004) asked people to read action words referring to face, arm, or leg actions (e.g., lick, pick, or kick), finding that activations of these words were either adjacent to or overlapped with areas activated by actual movement of the tongue, fingers, or feet. These results further elucidate embodied cognition, by showing that brain regions activated during actual motor movements were also activated when an individual processing verbally presented action information.

However, some studies challenged the notion that motor cortex engagement reflected the embodiment effect. For example, the fMRI study of G. de Zubicaray et al. (2013) reported that disyllabic nonwords containing endings with probabilistic cues predictive of verb status (e.g., -eve) evoked increased activity compared with nonwords with endings predictive of noun status (e.g., -age) in the identical motor area. They also found that nonwords matched to the action words in terms of their phonotactic probability elicit common patterns of activation (de Zubicaray et al., 2021). These results indicated motor cortex engagement during action word comprehension is more likely to reflect processing of statistical regularities in phonological features, rather than conceptual processing. To unravel these mixed

findings, a more comprehensive exploration of motor regions' functions in processing motor words is required.

Another set of studies has investigated regions activated when people perceive motion and their links with conceptual processing of motion (e.g., Assmus et al., 2007; Bedny et al., 2008; Bedny et al., 2014; Gennari, 2012; Glenberg & Kaschak, 2002; Kable et al., 2005; Peelen et al., 2012; Saygin et al., 2010). Compared with making actual movements, watching actions or motions may also activate frontal-parietal motor regions (Aziz-Zadeh et al., 2006). But most of the evidence points to lateral occipital temporal cortex (LOTC) as playing the central role in perceiving actions or motions, and in understanding corresponding concepts.

LOTC includes posterior middle temporal gyrus, extending to middle occipital gyrus near lateral occipital sulcus (Lingnau & Downing, 2015; Weiner & Grill-Spector, 2013). Parts of this region respond when watching human body movements, tool-related actions, and moving stimuli (Beauchamp et al., 2002; Cross et al., 2006; Hodgson et al., 2022; Lingnau & Petris, 2013; Tootell et al., 1995; Wall et al., 2008; Zeki et al., 1991). Damage to LOTC is associated with poor performance in naming, preparing, or imitating actions (Brambati et al., 2006; Buxbaum et al., 2014; Hoeren et al., 2014). It is also involved in body representation, with limb-selective regions in its posterior parts (Weiner & Grill-Spector, 2013).

LOTC also plays an important role in understanding action/motion concepts. It was found that some parts in LOTC were more activated by verbs than nouns (Bedny et al., 2014; Kable et al., 2005), and engaged in generating verbs for objects (Martin et al., 1995). But this does not mean that the response of LOTC is only sensitive to grammatical categories. Peelen et al. (2012) found that, even within verbs, posterior LOTC responded more to action verbs (e.g., 'walk') than static verbs (e.g., 'believe'). And using representational similarity analysis, Tucciarelli et al. (2019) reported that LOTC coded semantic similarity of motion pictures better than other brain regions. Lesion studies also associate LOTC with verbally presented actions: people with LOTC damage had worse performance when matching verbal descriptions of actions (Kalénine et al., 2010; Kemmerer et al., 2012; Urgesi et al., 2014).

All these results demonstrate that regions within LOTC are engaged in both perceiving visual motions and representing motion concepts. However, there is ongoing debate over how these 2 functions are undertaken by different parts of LOTC. Some studies suggested that the visual motion area in posterior LOTC (V5/hMT+) is responsible not only for perception of motions and body movements (Beauchamp et al., 2004; Dumoulin et al., 2000; Kourtzi & Kanwisher, 2000; Liu et al., 2016; Schultz et al., 2005; Thompson et al., 2005), but also for action concepts processing (Assmus et al., 2007; Glenberg & Kaschak, 2002; Revill et al., 2008; Rueschemeyer et al., 2010; Saygin et al., 2010).

Others argue that only the more anterior part of LOTC, such as posterior middle temporal gyrus (pMTG), is responsible for processing motion-related words (Bedny et al., 2008; Gennari et al., 2007; Kable et al., 2002; Noppeney et al., 2005; Watson et al., 2013). For instance, Bedny et al. (2008) asked participants to judge the semantic similarity of words (nouns and verbs), finding more activation for verbs in pMTG but not V5. Kable et al. (2002) used a conceptual matching task (matching related words or pictures) and observed that both pMTG and V5 responded to motion images, but only pMTG and other semantic processing regions were activated for motion words. These suggested V5 might not be recruited in representing motion concepts. Studies finding V5 engagement for action concepts, were criticized for their use of pictures and audio-visual stimuli (Assmus et al., 2007; Kable et al., 2002; Revill et al., 2008; Rueschemeyer et al., 2010; Saygin et al., 2010), since activation of V5 might be relate to perceptual rather conceptual aspects of motion processing. In contrast, some studies using motion and static sentences as stimuli only observed effects in regions anterior to V5 (Chen et al., 2008; Desai et al., 2013; Dravida et al., 2013; Humphreys et al., 2013; Wallentin et al., 2005). When comparing motion sentences (e.g 'The child fell under the slide') with static or abstract ones (e.g 'The merchant was greedy' / 'The congress is causing a big trade deficit again'), these studies found stronger responses in the pMTG region rather than V5. For example, Humphreys et al. (2013) presented participants a picture depicting a moving or static event first, followed by a recording of a sentence describing the event. They reported that V5 responded to the motion pictures, but not to the later sentence stimuli. These findings suggest that understanding motion language may not directly recruit the motion perception V5 region. In addition,

publication biases may distort the available literature on this topic. It might be more difficult to publish studies that do not find V5 effects for motion language, and so such findings may be underrepresented in the literature. It is also unclear how replicable these findings are.

These disagreements can be mapped to different forms of embodied accounts, which differ in the necessity of reactivation of embodied experience and modality-specific brain regions (for review, see Meteyard et al., 2012). Strong embodiment theories suggest that concept processing is re-enactment or 'full simulation' of relevant experiences, and sensory and motor brain regions are necessary for processing relevant concepts (Hauk et al., 2004; Kiefer et al., 2012; Pulvermüller, 2005; Saygin et al., 2010). Thus, understanding motion-related language necessitates the reactivation of corresponding visual experiences and V5. In contrast, weak embodiment theories suggest that semantic representations are at least partly constituted by sensory-motor information, but some degree of abstraction may take place (Meteyard et al., 2012). At a neural level, activations for concepts should be adjacent to primary sensory or motor cortices that process real experience, but the engagement of these sensory-motor regions depends on specific requirements of the given task (Barsalou, 2003; Bedny et al., 2008; Kable et al., 2002; Martin & Chao, 2001). According to these theories, motion concepts representation would principally involve pMTG, the region anterior to V5, and its level of engagement would depend on the specific requirements of the task being performed.

One possible reason for the inconsistences in the literature is that the above-mentioned studies relied on univariate neuroimaging analyses, where data from each voxel is analysed independently. But with more sensitive analyses, such as multi-voxel pattern analysis (MVPA), may lead to different conclusions about motion words' effects in LOTC. Wurm and Caramazza (2019) used MVPA to classify different motion types presented by videos and sentences, finding that LOTC regions encoded motion types in a crossmodal fashion. This crossmodal classification between videos and sentences suggested that LOTC was coding the conceptual properties of motion and not just involved in perception. However, the spatial distribution of these effects remains unclear, as the authors did not compare directly

effects in posterior LOTC (V5) with more anterior parts. Other MVPA studies have revealed that concrete and abstract action representations can be decoded from fMRI signals in posterior LOTC (Wurm et al., 2016; Wurm & Lingnau, 2015), but no studies have investigated MVPA effects to pure linguistic descriptions of motion across the LOTC region.

Overall, LOTC regions, including both V5 and pMTG, have been implicated in perceiving motions and representing motion concepts, although the exact roles of these regions remain unclear. To clarify the role of LOTC in action and motion concept representation, it is important to use multiple analyses to establish whether the processing of motion-related words engages the same parts of LOTC in the same ways as directly perceiving motion. Chapter 3 addresses this issue in a new fMRI study that combines univariate and MVPA analyses.

Although embodied theories emphasized the importance of sensory motor areas, they are not the only regions involved in semantic processing. Studies also identified amodal regions engaged in generalized semantics tasks, and networks for manipulating and controlling of semantic information, such as selecting between competing meanings of words or resolving ambiguity in language (Lambon Ralph et al., 2017). These will be discussed in next section.

1.3 Hub-and-spoke theory and semantic control

Embodied theories emphasized that concepts are grounded in perceptual experiences. The basic tenet of embodied cognition is now supported by studies of processing in various modalities, using both fMRI and lesion methodologies. These converge on the idea that a large portion of the knowledge we have about the world is related to perception and action and is represented in brain regions close to or overlapping with those involved in perceiving and acting (ALLPORT, 1985; Barsalou, 2008a; Martin, 2007; Saffran & Schwartz, 1994). However, these theories have unresolved questions about the importance of perceptual experiences and relevant brain regions – whether they are just crucial during the acquisition or updating of a concept or they need reactivation each time the concept is retrieved (for review, see Meteyard et al., 2012). Besides, the distribution of sensory and motor brain regions indicated that conceptual knowledge is distributed throughout the neural network

(e.g., knowledge of an objects' appearance is represented in occipital and ventral temporal regions, its movements are represented in lateral occipital-temporal regions). But this account faces challenges in computational principle and biological structure: namely, how is information relating to different modalities integrated into a single concept, and what neural underpinnings support this integration?

In contrast, symbolic theories suggested that manipulable, experientially independent symbols are the key for forming concepts (for review, see Fodor, 1983). Although these theories offer a framework for sophisticated concept processing and generalization, they have limitations in explaining the link between concepts and their associated experiential features or the genesis of concepts themselves.

To reconcile the embodied and symbolic views, researchers made efforts to form unifying theories: acknowledging the centrality of verbal and non-verbal experiences in concept formation, but introducing an amodal representation that can map experiences to concepts and facilitate knowledge generalization (e.g., Barsalou, 2008a; Smith & Medin, 1981). Additionally, some studies proposed 'convergence zones', which align with this perspective. They suggested modality-independent regions to mediate and integrate modality-specific features for each concept (Damasio & Damasio, 1994; Damasio et al., 1996).

The hub-and-spoke theory further extends these unifying theories by offering a neurocomputational explanation for how coherent, generalizable concepts are formed with experiences (Lambon Ralph et al., 2017). This theory proposes that experiences from modality-specific regions are used as ingredients for constructing a concept, and these multi-modal ingredients are mediated and integrated by a single hub, located anatomically in the bilateral anterior temporal lobes (ATLs).

The definition of ATL is variable across studies. Some researchers have focused on the most anterior part of temporal pole (e.g., Patterson et al., 2007), while some emphasize more ventral temporal regions like fusiform and parahippocampal gyri (e.g., Mion et al., 2010), or more posterior and lateral regions like middle and superior temporal gyrus (e.g., Visser et al., 2010). These regions are often collectively referred to as the "anterior temporal lobe (ATL)", and attributed a cross-modal role within a general semantic system (Bonner & Price, 2013; Lambon Ralph

et al., 2017). In this thesis, the term 'ATL' will be used to refer collectively to the anterior parts of all temporal gyri.

1.3.1 ATL as a hub

The hub role of ATL was initially inspired by observations of patients with semantic dementia (SD). As one form of fronto-temporal dementia (Snowden et al., 2002), SD is consistently associated with atrophy and dysfunction in bilateral ATLs (Desgranges et al., 2007; Diehl et al., 2004; Hodges et al., 1992; Nestor et al., 2006; Snowden et al., 2002), especially their ventral parts: polar and perirhinal cortices and the anterior fusiform gyri (Brambati et al., 2009; Williams et al., 2005). Behaviourally, SD is characterized by a gradual degeneration in expressive and receptive vocabulary, and a loss of knowledge about objects' properties, although other cognitive abilities and memory for recent events may remain intact (Schwartz et al., 1979; Snowden et al., 1989; Warrington, 1975). Lesion evidence in SD initially associated ATL damage with impaired semantic knowledge in multiple domains and modalities (Bozeat et al., 2000; Hodges & Patterson, 2007; Jefferies et al., 2009; Lambon Ralph & Patterson, 2008). Since impairment in multiple modalities/domains was associated with damage to a single brain region, this suggested the existence of a central semantic hub, in addition to distributed modality-specific representations. The central role of ATLs in semantic cognition was extensively observed by later studies, using a range of neuroimaging, electrophysiology and neurostimulation methods, in both healthy people and people with SD. Together, these works clarified how ATL is anatomically and functionally organized, and how it collaborates with other cortices to support generalised semantic processing.

The hub role of ATL was first demonstrated by its engagement in concepts across multiple domains (Jefferies et al., 2009; Pobric et al., 2007; Rogers et al., 2006). Studies of people with SD found that bilateral atrophy of the ATLs led to a deterioration of semantic knowledge, which could affect concepts of various domains (for review, see Lambon Ralph & Patterson, 2008). For example, a study of herpes simplex virus encephalitis (HSVE) and SD observed that, people with HSVE performed worse when retrieving concepts of living things than artefacts, but this effect was not found in people with SD (Lambon Ralph et al., 2007). Compared to ATLs, other regions also show category specificity: lesions in the posterior ventral

occipito-temporal region are associated with poor recognition of natural categories (Humphreys & Riddoch, 2003), damage in anteromedially centered temporal-lobe following HSVE might cause worse performance in processing natural things than artefacts (Lambon Ralph et al., 2007; Noppeney et al., 2007), and impairment to the temporoparietal region led to deficit of artefact-relevant knowledge (Buxbaum & Saffran, 2002; Campanella et al., 2010). In contrast, patients with SD show a category-general pattern. Along with the consistent findings from neuroimaging and TMS studies of healthy people (Binney et al., 2010; Chouinard & Goodale, 2010; Hasson et al., 2002; Pobric et al., 2010), these studies suggest that damage to some temporal regions gives rise to category-specific effects, in line with specialisation for particular modalities. But ATL damage shows a category-general effect, suggesting a hub function.

Engagement in semantic processing across modalities also indicates that ATL acts as a hub. It has been found that bilateral ATLs are engaged by semantic processing across modalities, including words presented visually or acoustically (Marinkovic et al., 2003), pictures (Vandenberghe et al., 1996), and sounds (Bozeat et al., 2000; Visser & Lambon Ralph, 2011). SD studies have found ATL damage leads to degeneration of semantic knowledge in both verbal and non-verbal modalities. For example, Bozeat et al. (2000) observed that, compared to healthy people, people with SD had poor performance in both word version and picture version of the Camel and Cactus test, as well as the task of matching sounds to pictures. Studies of healthy participants also reported ATL involvement in semantic decision tasks presented from different input modalities (Marinkovic et al., 2003; Vandenberghe et al., 1996; Visser & Lambon Ralph, 2011). In contrast, other parts of the temporal lobes, adjacent with parietal and occipital cortex, show preferences to different material modalities. The superior temporal regions (STS and STG) are specialized for auditory stimuli (Fullerton & Pandya, 2007; Liebenthal et al., 2005). The regions bordering occipital and temporal cortex are more sensitive to visual stimuli: for example, LOTC is highly involved in coding semantic knowledge for motion (Lingnau & Downing, 2015; Tucciarelli et al., 2019) and ventral occipital temporal cortex (VOTC) is more engaged in coding visual features like colour and shape, and its subregions also show strong category-selectivity to various object categorie (Bi et al., 2016). In contrast, ATL is widely engaged in processing different modalities'

stimuli, which makes it likely to be a hub for mediating and combining information from modality-specific regions.

Finally, as a hub, ATL must connect with other regions and integrate information from areas specializing for information in different modalities. This claim has been supported by more recent multivariate pattern analyses (MVPA) approaches in fMRI studies (Coutanche & Thompson-Schill, 2015; Peelen & Caramazza, 2012) and electrocorticography evidence (Chen et al., 2016). For example, by training pattern classification of ATL signal, Coutanche and Thompson-Schill (2015) found that ATL signals could decode object identities, while right V4 and lateral occipital cortex coded their colours and shapes respectively. They also found that ATL decoding was more likely to be successful when both colour and shape regions were representing object properties. Temporal evidence has also revealed the sequence of semantic effects in ATL and other regions (Chan et al., 2011; Clarke et al., 2013; Jackson et al., 2015; Shimotake et al., 2015a). For example, Clarke et al. (2013) presented images of concepts and observed perceptual effects in bilateral occipital cortex (starting at 74 ms post stimuli), then rapid semantic effects along the left ventral temporal lobe into left ATL (84-120 ms post stimuli). The ATL engagement after perceptual regions suggests a higher-level conceptual role. Finally, ATL shows structural connectivity with modality-specific areas in healthy participants, and in people with SD, worse comprehension is associated both with ATL atrophy and reduced hub-spoke connections (Guo et al., 2013).

Some neuroimaging studies have further revealed the gradations in function across the broader ATL. The ventrolateral ATL responds to generalized semantic tasks irre-spective of the stimuli domain or modality (Binney et al., 2010; Spitsyna et al., 2006; Visser et al., 2012; Visser & Lambon Ralph, 2011), but other ATL subregions are relatively specialized for stimuli of different categories and modalities. The medial ATL is more sensitive to picture materials and more concrete concepts (Clarke & Tyler, 2015; Hoffman et al., 2015; Visser et al., 2012), while the anterior part of superior temporal gyrus (STG) is activated more for auditory stimuli and more abstract concepts (Hoffman et al., 2015; Scott et al., 2000; Visser & Lambon Ralph, 2011). The polar and dorsal regions of the ATL have a preference for social concepts over other concepts (L. A. Ross & I. R. Olson, 2010; Zahn et al., 2007).

Overall, these findings indicate the centrality of the ventrolateral ATL as a cross-modal hub and extensively support the hub-and-spoke model's prediction: ATL plays a key role in coordinating connections among modality-specific 'spoke' regions and encoding semantic similarity structure among items.

1.3.2 Semantic control

Although a concept consists of features from multiple modalities, these features are not always relevant in every situation. Some tasks or situations require people to emphasize certain meanings, focus on less important features or suppress strong associations. For instance, cutting is a dominant feature of a knife, but this important feature would be inhibited when knife is used for other functions, like spreading butter. When dominant semantic information is not contextually appropriate, to avoid ambiguity and confusion, executive control processes are thought to shape the activation of semantic representations to fit the current situation. This is frequently termed semantic control (Badre et al., 2005; Jackson et al., 2021; Thompson-Schill et al., 1997; Wagner et al., 2001).

The controlled semantic cognition (CSC) framework suggests that although semantic control interacts with semantic representation, but they are based on different networks (Lambon Ralph et al., 2017). The network for semantic control supports working memory and executive processes relating to meaning, which encode information about the context relevant to current behaviour. These mechanisms affect how activation spreads through the semantic representation network. In well-practiced contexts, the representation network needs little input from semantic control. But in contexts requiring retrieval of weakly encoded information, the control network plays a more important role, since over-learned responses are suppressed and non-dominant features are emphasized. This view of controlled semantic processing is supported by empirical evidence and computational models (Badre et al., 2005; Hodgson et al., 2022; Rogers & McClelland, 2004; Thompson-Schill et al., 1997; Wagner et al., 2001).

Distinction between representation and control is supported by neuropsychological evidence. Some studies found people with damage on prefrontal or temporoparietal regions show semantic processing issues that are different from SD: although these

people might also have concept access issues, their main difficulty is in using and manipulating knowledge appropriately (Corbett et al., 2009; Head, 2014; Jefferies & Lambon Ralph, 2006; Luriia, 1973; Noonan, Jefferies, Corbett, & Lambon Ralph, 2010; Rogers et al., 2015). This pattern is named 'Semantic Aphasia'(SA).

Some case studies have highlighted notable behaviour differences between SD and SA, in both verbal and non-verbal domains (Corbett et al., 2009; Noonan, Jefferies, Corbett, & Ralph, 2010). Compared to people with SD, those with SA had more difficulties on semantic tasks with high executive demands: they had worse performance when processing words with more ambiguity or semantic diversity (e.g., 'bark'), and found it difficult inhibit items that were strongly activated by context (e.g. choose marmalade when need to spread cheese) or associated concepts (e.g. saying 'milk' when naming a picture of a cow) (Corbett et al., 2009; Hoffman et al., 2011; Jefferies et al., 2007; Jefferies & Lambon Ralph, 2006; Noonan, Jefferies, Corbett, & Lambon Ralph, 2010; Rogers et al., 2015).

Anatomically, meta-analyses of neuroimaging data (Humphreys & Lambon Ralph, 2015; Jackson, 2021; Noonan et al., 2013) and TMS studies (Davey et al., 2015; Hoffman et al., 2010; Whitney et al., 2011, 2012) located several regions involved in semantic control: inferior frontal gyrus (IFG), dorsomedial prefrontal cortex (PFC), pMTG, and intraparietal sulcus (IPS) were consistently identified in semantic control tasks. These regions are suggested to be jointly important for executive regulation of semantic knowledge.

Functional subdivisions have also been observed within the semantic control network. The ventral PFC and pMTG exhibit greater activation during weak semantic association retrieval, while the dorsolateral PFC and IPS areas demonstrate increased responses under high selection demands (Davey et al., 2016; Hodges & Patterson, 2007; Nagel et al., 2008). Studies of functional and anatomical connectivity have also reported connections between pMTG and ATL hub, but these connections with ATL were not observed in superior regions of the control network (Binney et al., 2012; Jackson et al., 2016). In addition, TMS studies also found that inhibition to pMTG selectively slowed semantic judgments (Hoffman et al., 2010; Whitney et al., 2011), but inhibition to IPS delayed both difficult semantic and non-semantic decisions (Whitney et al., 2012). These findings implicated a graded

structure of the semantic control network. Superior regions, including the pre-supplementary motor area and anterior cingulate cortex, may contribute to more general control functions. But inferior regions appear to support retrieval of weakly encoded semantic information, due to their connections to the semantic representation network (Duncan, 2010). Semantic control engages similar LOTC regions (e.g., pMTG) to those implicated in verb and action processing. Some researchers suggested this could be explained by action processing requiring more semantic control (e.g., Davey et al., 2016). To test this possibility, it is critical to investigate which areas of cortex within LOTC are selectively engaged by action and motion. This question is addressed in Chapter 3 of the thesis.

1.4 Dual hub theory and feature reliance

In hub-and-spoke theory, hub refers to an amodal region which processes multi-modal information and integrates them for high-level cognition. ATL has been identified as a semantic hub in many studies (for review, see Lambon Ralph et al., 2017). However, some researchers propose that ATL is a hub specialized for visual features more relevant to ventral pathway, such as colour and shape (Kravitz et al., 2013). Another hub may exist in temporal-parietal cortex (TPC), which also mediates cross-modal information like ATL, but specialized for action and spatial information, which are more relevant to the dorsal visual pathway (Buxbaum & Kalénine, 2010; Husain & Nachev, 2007). The semantic representation is supported by both hubs in ATL and TPC. The TPC region encompasses a large area of the posterior temporal and inferior parietal cortex. This theory is commonly referred to as the "dual-hub" hypothesis (for review, see Mirman et al., 2017). Some researchers suggested that the disassociation of taxonomic relation and thematic relation is caused by the different specializations of ATL and TPC hubs.

1.4.1 Taxonomic and thematic relations

Taxonomic relations, also known as categorical relations, arise when two concepts belong to the same category, such as "dog" and "wolf" both being canines. These related concepts usually share many sensorimotor characteristics, such as colour and shape (Dilkina & Lambon Ralph, 2013). In contrast, thematic relations, or associative relations, arise when two concepts frequently co-occur in events or

situations, such as "dog" and "bone," with an emphasis on the interaction or association between the concepts (Mirman et al., 2017). Behavioural evidence has indicated that taxonomic and thematic relations are based on different learning and cognitive processes. For example, one eye-tracking study reported that participants fixate on thematically-related pictures faster than taxonomically-related ones (Kalénine, Mirman, Middleton, et al., 2012). Furthermore, switching between taxonomic and thematic relatedness judgments incurs a processing cost, indicating that the two relation types involve different cognitive systems (Landrigan & Mirman, 2018). Taxonomic and thematic relations are two crucial components of semantic representation, and it is still a challenge to decipher how the human semantic system encodes them and which brain regions may specialise in representing each type.

At a neural level, some studies have associated taxonomic relations with the ATL (Geng & Schnur, 2016; Lewis et al., 2015; Merck et al., 2019; Schwartz et al., 2011). An MEG study by Lewis et al. (2015) measured participants' brain responses to words preceded by either a taxonomically or thematically related item (e.g., cottage and castle, king and castle), finding stronger ATL activity for taxonomic pairs. Geng and Schnur (2016) also fMRI scanned participants, when viewing word pairs with occasional attention catch-trials (where they identified the more familiar object in the pair), and reported more left ATL engagement for taxonomic pairs. Some consistent evidence comes from lesion studies. Schwartz et al. (2011) collected picture-naming errors and lesion maps from 86 people with poststroke language impairment (aphasia), then did voxel-based lesion-symptom mapping (VBLSM) to assess the association between behaviour and damage. It was found taxonomic errors were localized to the left ATL. Furthermore, a more recent study observed that people with semantic dementia preserved more thematic knowledge compared to taxonomic knowledge, relative to those with Alzheimer's disease (Merck et al., 2019).

However, some fMRI studies have not found greater ATL activation for taxonomic (e.g., Jackson et al., 2015; Kuchinke et al., 2009; Lee et al., 2014; Sachs, Weis, Zellagui, et al., 2008). And another SD study found no difference in knowledge for taxonomic vs. thematic relations (Hoffman et al., 2013). Thus, though dual-hub theory proposes this specialisation, the current literature appears to be inconsistent about this hypothesis.

In contrast, thematic relations have been frequently associated with TPC. Using triads tasks (e.g., is dog more related to bone or feather?), some fMRI studies have observed more activation for thematic relations in left supramarginal and angular gyrus (Jackson et al., 2015), bilateral inferior parietal lobe (IPL) and MTG (Kalénine et al., 2009), and especially more activation for tool or action-related thematic decisions in left pMTG (Davey et al., 2016). And a set of evidence implicates the TPC in processing of actions, spatial relations, and conceptual combination, which are all critical aspects of thematic processing (for review, see Mirman et al., 2017).

Action associations between objects (e.g. corkscrew – wine bottle), as a main content of thematic relations, are especially affected by damage to left pMTG (Kalénine & Buxbaum, 2016; Tsagkaridis et al., 2014). Therefore, the pMTG activation for thematic relations are usually explained as effects caused by action or motion relevant semantics. However, semantic control effect is another factor should be considered. Thematic relation might require a higher level of semantic control compared to taxonomic relations, due to the need to actively search for the specific context in which the items co-occur (Thompson et al., 2017). Given that pMTG is a part of semantic control network which respond more for higher demanding semantic tasks (Davey et al., 2015; Jackson, 2021; Noonan, Jefferies, Corbett, & Ralph, 2010; Whitney et al., 2011, 2012), the pMTG effects for thematic relation might be partially due to the efforts for retrieving and manipulating semantic information in certain contexts.

Spatial relations, another aspect of thematic knowledge, are more linked to parietal parts in TPC (Husain & Nachev, 2007), such as spatial working memory and spatial attention (Wager & Smith, 2003; Yantis & Serences, 2003). Damage to these parietal areas often leads to disorders like spatial neglect (Buxbaum et al., 2004; Corbetta & Shulman, 2011). AG was also associated with thematic relation since it was found to be critical for integrating spatially distributed objects into a single coherent percept (Huberle & Karnath, 2012; Lestou et al., 2014). For example, by presenting participants graphs of hierarchically organized visual stimuli, Huberle and Karnath (2012) reported that global Gestalt cognition activated a network including AG, anterior cingulate cortex (ACC) and the precuneus. Furthermore, AG has been implicated in combinatorial semantics (Bemis & Pylkkänen, 2013; Price et al., 2015),

and showed more sensitivity to verbs than nouns (Bedny et al., 2008; Bedny et al., 2014; Boylan et al., 2015). For instance, Boylan et al. (2015) found left AG also showed higher neural activation similarity of two phrases sharing a motion (e.g. 'eats meat' and 'eats quickly') compared to two phrases sharing a noun argument (e.g. 'eats meat' and 'with meat'). However, AG also shows domain-general deactivation effects for more difficult tasks (e.g., Humphreys et al., 2015; Humphreys et al., 2021). Considering many studies reported longer reaction times for taxonomic relation (e.g., Abel et al., 2009; G. I. De Zubicaray et al., 2013; Kotz et al., 2002; Sachs, Weis, Krings, et al., 2008; Sass et al., 2009), taxonomic relations may tend to be more difficult to process than thematic relation. This difficulty difference might also lead to more AG activation for thematic relation than taxonomic relation. Thus, the role of AG has to be considered carefully in representing thematic relations.

Although the dual-hub theory is a prominent account of neural underpinnings for taxonomic and thematic relations, it has received mixed support from empirical studies, particularly the neuroimaging literature. One issue is that different fMRI studies have used a range of different paradigms, including triads task (e.g., Davey et al., 2016; Jackson et al., 2015; Sachs, Weis, Krings, et al., 2008), relatedness judgement task (e.g., Kuchinke et al., 2009; Lewis et al., 2019; Zhang et al., 2021), picture-word interference (e.g., Abel et al., 2009; G. I. De Zubicaray et al., 2013), primed lexical decision (e.g., Lee et al., 2014; Sachs et al., 2011; Sass et al., 2009) and primed picture naming (e.g., De Zubicaray et al., 2014). Thus far, there has been no attempt to assess which areas are reliably activated across studies. Chapter 4 addresses this by conducting the first neuroimaging meta-analysis of taxonomic and thematic relations.

1.4.2 Object and event semantic representation

One final important issue for this thesis is the distinction between semantic knowledge of objects and that of events. This distinction partially overlaps with the thematic vs. taxonomic dissociation just reviewed.

The taxonomic relation is based on comparing the core properties of objects: isolated from their surroundings and treated as independent entities. In contrast, thematic relations depend more on event representation: connecting an object to

other objects and its context, then determining how different objects relate to one another. As 2 necessary abilities for daily life, object representation and event representation have been separately investigated in many studies (e.g., Baldassano et al., 2017; Bi et al., 2016; Hutchison et al., 2014; Morton et al., 2020). However, neural bases for object and event representation are rarely compared directly.

In object semantics, many studies have indicated the importance of ventral ATL (vATL). Multivariate pattern analyses of both ECoG and fMRI data have indicated that vATL regions encode semantic similarities between objects (Chen et al., 2016; Fairhall & Caramazza, 2013; Rogers et al., 2021). For instance, in a picture naming task, Chen et al. (2016) used iEEG and observed significant correlation between similarities of vATL neural signal and objects' semantics. The perirhinal cortex, specifically located in the medial part of vATL, also distinguishes objects that share many semantic features (for review, see Clarke & Tyler, 2015). Damage to this area was associated with difficulties in naming semantically more-confusable objects (Wright et al., 2015). RSA analyses provide more direct evidence by showing that similar objects produce similar activation patterns in this region (Bruffaerts et al., 2013; Devereux et al., 2018; Liuzzi et al., 2015; Naspi et al., 2021). For example, by fMRI scanning people viewing written object names, Liuzzi et al. (2015) found that similarity in activation patterns of left perirhinal cortex was predicted by semantic feature similarity.

In contrast, some studies suggested associations between event representation and AG (for review, see Binder & Desai, 2011; Humphreys et al., 2021). An event usually includes multiple objects and their interactions in a certain environment (Altmann & Ekves, 2019). Thus, in addition to representing objects, event representation also requires the relations between objects and their context. Where these relations are experienced consistently across many different events, they can be integrated into conceptual units as 'event concepts' (e.g., 'bride and groom receive congratulations and celebrate with guests' can be compressed into 'a wedding'). Thus, representing the conceptual features of events is a key function of the semantic system. This representation of contexts and inter-item associations are also critical for understanding thematic relations, which may mainly rely on TPC (as above discussed), especially the AG. Binder and Desai (2011) proposed that AG belongs to the hub that store increasingly abstract representations of entity and event

knowledge. AG is proximal to regions involved in spatial, action and motion processing (as reviewed earlier in the chapter). Binder and Desai (2011) argued that this means AG was well-placed to integrate these features and represent the properties of events. While there are some differences in these models, they agree on fundamental features that shape the AG function, including cross-modal associations, integration, and event representations. A role for AG in event knowledge is supported by many recent studies, which have reported the critical role of this region in integration of spatial-temporal information (Bonnici et al., 2016; Yazar et al., 2014, 2017), and combining semantics of concepts for both noun+noun and verb+noun compositions (Boylan et al., 2015; Price et al., 2015). In addition, AG is a key node in the default mode network (DMN), which is implicated in coding situation models and segmenting events (Baldassano et al., 2017; Morales et al., 2022; Ranganath & Ritchey, 2012; Swallow et al., 2011; Yeshurun et al., 2021; Zacks et al., 2010). These various lines of evidence suggest that AG might act as a hub for representing dynamic and complex combinations of people, concepts, objects, and actions – in other words, for events.

Some studies suggested that AG function is better explained in terms of episodic memory or working memory functions (for review, see Humphreys et al., 2021). AG is closely associated with processes that contribute to successful episodic retrieval (Konishi et al., 2000), and increased activation in AG occurs during memory tasks requiring recalling context in which stimuli were previously encountered, suggesting AG is crucial for conscious recollection (Henson et al., 1999). Some neuroimaging experiments also revealed that AG activity is sensitive to qualitative characteristics of retrieved memories, including their rated vividness, confidence, and precision (Kuhl & Chun, 2014; Richter et al., 2016; Tibon et al., 2019). In meta-analyses of fMRI studies related to episodic retrieval, AG is even more consistently activated during recollection compared to regions traditionally considered critical for episodic memory (Simons et al., 2008; Skinner & Fernandes, 2007). According to these evidence, AG activation in event processing might be partially caused by retaining event characteristics or linking them with specific past experiences. The role of AG in event representation still needs further invesitgation.

Besides, although vATL has been robustly demonstrated to code object properties, few studies have investigated whether it codes event knowledge as well. Thus, empirical evidence is still needed, to support the theory that vATL and AG have functional dissociation in processing objects and events. In Chapter 5 of the thesis, I address this by using RSA to directly compare the ability of each region to encode the semantic properties of events and objects.

1.4.3 A feature reliance explanation for dual hubs

There is one final issue to consider in this thesis introduction: why might these regions specialise in this way? According to Mirman et al. (2017), the dual-hub structure might be explained by different brain regions' specializations for different types of sensorimotor features. Mirman et al. proposed that when representing single objects and their taxonomic relations, visual features like colour and shape are most important. But when representing events or objects' thematic relations, interaction (i.e.., actions) or contextual information (e.g., locations) are most important. This is referred to as the feature reliance hypothesis in this thesis.

The organization of visual system may explain how this feature reliance gives rise to ATL and TPC hubs. The visual system is commonly divided into two streams - the dorsal and ventral pathways. The dorsal pathway extends from the early visual cortex to the frontal-parietal regions, and courses through the TPC (Kravitz et al., 2013; Mishkin et al., 1983). This pathway is known as the 'where/how' pathway as it supports visually-guided action, spatial cognition, and motion processing (Andersen & Cui, 2009; Buxbaum & Kalénine, 2010; Husain & Nachev, 2007; Wager & Smith, 2003; Watson & Chatterjee, 2011). As the posterior part of temporal-parietal junction, AG is close to these regions specialized for processing interaction and contextual information. Therefore, AG might be an ideal hub for representing thematic relations, and its converging functions also make it suitable for integrating these in event representations.

The ventral pathway runs between the early visual cortex and the vATL, coursing through the inferior parts of the temporal lobe (Kravitz et al., 2013; Mishkin et al., 1983). It is known as the 'what' stream as it is more specialized in identifying and categorizing objects. The ventral stream is involved in processing and integrating

perceptual features such as colour, size, and brightness (Baron et al., 2010; Coutanche & Thompson-Schill, 2015; Martin et al., 2018). Different parts of ventral stream also showed different sensitivities to various object categories such as tools, animals, and human faces (Bi et al., 2016; Hutchison et al., 2014). Thus, as the terminus of ventral stream, the vATL may engage more in representing the semantics of single objects and their similarities, due to the importance of visual perceptual features in this domain.

Chapter 4 of this thesis directly tests the feature reliance hypothesis by testing whether taxonomic relations are primed when participants think about colour and shape, and whether thematic relations are primed when they think about action and location.

1.5 Motivations of current studies

The present thesis tackles a number of the issues raised in this chapter. First, although neuroimaging and lesion studies have provided much evidence for explaining semantic representation, there is still debate between strong and weak embodiment accounts. Specifically, LOTC has been long associated with motion perception and understanding, but there is ongoing debate about the exact location of these effects and how they should be interpreted. V5, as the posterior part of LOTC, has been found engaged in some tasks of understanding action semantics, but was absent in other studies. However, it is important to note that most existing studies used univariate analyses, which might ignore some effects. By contrast, multi-voxel pattern analysis (MVPA) might provide more sensitive analysis of motion effects in LOTC and reveal its content of representation. Wurm and Caramazza (2019) used MVPA and found LOTC encodes different motion types in a crossmodal fashion. But they did not compare posterior LOTC (V5) with more anterior regions (pMTG), leaving the spatial distribution of motion effects unclear. Other MVPA analyses also showed that the fMRI signal in posterior LOTC could be used to decode concrete and abstract action representations (Wurm et al., 2016), and decode actions by transitivity and sociality (Wurm et al., 2017). However, there is a lack of investigation into LOTC subregions' effects for linguistic descriptions of motion.

Thus, in Chapter 3, I used multiple analysis methods to examine how different parts of LOTC respond to motion descriptions. The LOTC was divided into 3 subregions from anterior to posterior. Then we employed univariate and MVPA analyses, to explore activation patterns of these areas in processing sentence descriptions of moving and static events. I also conducted PPI analyses to examine which areas had varied functional connectivity with LOTC subregions in motion and static conditions.

Second, the ATL has been identified as a hub in generalised semantic cognition, but the AG in TPC was suggested as another hub working together with ATL to support different semantic contents. Studies suggested that ATL might be more specialized for representing taxonomic relations and single objects, and AG might be more specialized for representing thematic relations and events. But not all studies are consistent on this neural disassociation of taxonomic and thematic relations. Several fMRI studies have failed to observe the expected distinction between ATL and TPC. Some have observed stronger activation in ATL areas (e.g., anterior STG and MTG) when processing thematic relations rather than taxonomic relations (G. I. De Zubicaray et al., 2013; Lewis et al., 2019; Sass et al., 2009), while other studies have reported greater activation in temporal-parietal regions for taxonomic versus thematic relations (Kuchinke et al., 2009; Lee et al., 2014; Sachs, Weis, Zellagui, et al., 2008). Overall, although many studies have established that different cognitive and neural systems are involved in processing taxonomic and thematic relations, their corresponding neural underpinnings are not yet fully understood.

Thus, in Chapter 4, we first conducted activation likelihood estimation (ALE) meta-analysis, using fMRI studies comparing taxonomic and thematic conditions in 332 participants to examine effects in ATL and TPC. Then we further examined the dual-hub view by testing the feature reliance hypothesis. This hypothesis argues that the 2 hubs are formed by the division of ventral and dorsal visual pathways, and their specializations in processing different information (colour, shape, action, location). However, empirical evidence for this idea is lacking. Therefore, we used a behavioral task to evaluate the hypothesis, using a modality-priming paradigm to test if colour/shape processing facilitates taxonomic relation retrieval, and if action/location processing facilitates thematic relations.

Finally, in chapter 5, we focus on object and event representation. We used fMRI to scan participants viewing event and object concepts, conducting RSA to test semantic similarity effects in vATL and AG. RSA was used to investigate whether vATL codes the similarity structure of objects more than events, and if the reverse was true in AG. Univariate analysis examined general activation differences and PPI was used to explore whether the 2 semantic hubs have different connective patterns with other areas.

Chapter 2: Methodology

This chapter introduces the brain imaging techniques and statistical approaches used in the thesis. To explore cortical specialisations for different types of semantic knowledge, functional magnetic resonance imaging (fMRI) was used for acquiring neural data. A variety of analyses, including univariate analysis, MVPA analysis, PPI analysis, and ALE meta-analysis, are combined to give a comprehensive sight of this question.

2.1 Principles of functional neuroimaging

In neuroimaging methods, fMRI is a non-invasive technique for measuring brain activity. This technique is based on the principle that neural activity changes in different brain regions are associated with changes in blood oxygenation levels (Ogawa & Lee, 1990; Ogawa et al., 1990). When a brain region becomes more active, it requires more oxygenated blood, which increases blood flow to that region. The increase in blood flow is accompanied by changes in the magnetic properties of the blood, specifically the level of oxygenation. During scanning, the scanner does not measure neural activity directly, but tracks the blood oxygenation level dependent (BOLD) signal.

To capture detailed images of brain activity, fMRI scanning typically divides a brain into multiple slices (Buxton, 2009). Each slice is divided into small voxels (the size of each one is usually a few millimetres). A voxel is considered as a small volume element in the brain, and used as the smallest unit to record BOLD signal changes. The number and size of each slice and voxel can vary for different studies. Smaller voxel sizes result in higher spatial resolution, allowing researchers to localize brain activity to specific brain regions.

The scanning results are a series of activation maps that highlight brain regions that showed activity during certain cognitive tasks. These maps are usually overlaid on the structural MRI image to provide anatomical context.

Although fMRI is a non-invasive high spatial resolution technique, it has limitations (Heeger & Ress, 2002; Logothetis, 2008). Low temporal resolution is a main

disadvantage, since fMRI measures changes in blood oxygenation levels to infer neural activity, rather than directly record neural activity (Jueptner & Weiller, 1995; Poldrack & Farah, 2015). The hemodynamic response is a relatively slow process compared to the electrical activity of neurons. When a particular brain region becomes active, it takes several seconds for the blood flow to increase and reach its peak. Similarly, it takes time for the oxygenated blood to return to baseline levels. This delay in the hemodynamic response leads to the lower temporal resolution of fMRI.

In addition, spatial smoothing may reduce spatial accuracy (Friston et al., 2000). To improve the signal-to-noise ratio and enhance statistical analysis, fMRI data are often spatially smoothed. Averaging signals across neighbouring voxels may blur the spatial information and reduce the accuracy for locating exact brain activity.

Signal sensitivity is also a limitation. The fMRI signal can be affected by noise and artifacts, such as head motion, physiological processes, and scanner-related artifacts (Liu, 2016; Van Dijk et al., 2012). These factors may reduce the signal sensitivity for detecting brain activity for target cognitive tasks. Careful preprocessing and data quality control measures are essential to mitigate these issues.

These limitations lead to challenges when interpreting fMRI results. However, fMRI is still a valuable tool in neuroscience and cognitive research. By carefully considering these limitations and combining multiple analysis approaches, this thesis aims to obtain valuable insights into brain functions of semantic processing and their relationships with behaviour and cognition.

The next sections outline the methodological approaches taken in Chapters 3 and 5, where new fMRI data were collected.

2.2 Image acquisition

For Chapters 3 and 5, images were acquired on a 3T Siemens Prisma scanner with a 32-channel head coil. For the functional images, the multi-echo EPI sequence included 46 slices covering the whole brain with repetition time (TR) = 1.7 sec, flip angle = 73, 80 * 80 matrix. Voxel size was $3mm^3$. In chapter 3, the T1-weighted structure scan was acquired with TR = 2.62s, TE = 4.5ms and 0.8 mm^3 voxels. In

chapter 5, the T1-weighted structure scan was acquired with TR = 2.5 sec, TE = 4.6 msec and 1 mm^3 voxels. To minimize the impact of head movements and signal drop out in the ventral temporal regions (Kundu et al., 2017), studies employed a whole-brain multi-echo acquisition protocol, in which data were simultaneously acquired at 3 echo times: 13 msec, 31 msec and 48 msec. Data from the three-echo series were weighted and combined, and the resulting time-series were denoised using independent components analysis (ICA). The vATL is a critical region for semantic processing (see Chapter 1) but has traditionally been overlooked in fMRI studies because signal in this region is susceptible to distortion and loss, due to the proximity of air-filled sinuses (Devlin et al., 2000; Visser et al., 2010). The multi-echo acquisition protocol addresses this issue by acquiring images at short as well as long echo times (in our case 13ms). Short echo times produce less signal artefact in this region.

2.3 FMRI analysis

Analyses of fMRI data included preprocessing, univariate analysis (general linear model, GLM), multivariate analysis, functional connectivity analysis and meta-analysis.

2.3.1 Preprocessing

For fMRI data of chapter 3 and 5, preprocessing was conducted with SPM12 and TE-Dependent Analysis Toolbox 0.0.7 (Tedana) (Kundu et al., 2013; Kundu et al., 2012) in the following pipelines.

- **Slice Timing Correction:** Data are acquired as a series of slices, which are acquired at slightly different time points. This step adjusts the time delay between slices, ensuring that the data from different slices accurately represent the same time point in the acquisition sequence. This correction helps to align the temporal information across slices.
- **Motion Correction:** Head motion during the fMRI scan may bring artifacts and distortions in signal. This step aligns each volume in the fMRI time series to a reference volume, minimizing the effects of head motion. This step is particularly important to reduce motion-related confounds in the subsequent analyses.

- **Multi-echo Combination:** This step combines fMRI signal acquired at the various echo times into one single time-series and denoise images in each run (Kundu et al., 2017). In multi-echo fMRI scanning, images are acquired at various echo times for each trial, offering different information into the temporal dynamics of the signal. The integration of these images from multiple echo times facilitates denoising and component analysis. This step enhances the modelling of fMRI temporal properties, increasing sensitivity in identifying specific neural activity targets. In the chapter 3 and 5, Tedana software is used for this step, with the echo times used by Kundu et al. (2017).

- **Registration:** This step aligns the fMRI signal to the anatomy of the participant's brain. It involves aligning the functional data to the structural data (e.g., T1-weighted image) before aligning the structural data to a standard brain template.

- **Normalization:** This step transforms the data to a standardized coordinate system (MNI space), allowing for group-level analyses and comparison across individuals or studies.

- **Smoothing:** This step averages the fMRI signal across neighboring voxels to improve the signal-to-noise ratio, for enhancing power of later analysis. Smoothing can help reduce high-frequency noise and increase the detectability of underlying brain activity. However, it is important to balance the amount of smoothing applied to avoid blurring fine-scale spatial information. In chapter 3 and 5, fMRI data were smoothed with a kernel of 8 mm FWHM for univariate and PPI analysis and 4 mm FWHM for MVPA analysis.

2.3.2 General linear model (GLM)

The General Linear Model (GLM) is a widely used statistical framework for analyzing fMRI data. This approach is based on the assumption that the fMRI signal of each voxel can be modelled as a linear combination of predictors or regressors. The GLMs for fMRI analysis in this thesis are built with following steps.

- **Design Matrix:** This step specifies the experimental conditions and their timings. Each condition is represented by a regressor in the design matrix. The regressors models the shapes of the hemodynamic responses.
- **Convolution:** The design matrix is convolved with a canonical hemodynamic response function (HRF) or a subject-specific HRF to account for the delayed and sustained nature of the hemodynamic response. The convolution process generates the predicted response of each regressor at each time point.
- **Model Estimation:** This step estimates the regression coefficients or betas that represent the strength of the relationship between each regressor and the fMRI signal at each voxel.
- **Contrast and multiple comparisons correction:** This step first assesses the significance of the effects, by comparing the activation between conditions or comparing against baseline. Then correct results for multiple statistical comparisons to control for false positives. In this thesis, chapter 3 and 5 use family-wise error (FWE) correction for reporting results.
- **Individual-level and group-level analysis:** GLMs are first built for each participant with above steps, then they are used for establishing group-level analysis, to examine common activation patterns across participants.
- **Whole-brain and region of interest (ROI) analysis:** Whole-brain analysis examines the entire brain for regions that show significant activation differences across conditions, or other effects of interest. In whole brain analysis, statistical tests are performed at each voxel independently, allowing for a comprehensive exploration of the entire brain. In contrast, ROI analysis selects specific regions of interest for further investigation. A ROI refers to a specific brain area or volume selected for more focused analysis. ROIs in neuroimaging can be defined based on anatomical landmarks, functional characteristics, or priori hypotheses (Poldrack, 2007). ROI analysis usually involves defining ROIs, extracting fMRI data from ROIs (averaging or summarizing the signal in the ROI), and applying statistical tests to the extracted fMRI data of ROIs. ROI analysis focus on specific brain regions or networks of interest, allowing test of hypotheses or functional connectivity patterns of a specific regions. In chapter 3 and 5, Marsbar 0.45 is used for ROI analysis. In chapter 3, ROIs are defined as 5 mm radius spheres. In chapter 5, ROIs are defined as 10 mm radius sphere. In each case, these

spheres are centred on peak co-ordinates of interest obtained from independent datasets.

2.3.3 Multivariate pattern analysis (MVPA)

Univariate analysis primarily focuses on the magnitude of activation. It assesses whether the average signal across voxels differs significantly between experimental conditions. Although univariate analysis provides straightforward and interpretable results, voxels' activation pattern information might be lost in computing their average activation (Cox & Savoy, 2003; Haynes & Rees, 2006). In different experimental conditions, a cluster of voxels might have different activation patterns but show the same averaged activation level.

Comparatively, MVPA focus on the spatial patterns of activity across multiple voxels (Haxby et al., 2014; Haynes & Rees, 2006). It uses activation pattern differences across voxels to discriminate between different experimental conditions. MVPA is particularly sensitive to information encoded in fine-grained spatial patterns that might not be evident in traditional univariate analyses.

However, MVPA also has limitations: the results can be complex to interpret. The lack of a clear mapping between neural patterns and cognitive processes can limit the meaningful interpretation of results (Haynes, 2015).

Considering the properties of univariate and MVPA analysis, the combination of them in neuroimaging studies is a complementary and advantageous approach (Davis et al., 2014; Jimura & Poldrack, 2012). MVPA can explore distributed patterns, capturing the complex information ignored by traditional univariate analyses. Univariate analyses can serve as a validation tool, confirming the reliability and validity of MVPA findings. Thus, the chapter 3 and chapter 5 combined univariate and MVPA approaches in analyzing fMRI data, to get a more comprehensive understanding of neural responses to different types of semantic knowledge. In this thesis, univariate analysis for fMRI were conducted with SPM12 (Ashburner et al., 2014), classification analysis and RSA were conducted with CosMoMVPA (Oosterhof et al., 2016).

2.3.3.1 Classification Analysis

Chapter 3 investigate differences in the neural responses to 2 motion events and 2 static events. Classification analysis is used here due to the small number of contrasting classes.

Classification analysis involves training a classification model using a subset of the data and testing the model performance on the remaining data.

The training set consists of labelled examples, where each example represents a pattern of neural activity in a certain condition. A machine learning algorithm can be selected to learn distinguishing patterns of different conditions, with the labelled examples in training set.

The trained model is applied to the testing set to predict the conditions based on the patterns of neural activity. The model performance is evaluated by comparing its predictions with the true labels of the testing examples.

For better model generalizability, cross-validation is often used in classification analysis. Data are divided into training and testing sets for multiple times. Then training and testing are repeated multiple times, each time with a different combination of training and testing sets. This helps enhancing model performance on novel data and reducing overfitting risk.

In chapter 3 of this thesis, CosMoMVPA is used for training SVM classifier to distinguish motion and static sentences. Cross-validation is achieving by using different combinations of motion and static sentences for training and testing. Other details can be found in chapter 3.

2.3.3.2 Representation similarity analysis (RSA)

Chapter 5 investigates neural relationships between 30 event concepts and 30 object concepts. RSA analysis is used here due to the relatively large number of contrasting classes.

RSA computes a similarity matrix that represents the similarity between all pairs of conditions based on their corresponding activation patterns.

The neural activity of voxels in a certain size cluster is extracted as an activation pattern. The similarity between activation patterns of different conditions is quantified by computing the correlation between their activation patterns. This results in a square similarity matrix, where each cell represents the similarity between two conditions in the specific cluster. The similarity matrix is used for statistical analysis to determine the factors that influence activation similarity (e.g., whether activation similarity can be predicted by theoretical or empirically-determined similarities between the stimuli used in each condition).

In searchlight analysis, each voxel is used as the centre for a cluster, and each cluster generates a similarity matrix. Statistical analysis is conducted on similarity matrices of each cluster, and the results are mapped onto the brain as a representation map. In ROI analysis, in contrast, one similarity matrix is generated for each ROI and these are used for statistical analysis.

In chapter 5 of the thesis, CosMoMVPA is used for computing dissimilarity matrices (DSMs) of neural activation patterns. Then to compare event and object concepts' similarity representations; the analysis computes correlations between semantic DSM and neural DSMs. Other details can be found in chapter 5.

2.3.4 Psychophysiological Interaction (PPI) analysis

Although MVPA and univariate analysis focus on pattern discrimination or univariate effects, they typically do not directly capture the context-dependent changes in connectivity between regions. However, PPI analysis, as a functional connectivity analyses, is effective for examining how the relations between brain regions changes during cognitive tasks (Ashburner et al., 2014; K. J. Friston et al., 1997). Increases in functional connectivity identified by PPI suggest a task-specific increase in the exchange of information between brain areas. Compared to other functional connectivity analyses, PPI is more suitable for more focused, hypothesis-driven studies. It connects certain psychological states with corresponding connectivity variations, revealing how different regions interact during various psychological processes (O'Reilly et al., 2012). However, PPI is also limited by deconvolution challenges and lack of power (Gitelman et al., 2003; O'Reilly et al., 2012). PPI aims to model the interaction between psychological context and brain activity. However,

brain activity measurements have a lag due to the hemodynamic response function (HRF), leading to temporal blurring. To align the psychological context with brain activity data, both need to be convolved with the HRF or expressed in terms of underlying neural activity (deconvolved). This process introduces complexity as it is hard to accurately deconvolve the HRF if its shape is not precisely known (Gitelman et al., 2003). Besides, PPI tends to have lower power to detect effects, increasing the chances of missing real effects (false negatives). These are particularly challenging in event-related designs, since the shape of the HRF significantly influences the analysis, and event-related designs usually have smaller effect size than block designs (O'Reilly et al., 2012).

In this thesis, both chapter 3 and 5 aimed to test certain brain regions' connectivity with other areas during processing different concept types. Chapter 3 planned to test which regions' activity would show increased correlation with LOTC sub-regions during processing of motion (relative to static) sentences, and chapter 5 planned to examine which regions would show increased correlation with vATLs and AGs when representing event concepts relative to object concepts, or vice versa. Therefore, PPI was chosen to reveal the task-specific connection changes between brain regions.

In a PPI analysis, first step is choosing a seed region based on prior hypotheses about its involvement in certain cognitive process. The seed region can be defined anatomically or functionally using criteria such as activation peaks or anatomical atlases. Then the fMRI data within the seed region are extracted, as a time series that represents the regions' activity fluctuations over time. When building the GLM model, three types of regressors are included: the seed region time series, regressors representing experimental conditions, and the interaction between the seed region time series and the task-specific regressors. The GLM is fitted to the fMRI data, and statistical tests are conducted to assess the significance of the PPI effects.

In this thesis, SPM12 is used to conduct PPI analyses. Details can be found in chapter 3 and chapter 5.

2.3.5 Activation likelihood estimation (ALE) meta-analysis

Integrating univariate, MVPA and PPI analysis can provide a comprehensive insight of specific cognitive processes within a single study. But ALE meta-analysis still offers unique information that complements findings from above methods. It combines results from a large set of experiments that involve the same specific cognitive process, to identify brain regions consistently activated for this cognitive function across multiple studies.

For ALE meta-analysis, the preparation involves collecting studies that investigate the same or similar research questions, and getting coordinate data (e.g., peak activation coordinates) representing regions of brain activity from these studies. Then these coordinates are transformed into a standard stereotactic space, such as the Montreal Neurological Institute (MNI) or Talairach space.

In the ALE meta-analysis, the extracted coordinate data are spatially modeled by converting them into three-dimensional Gaussian probability distributions centered at each coordinate. The spread of the Gaussian distribution is determined based on the sample size of each study to account for the uncertainty associated with smaller sample sizes. The ALE algorithm computes a value for each voxel, representing the overlap of activation probabilities in the voxel. Voxel-wise statistical tests are then used to determine the statistical significance of the ALE values. When reporting results, clusters of significantly activated voxels are identified based on a predefined threshold, and corrected for multiple comparisons.

In this thesis, GingerALE 3.0.2 (Eickhoff et al., 2012; Eickhoff et al., 2009) is used for meta-analysis in chapter 4. Details can be found in Study 1 of chapter 4.

Chapter 3: Representation of motion concepts in occipitotemporal cortex: fMRI activation, decoding and connectivity analyses

The contents of this chapter have been published in the following paper:

Zhang, Y., Lemarchand, R., Asyraff, A., & Hoffman, P. (2022). Representation of motion concepts in occipitotemporal cortex: fMRI activation, decoding and connectivity analyses. *NeuroImage*, *259*, 119450.

3.1 Abstract

Embodied theories of semantic cognition predict that brain regions involved in motion perception are engaged when people comprehend motion concepts expressed in language. Left lateral occipitotemporal cortex (LOTC) is implicated in both motion perception and motion concept processing but prior studies have produced mixed findings on which parts of this region are engaged by motion language. We scanned participants performing semantic judgements about sentences describing motion events and static events. We performed univariate analyses, multivariate pattern analyses (MVPA) and psychophysiological interaction (PPI) analyses to investigate the effect of motion on activity and connectivity in different parts of LOTC. In multivariate analyses that decoded whether a sentence described motion or not, the middle and posterior parts of LOTC showed above-chance level performance, with performance exceeding that of other brain regions. Univariate ROI analyses found the middle part of LOTC was more active for motion events than static ones. Finally, PPI analyses found that when processing motion events, the middle and posterior parts of LOTC (overlapping with motion perception regions), increased their connectivity with cognitive control regions. Taken together, these results indicate that the more posterior parts of LOTC, including motion perception cortex, respond differently to motion vs. static events. These findings are consistent with embodiment accounts of semantic processing, and suggest that understanding verbal descriptions of motion engages areas of the occipitotemporal cortex involved in perceiving motion.

3.2 Introduction

Embodied theories of semantics hold that we represent knowledge of concepts by simulating the sensory, motor and other sensations they elicit (Barsalou, 1999; Decety & Grezes, 2006; Gallese & Lakoff, 2005). In terms of motion concept representation, there is evidence that brain areas involved in perceiving and controlling movements are also engaged when we process concepts relating to motion (Barsalou, 2003; Beilock et al., 2008). In particular, the lateral occipital-temporal cortex (LOTC) has been implicated in processing, perceiving and representing embodied experiences of perceived motion (Lingnau & Downing, 2015; Tucciarelli et al., 2019). The LOTC is typically assumed to encompass the posterior portion of the middle temporal gyrus, extending back into middle occipital gyrus as far as the lateral occipital sulcus (Lingnau & Downing, 2015; Weiner & Grill-Spector, 2013) (see Figure 1). This broad region of the cortex includes areas implicated in motion and action perception as well as sites associated with language processing. As an important area for action perception, parts of LOTC respond when participants watch videos or pictures of human body movements (Cross et al., 2006; Lingnau & Petris, 2013), tool-related actions (Beauchamp et al., 2002), and abstract moving stimuli formed by dots (Tootell et al., 1995; Wall et al., 2008) or geometries (Zeki et al., 1991). In addition, lesion studies have showed that damage to LOTC leads to poor performance in naming, preparing or imitating actions (Brambati et al., 2006; Buxbaum et al., 2014; Hoeren et al., 2014). Body representation is also a function of LOTC, with posterior parts of the region identified as 'limb-selective' regions (Weiner & Grill-Spector, 2013).

Beyond perception, understanding action/motion concepts also engages LOTC. Some positron emission tomography (PET) studies and functional magnetic resonance imaging (fMRI) studies have observed LOTC activity when participants generate appropriate verbs for objects (Martin et al., 1995) or match motion pictures with similar semantic meanings (Tucciarelli et al., 2019). Lesion studies have also reported that patients with damage in LOTC showed deficits of matching verbal descriptions of actions to related pictures (Kalénine et al., 2010; Kemmerer et al., 2012; Urgesi et al., 2014). Some researchers suggested that the response of LOTC is also sensitive to grammatical categories. For example, compared with nouns, verbs elicit stronger activation in parts of LOTC (Bedny et al., 2014; Kable et al., 2005). Within verbs,

Peelen et al. (2012) found that the posterior part of LOTC showed a preference for action verbs (verbs describing dynamic activities, like 'to walk') than state verbs (verbs describing state or mental actions, but no obvious body actions, like 'to believe').

These results have shown that LOTC includes areas involved in both perceiving action and motion visually and in understanding related semantic concepts. However, there remains considerable debate over the degree to which the precise regions engaged by these functions overlap and consequently, researchers hold different views about the role of LOTC in motion concept representation. Strong re-enactment theories claim that understanding motion words requires reactivation of corresponding perceptual experiences, and thus predict that understanding motion words elicits similar neural responses to perceiving motion directly (Hauk et al., 2004; Kiefer et al., 2012; Pulvermüller, 2005; Saygin et al., 2010). Weaker embodiment theories argue that representation of motion concepts recruit regions close to relevant sensory areas, but do not necessarily activate the perceptual regions themselves (Barsalou, 2003; Bedny et al., 2008; Kable et al., 2002; Martin & Chao, 2001). Finally, modality-independent views propose that LOTC activation for motion words is driven by retrieval of event concepts or grammatical information linked with verbs, rather than effects of sensory-motor simulation (Bedny & Caramazza, 2011; Bedny et al., 2012).

To understand the role of LOTC in action/motion concept representation, it is critical to determine whether processing motion-related words engages the same parts of LOTC, in the same ways, as perceiving motion directly. Evidence on this issue has been somewhat inconsistent. Many studies have focused on area V5 (also frequently termed hMT+), a critical region for perception of visual motion located in the posterior part of LOTC. As an important region for encoding visual information concerning motions and body movements (Beauchamp et al., 2004; Dumoulin et al., 2000; Kourtzi & Kanwisher, 2000; Liu et al., 2016; Schultz et al., 2005; Thompson et al., 2005), V5 was also found to activate during action concept processing (Assmus et al., 2007; Glenberg & Kaschak, 2002; Revill et al., 2008; Rueschemeyer et al., 2010; Saygin et al., 2010). It was reported that, compared with processing language or images of static events, more activation of V5 was observed when participants read and listened to sentences describing motion events (Rueschemeyer et al., 2010; Saygin et al., 2010), made semantic decisions to words (Kable et al., 2002) or sentences (Revill et al., 2008)

describing motion, or comprehended action knowledge represented in static pictograms (Assmus et al., 2007).

However, studies finding V5 activation have been criticized for using pictures as stimuli (Assmus et al., 2007; Kable et al., 2002), or for combining motion-related language stimuli with other visual stimuli (Revill et al., 2008; Rueschemeyer et al., 2010; Saygin et al., 2010). Since pictures of static objects or humans can also elicit responses in V5 (Kourtzi & Kanwisher, 2000; Senior et al., 2000), it is hard to determine the contribution of conceptual processing when language and pictures are presented together. In addition, integrating audio-visual language stimuli could activate V5 (Calvert et al., 1999; 2000), thus the V5 effect in some studies might be caused by the use of audio-visual stimuli (Saygin et al., 2010), instead of the motion content.

In addition, not all studies have supported the view that V5 is engaged when processing motion-related words. Some evidence suggests that only the more anterior part of LOTC, typically referred to as pMTG (posterior middle temporal gyrus), shows such effects. Several studies using pure language stimuli have only found motion effects in areas anterior to V5, such as pMTG (Bedny et al., 2008; Gennari et al., 2007; Noppeney et al., 2005). For instance, Bedny et al. (2008) asked participants to judge the semantic similarity of words (nouns and verbs), finding more activation for verbs in pMTG but not V5. Kable et al. (2002) used a conceptual matching task (matching related words or pictures) and observed that both pMTG and V5 responded to motion images, but only pMTG and other semantic processing regions were activated for motion words. These indicated that representing motion concepts might not recruit V5 directly, a view supported by a meta-analysis by Watson et al. (2013), which reported that activation for action verbs was more anterior in LOTC than for action images.

The absence of V5 effects has also been reported in studies using motion and static sentences as stimuli (Chen et al., 2008; Desai et al., 2013; Dravida et al., 2013; Humphreys et al., 2013; Wallentin et al., 2005). When comparing motion sentences (e.g., 'The child fell under the slide') with static or abstract ones (e.g., 'The merchant was greedy' / 'The congress is causing a big trade deficit again'), these studies found stronger responses in the pMTG region anterior to V5, but not in V5 itself. In particular, Humphreys et al. (2013) separated motion sentences from static images depicting motion in every trial. They showed participants a picture depicting a moving or static

event first, followed by a recording of a sentence describing the event presented after a short interval. They reported that V5 responded to the motion pictures, but not to the later sentence stimuli. These findings have made some researchers skeptical about the role of lower-level perceptual areas such as V5 in understanding motion language (Gennari, 2012; Humphreys et al., 2013). In addition, publication biases may distort the available literature on this topic. It might be more difficult to publish studies that do not find V5 effects for motion language, and so such findings may be underrepresented in the literature. It is also unclear how replicable these findings are. A more comprehensive investigation of V5 and motion concept representation is required.

It is important to note that the studies reviewed above relied on univariate neuroimaging analyses, in which data from each voxel is analyzed independently. Multi-voxel pattern analysis (MVPA) has the potential to provide more sensitive analyses of motion effects in LOTC and to uncover the content of representations in this brain region, but has only recently been applied to this research question. Wurm and Caramazza (2019) used MVPA to investigate representation of different types of motion elicited by videos and sentences (e.g., "the girl opens the bottle"). They found that regions in LOTC encoded motion types in a crossmodal fashion (generalizing between videos and sentences), supporting the general view that this area is involved in conceptual representation of motion and action. However, these authors did not directly compare effects in posterior LOTC (V5) with those more anterior parts (pMTG), thus the spatial distribution of these effects remains unclear. Other MVPA studies using video stimuli have revealed that both concrete and abstract action representations can be decoded from fMRI signal in posterior LOTC (Wurm et al., 2016), and that the neural responses to observed actions can be classified in terms of transitivity and sociality (Wurm et al., 2017). However, no studies have yet investigated how MVPA effects to pure linguistic descriptions of motion vary across the LOTC region.

In summary, while it is clear that LOTC is engaged by motion understanding as well as motion perception, the precise locus of these effects, and hence their interpretation, remains under debate. In present study, we used multiple analysis methods to construct a more detailed picture of how the response to motion sentences varies across LOTC. We re-analysed data collected by Asyraff et al. (2021), in which participants were asked to make simple semantic decisions of sentences describing 4

events. We categorized the 4 events as 2 motion events and 2 static events. We used univariate analysis, MVPA, and psychophysiological interaction (PPI) analysis to explore activation patterns within LOTC and its functional connectivity with other areas. We used sentences rather than words or phrases as stimuli, as sentences are more likely to elicit strong sensory-motor imagery (Dravida et al., 2013). We planned to ask three questions. The first is similar to those in previous univariate studies: Which areas within LOTC activate more to motion sentences than to static ones? Going beyond this, however, we used MVPA to investigate the degree to which neural patterns in LOTC could distinguish motion from static sentences as well as between different forms of motion. This allowed us to ask what level of motion knowledge is represented in LOTC during sentence processing. Finally, we used PPI to investigate how connectivity between LOTC and other brain regions changed as a function of sentence type. This allowed us to gain additional information about the role of LOTC regions by revealing their interactions with other neural systems. To guide our analyses, we divided LOTC into three sub-regions along its anterior to posterior axis (see Figure 1), guided by peak meta-analytic activations for semantics and motion processing. By doing this, we aimed to establish a better understanding of how function varies across the LOTC region during processing of motion language.
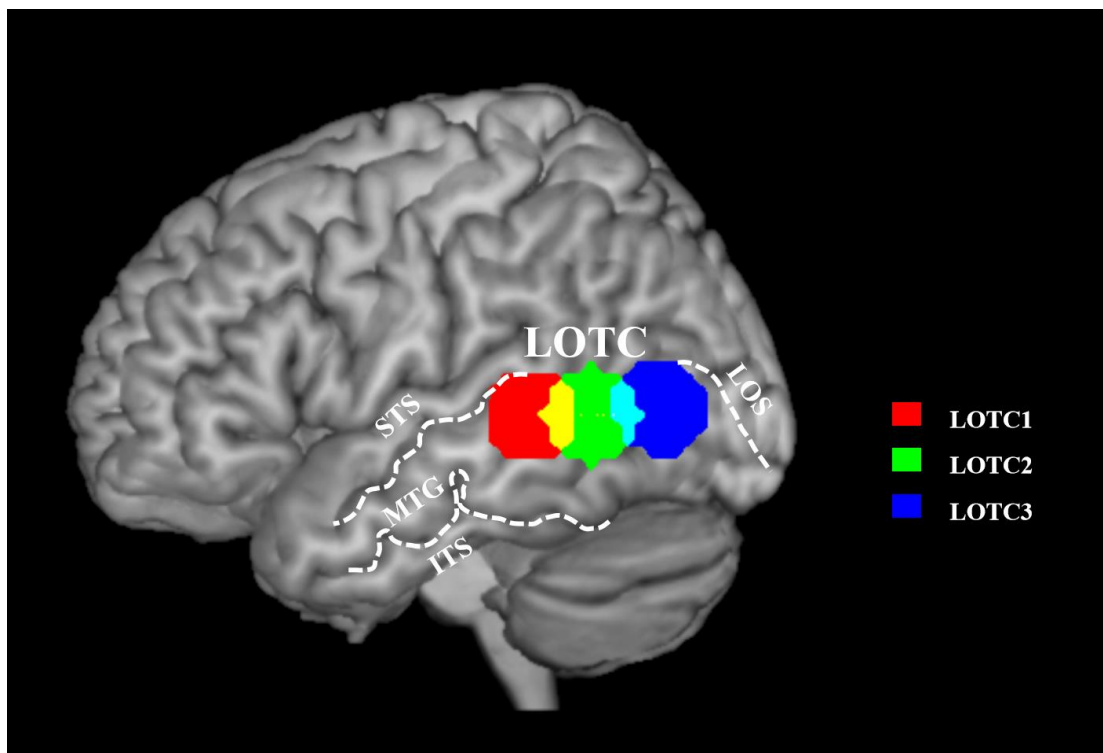
ITS, inferior temporal sulcus; MTG, middle temporal gyrus; STS, superior temporal sulcus; LOS, lateral occipital sulcus.

3.3 Method

3.3.1 Participants

26 healthy participants were recruited (20 female; mean age 22.48, range 18-35 years). All participants were right-handed native English speakers, and no one reported history of dyslexia or other neurological disorders. The study was approved by University of Edinburgh School of Philosophy, Psychology & Language Sciences Research Ethics Committee. Other analyses of the data presented here have been reported by Asyraff et al. (2021). This previous study used MVPA to investigate semantic representation of general event concepts; here, we specifically investigated differences between motion and static sentences, with a focus on LOTC.

3.3.2 Materials

32 sentences were created as stimuli (see Appendices Supplemental material of chapter 3: Supplementary Table 1). Half of these (16) were target stimuli and the other half were fillers. The target sentences described four different events, each with a different agent, patient and verb (see Table 1). Two events involved an agent making a visualizable movement in relation to the object, while the other two involved static acts. Four descriptions of each event by substituting lexical terms with similar meanings (e.g., 'cow' and 'bull') and by varying the syntactic structure of the sentence (active vs. passive). The 16 fillers were anomalous sentences created with words used in target stimuli, and with the same syntactic structures. Fillers did not describe a coherent, meaningful event (e.g., The computer jumped over the bull).

In Asyraff et al. (2021), all 32 sentences were rated by 18 participants who did not take part in the main experiment. A five-point scale was used for rating how meaningful a sentence was; target stimuli received significantly higher scores than fillers (Target M = 4.56, SD = 0.32; Filler M = 1.53, SD = 0.57; t(30) = 18.6, p<0.001). For the current

study, in order to verify our assignment of sentences as motion events and static events, the 16 target sentences were rated with a seven-point scale by 22 native English speakers (who did not participate in the main experiment) for the degree to which each sentence brings to mind an experience of motion. Motion events received significantly higher scores than static events (Motion M = 5.42, Static M = 2.23, mean difference = 3.18, $t(9.66)=17.76$, $p<0.0001$). Raters also rated each sentence for visual, auditory and emotional experiences. No difference for found for emotion (mean difference = 0.24, $t(12.23)=0.67$, $p=0.52$); however, motion events were more associated with visual (mean difference = 2.23, $t(13.23)=11.87$, $p<0.0001$) and auditory experiences (mean difference = 1.92, $t(7.99)=7.84$, $p<0.0001$). Importantly, the difference between conditions was considerably larger for the motion ratings than for either visual or auditory. Thus, the perception of motion was the most salient difference between our sets of stimuli, but motion events also brought to mind richer auditory and visual experiences for participants, in line with the real-word perceptual correlates of motion.

We also computed word frequency and concreteness for every target sentence by averaging values of the content words in each sentence. Concreteness values were obtained from Brysbaert et al. (2014) and frequency values from Van Heuven et al. (2014). There was no significant difference in word frequency (Motion M=5.69, Static M=5.72, $t(11.77)=-0.025$, $p=0.89$) but motion events were described with more concrete words than static events (Motion M =3.04, Static M =2.54, $t(13.27)=3.65$, $p<0.01$). This reflects the fact that motion verbs are easier to visualize than static verbs. Importantly, neuroimaging meta-analyses indicate that activation differences between concrete and abstract concepts are not typically observed in LOTC (Bucur & Papagno, 2021; Wang et al., 2010). Thus effects observed in this study are unlikely to be due to the concreteness difference between motion and static events. The list of all sentences and their properties can be found in Supplementary Materials (see Appendices Supplemental material of chapter 3: Supplementary Table 2, Supplementary Table 3).

Table 1: Target stimuli used in the experiment

Condition	Event	Syntactic form	Lexical items 1	Lexical items 2

Motion	Event1	Active	The bull leapt over the gate.	The cow jumped over the fence.
		Passive	The gate was leapt over by the bull.	The fence was jumped over by the cow.
	Event2	Active	The lorry bumped the lamp post.	The truck hit the street light.
		Passive	The lamp post was bumped by the lorry.	The street light was hit by the truck.
Static	Event3	Active	The computer processed the file.	The laptop analysed the document.
		Passive	The file was processed by the computer.	The document was analysed by the laptop.
	Event4	Active	The student considered the problem.	The pupil pondered the issue.
		Passive	The problem was considered by the student.	The issue was pondered by the pupil.

3.3.3 Experiment procedure

On each trial, a fixation cross was presented for 500ms, followed by one of the 32 sentences presented in the centre of the screen for 4000ms. Participants were required to judge whether the sentence was meaningful by pressing buttons held in the left and right hands. The order of sentence presentation was randomized separately for each participant in each run. By fully randomizing presentation orders for each run and participant, we ensured that there was no temporal structure present in the data that could lead to false positive errors during MVPA classification (Mumford

et al., 2014). After each trial, there was a jittered interval of 4000ms to 8000ms. The length of the interval was randomized independently of sentence order randomization. Each run presented all 32 sentences once and each participant was asked to complete 6 runs in total. We note that, because the same sentences were used in each run, neural responses are potentially subject to the repetition suppression effect, whereby activation decreases when the same stimuli are processed repeatedly (Barron et al., 2016). There are two reasons why we do not believe this poses a problem for the present study. First, repetition suppression effects in fMRI are short-lived, dissipating on the order of seconds, and are strongest when few other stimuli are presented between repetitions (Barron et al., 2016). In the present study, stimulus repetitions were separated by a mean of 32 stimuli and 360s (the length of one run). Second, motion and static sentences were repeated equally often, so any repetition suppression should affect both sentence types equally.

For the behavioral data, T-tests were used to compare reaction time and accuracy for motion vs. static sentences. In addition, R-4.0.3, with the 'lme', 'effects' and 'afex' packages, was employed to build a linear mixed effect model predicting RTs on trials with correct responses. Fixed effects included the type of events (motion/static), run number in the experiment and sentence length (number of characters in each sentence). Sentence length was set as a fixed effect as sentences were not precisely matched for length. Participant was set as the random effect with intercepts and random slopes for event types.

3.3.4 Data acquisition

A 3T Siemens Prisma scanner and 32-channel head coil were employed for the data acquisition. The T1-weighted structure scan was acquired with TR = 2.62s, TE = 4.5ms and 0.8mm^3 voxels. For functional scanning, each image contained 46 slices of 3mm^3 isotropic voxels with an 80*80 matrix and the TR for scanning was 1.7s. To improve fMRI signal quality and reduce the influence caused by movement and other artefacts, a whole-brain multi-echo acquisition protocol was used. The signal was collected at 3 echo times (13ms, 31ms, 48ms) simultaneously (Feinberg et al., 2010; Moeller et al., 2010; Xu et al., 2013), then the images were weighted and combined and independent components analysis (ICA) was used to remove noise components.

3.3.5 Preprocessing

SPM12 and TE-Dependent Analysis Toolbox 0.0.7 (Tedana) (DuPre et al., 2019) were employed for preprocessing. Slice-timing correction and motion correction were performed first. The data acquired at the first echo time (13ms) was used for estimating motion parameters (Power et al., 2017). Next, we used Tedana to combine the data acquired at the 3 echo times into one single time-series and denoise images in each run (Kundu et al., 2017). Tedana uses ICA to discriminate noise and task-related signal, based on their different patterns of signal decay over increasing TEs. Finally, we employed SPM12 to coregister functional scans to the anatomical images and normalise them to MNI space with DARTEL (Ashburner, 2007).

For univariate and PPI analyses, images were smoothed with a kernel of 8mm FWHM. We processed data with a high-pass filter with a cut-off of 128s and used one general linear model for analyzing all 6 runs. In a model of a run, 3 regressors modelled motion events, static events and anomalous events respectively. Covariates consisted of six motion parameters and their first-order derivatives.

3.3.6 Regions of Interest

We divided left LOTC into 3 sub-regions horizontally: LOTC1, LOTC2 and LOTC3 (Figure 1). Each sub-region was defined as a 5mm radius sphere centered on specific MNI co-ordinates. Co-ordinates for LOTC1 and LOTC3 were obtained from automated meta-analysis of the neuroimaging literature using the Neurosynth database (Yarkoni et al., 2011).

The centre of LOTC1 was located at [-52 -40 2], the peak co-ordinate in LOTC for activations associated with the term "semantic" in Neurosynth (see Figure 2A). Thus, LOTC1 represented an anterior location within LOTC associated with general semantic processing. Studies of semantic processing frequently refer to this area as pMTG. In contrast, LOTC3 was centered at [-44 -72 5], the peak co-ordinate from activations associated with the term "motion" in Neurosynth (see Figure 2A). Figure 2B shows the overlap between LOTC3 and area V5, as defined in the probabilistic atlas of Malikovic et al. (2007). In addition, the centre co-ordinates of LOTC3 are very close to those obtained in studies that used motion perception tasks to localize this area (Dravida et al., 2013; Humphreys et al., 2013; Saygin et al., 2010). Finally, for

LOTC2 we needed to identify a region located between the anterior and posterior extremes of LOTC1 and LOTC3. We selected the peak co-ordinate from the whole-brain analysis of meaningful sentences > rest in our own study [-54 -55 3], as this fell midway between the other two regions. Note that the use of this peak did not bias us towards finding any particular effect of motion over static sentences, since the meaningful sentences condition contained equal numbers of both types of sentence. The 3 sub-regions overlapped each other slightly so that we could plot graded changes in the functional profile of LOTC along its anterior-to-posterior axis. Together they covered the entire cortical territory thought to comprise LOTC.

3.3.7 Univariate fMRI analysis

Both whole-brain analysis and ROI analyses were conducted, contrasting motion and static sentences. The whole-brain analysis was corrected for multiple comparisons ($p < 0.05$) at the cluster level using SPM's random field theory, with a cluster-forming threshold of $p < 0.005$. For the univariate ROI analyses, we first used SPM12 to extract the mean beta values of LOTC1, LOTC2 and LOTC3 in motion event and static event conditions, which represent activation relative to the implicit baseline (rest). The beta values were imported into R-4.0.3, and an ANOVA analysis was completed to assess effects of event type (motion, static), ROI and their interaction.
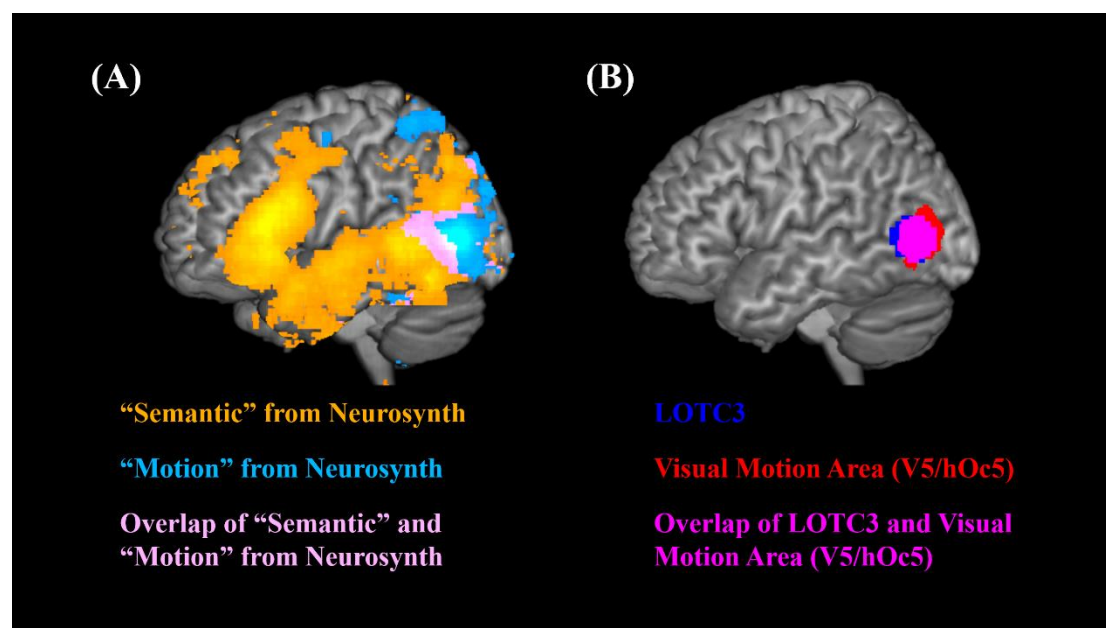
Figure 2. Details about ROI definitions. (A). Regions significantly associated with "Semantic" and "Motion" keywords in Neurosynth, (FDR p < 0.01); (B). Overlap of

3.3.8 Multivariate pattern analysis (MVPA)

We employed MVPA to investigate which areas discriminate between different types of event. Since some studies have reported that smoothing slightly improves performance in decoding models (Gardumi et al., 2016; Hendriks et al., 2017), images used for MVPA were normalized and smoothed at 4mm FWHM. To obtain T-maps for each of the 32 sentences, a general linear model was built for each run. In each model, each sentence was modelled with a separate regressor. We used CoSMoMVPA (Oosterhof et al., 2016) for processing the T-maps generated by these models.

Previous studies have shown that MVPA can be very sensitive to differences in reaction time between classes (Todd et al., 2013; Woolgar et al., 2014). In the present study, participants were reliably slower to respond to motion sentences when compared with static sentences (see Results). To avoid the possibility that this difference could lead to successful classification, we regressed out the effect of RT on each voxel's t-values prior to MVPA. We did this by estimating a linear model for each voxel predicting t-values from RT on a trial-by-trial basis. The residuals of these models, which were uncorrelated with RT, were used as the patterns in the classifier (Todd et al., 2013).

Three analyses were performed, repeated at the searchlight and ROI level (with the ROIs defined earlier). For the first analysis, a decoding model was trained to classify whether activation patterns belonged to motion or static sentences. This analysis was intended to reveal which regions were sensitive to the presence of motion in event descriptions. For the other 2 analyses, we trained 2 models separately to discriminate between the 2 kinds of motion events and the 2 kinds of static events used in the study. These 2 analyses were intended to identify areas that coded for the semantic content within the motion and static domains. Details of each decoding model are as follows:

<u>Decoding event types (motion vs. static):</u> An example of train and test patterns for this classifier is shown in Figure 5B. Because each event could be described using four different sentences (differing in lexical or syntactic forms), we were able to test the ability of activation patterns to classify motion in a way that generalizes to novel

sentences. For one iteration, the classifier was trained on 3 of the 4 sentences describing each event and tested on the remaining sentences (one for each event) that were not used for training. This process was repeated 16 times, until all possible combinations of the various lexical forms and syntactic forms were used as the training set. We adopted this "leave-one-stimulus-out" approach, as opposed to the more common "leave-one-run-out" method, because it provides a stronger test of our hypothesis. Specifically, requiring generalization to novel sentences ensures that successful decoding is driven by conceptual content and not by lower-level characteristics of particular stimuli (Asyraff et al., 2021). The first searchlight analysis gave us a whole-brain decoding accuracy map (Figure 5A). The ROI analysis used patterns in LOTC1, 2 and 3 for decoding (Figure 7A), and tested whether these accuracies were significantly higher than 50% (chance level for classifying two categories).

Decoding specific motion events: A example of one iteration in this analysis can be seen in Figure 6B. The training sets and testing sets were partitioned in a way similar way to decoding event types, except that only motion sentences were used and the classifier was required to discriminate between the two events that involved motion. The process was also repeated 16 times, until all possible combinations of different event descriptions had been used as the training set.

Decoding specific static events: This took the same form at decoding specific motion events, except that the classifier was trained to discriminate the two static events. An example of one iteration can be seen in Figure 6D.

All classifiers were trained with a support vector machine (LIBSVM) with the regularization parameter C set to 1. To test whether the models could classify better than chance level, we used a two-stage method to perform permutation tests (Stelzer et al., 2013). Specifically, a decoding model was trained and tested 100 times for each participant (divided equally between all iterations of the training set), with the class labels randomly permuted in each run. This process provided a distribution of accuracies under the null hypothesis for each participant. Then we used a Monte Carlo approach to compute a null accuracy distribution at the group level (over all participants). From each participant's null distribution, we selected one random accuracy value/map for each training iteration and averaged them to generate a group

mean. This process was repeated 10,000 times to generate a distribution of the expected group accuracy under the null hypothesis. In searchlight analyses, we entered the observed and null accuracy maps into the Monte Carlo cluster statistics function of CoSMoMVPA to generate a statistical map corrected for multiple comparisons using threshold-free cluster enhancement (Smith & Nichols, 2009). These maps were thresholded at corrected $p < 0.05$. For ROI analyses, we used the position of the observed group accuracy in the null distribution to determine the p-value (e.g. if the observed accuracy was greater than 95% of accuracies in the null distribution, the p-value would be 0.05).

3.3.9 Psychophysiological interaction (PPI) analysis

PPI analysis is a method for investigating task-specific changes in the relationship between different brain regions' activity (K. Friston et al., 1997). PPI is a form of functional connectivity analysis. However, while functional connectivity analyses often consider the temporal correlations between different brain regions in all conditions (including the resting state), PPI focuses specifically on *changes* in connectivity caused by experimental manipulations (Ashburner et al., 2014; Gitelman et al., 2003; O'Reilly et al., 2012). In current study, we used PPI analysis to investigate which brain regions' activity would show increased correlation with LOTC sub-regions during processing of motion (relative to static) sentences. The PPI analysis for each seed region (LOTC1, LOTC2, LOTC3) was conducted using SPM12 with the following steps. First, the seed region was defined as described in the Region of Interest section above, and the BOLD signal time-series from the seed region was extracted using the first eigenvariate. Then, a general linear model was built with the following regressors:

1. The signal in the seed region.
2. A regressor coding for the experimental effect of interest, where motion sentence trials were coded as '+1' and static sentences '-1'.
3. The interaction between the signal in the seed region and the experimental effect (motion/static).
4. An additional regressor coding for the presentation of anomalous sentences, as a nuisance covariate.
5. Head movement covariates as included in the main univariate analysis.

This model was used for testing effects of the PPI regressor (i.e., changes in

connectivity driven by sentence type) in the whole brain. Results were corrected for multiple comparisons ($p < 0.05$) at the cluster using SPM's random field theory, with a cluster-forming threshold of $p < 0.005$.

Data and code availability

Group-level results maps and ROI masks are archived at: https://neurovault.org/collections/11009/. Other study data and code are available at: https://osf.io/d3nkc/.

3.4 Results

3.4.1 Behavioural data

Paired t-tests were conducted to examine whether participants responded differently to static vs. motion events. No significant difference was found in their accuracies (static M = 93.35%, SD = 0.09, motion M = 95.11%, SD = 0.08, t(25) = -1.06, p < 0.3), but participants reacted faster when processing static events (static M = 1799ms, SD = 452.02, motion M = 1931ms, SD = 459.91, t(25) = -4.27, p < 0.0002). In a linear mixed effects model controlling for the effect of run order and length of sentences, the event type still had a significant effect on reaction time (t(2267)=-7.316, p< 0.001).

3.4.2 fMRI data

Three sets of analysis were formed on the fMRI data: univariate analyses, multivariate pattern analyses (MVPA) and psychophysiological analyses (PPI).

3.4.2.1 Univariate analysis

In the whole-brain analysis contrasting motion vs. static sentences, there were no significant differences with cluster FWE correction. However, some small clusters of activation for motion > static events were observed at uncorrected p<0.005 (Figure 3). These included a small cluster in LOTC and clusters in regions of parahippocampal gyrus and lateral occipital cortex.
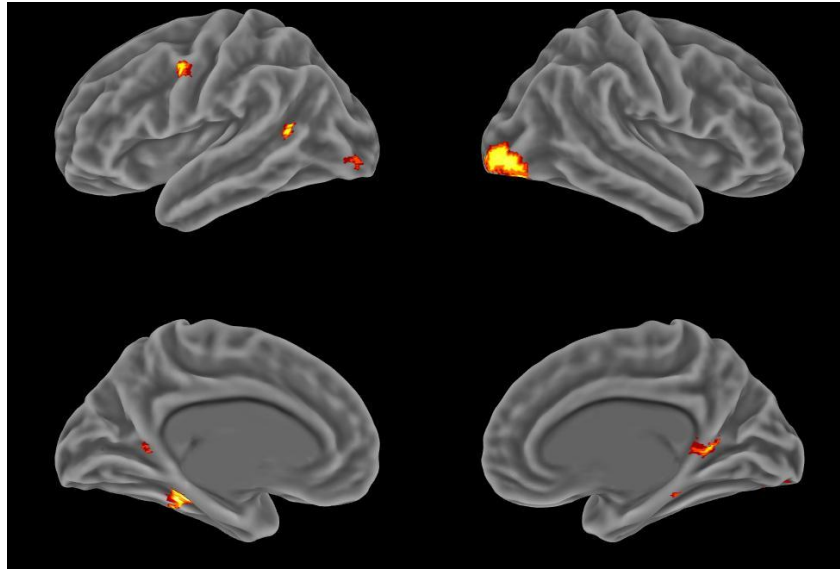
Figure 3. Univariate effects of motion events minus static events at a liberal threshold (p<0.005, uncorrected)

Figure 4 shows activation estimates for the contrast of motion and static events in the three ROIs comprising LOTC. We used two-way repeated measures ANVOA to test whether the effect of motion varied across the sub-regions of LOTC. The analysis revealed a significant main effect of sub-region ($F_{(1.43, 35.83)}$ = 13.057, $p<0.001$) and an interaction between sub-region and condition ($F_{(2, 50)}$ = 5.947, $p<0.005$). Post-hoc tests in each ROI found greater activation for motion events in LOTC2 only ($t_{(25)}$=2.56, $p<0.017$). A comparison of all meaningful sentences vs. rest revealed activation in LOTC1 and LOTC2 (see Appendices Supplemental material of chapter 3: Supplementary Figure 1).
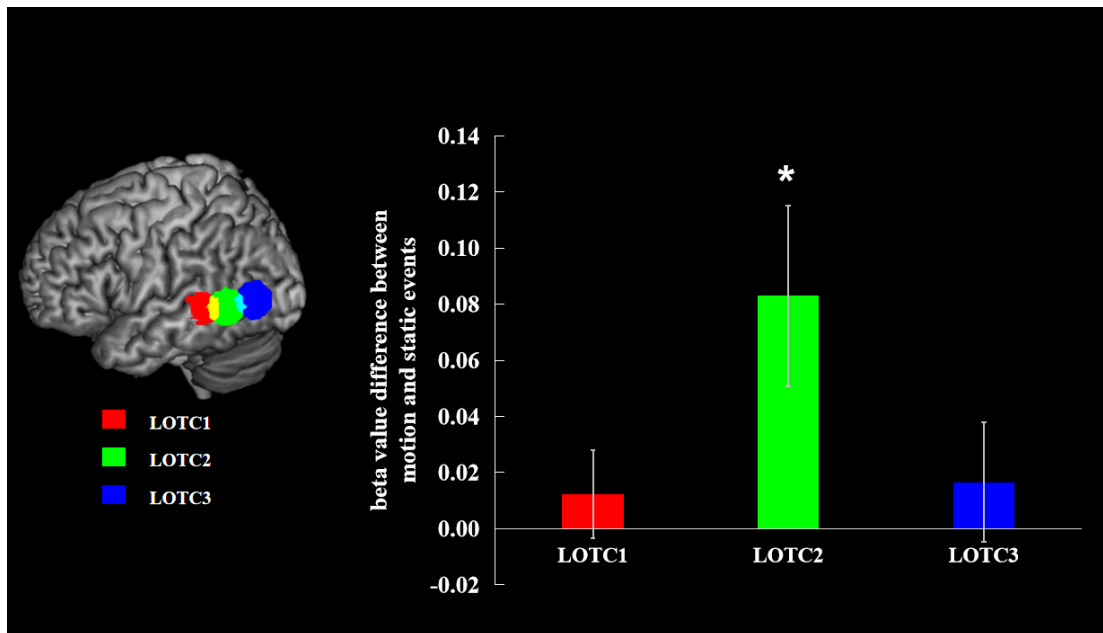
Figure 4. Effects of motion minus static events in LOTC ROIs. Bars show one standard error of the mean.

3.4.2.2 MVPA analysis

Figure 5 displays the result of the first analysis, which discriminated between motion and static events. Coloured areas indicate regions where decoding accuracy significantly exceeded chance levels (cluster-corrected p<0.05). Successful decoding was achieved in left hemisphere temporal and occipital regions. The highest decoding accuracy was found in left LOTC. The right lingual gyrus also showed above-chance level decoding accuracy.
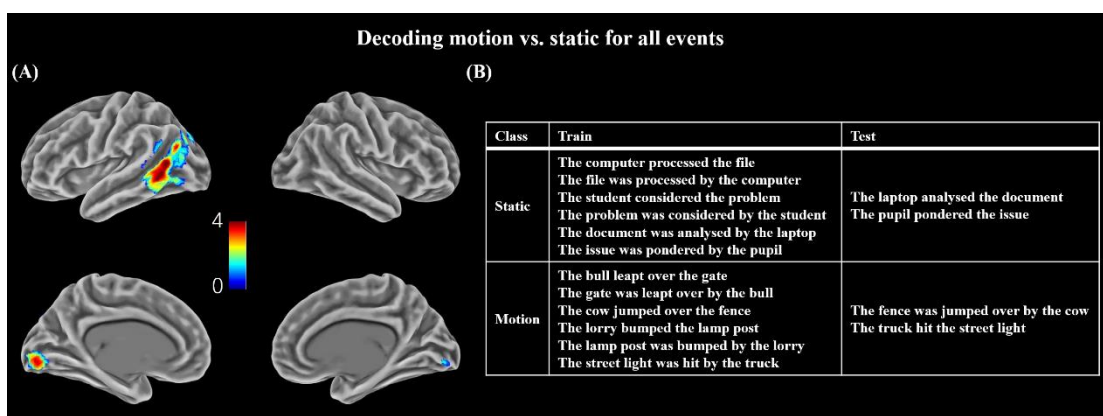
Figure 5. Decoding of event types (motion vs. static). (A) Decoding accuracy map, showing regions where classifier performance exceeded chance (corrected p < 0.05).

(B) Example of train and test patterns for one iteration of the analysis.

Figure 6 shows the results of classifiers trained to discriminate between the two motion events and the two static events used in the study. For the static events, successful decoding was observed in a wide range of regions in both hemispheres, including LOTC. However, parts of left occipital and parietal cortex showed the best decoding performance. Discrimination between the two motion events was unsuccessful: above-chance decoding was not observed anywhere in the brain.
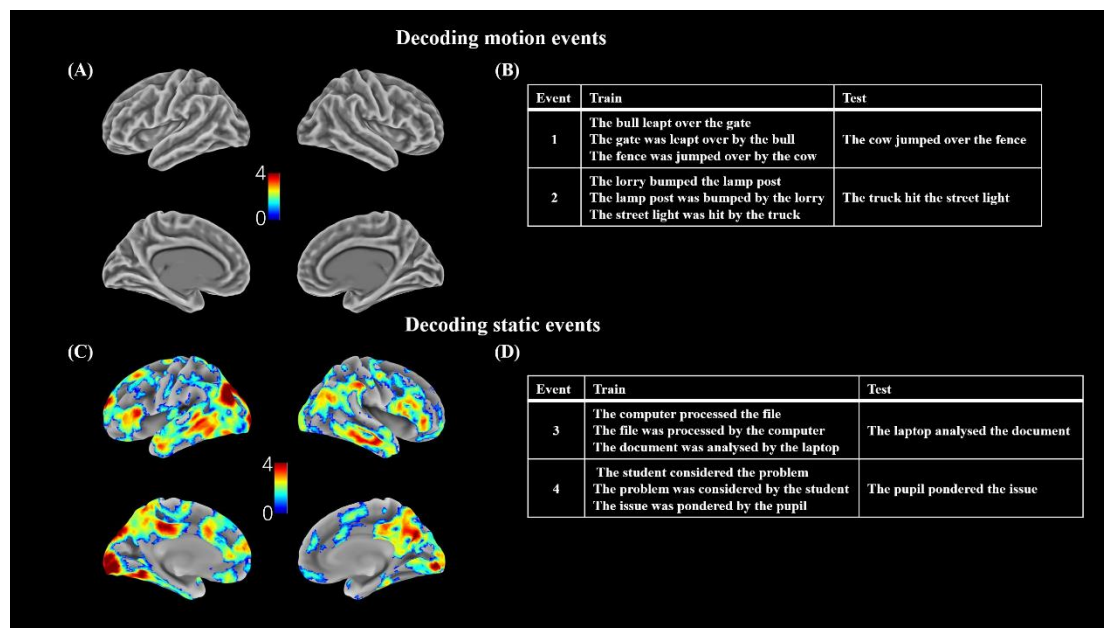

Figure 6. Decoding of specific motion and static events. (A) and (C) Decoding accuracy map, showing regions where classifier performance exceeded chance (corrected p < 0.05). (B) and (D) Examples of train and test patterns for one iteration of each analysis.

Figure 7 shows accuracies for each classifier for the LOTC regions of interest. When classifying the event type (motion/static), LOTC2 and LOTC3 showed significantly above-chance decoding accuracy, with highest accuracy in LOTC2. In contrast, none of the LOTC regions could successfully discriminate between the two different motion events. All regions could, however, distinguish between the two static events, in common with large swathes of temporal and occipital cortices (see Figure 6C).

Finally, as a control analysis, we took the searchlight classifier trained to discriminate the two motion events and tested its ability to categorize the static events. Since

motion and static events do not correspond to one another, this attempt at classification should not be successful. As expected, no voxels showed above-chance decoding at our cluster-corrected threshold.
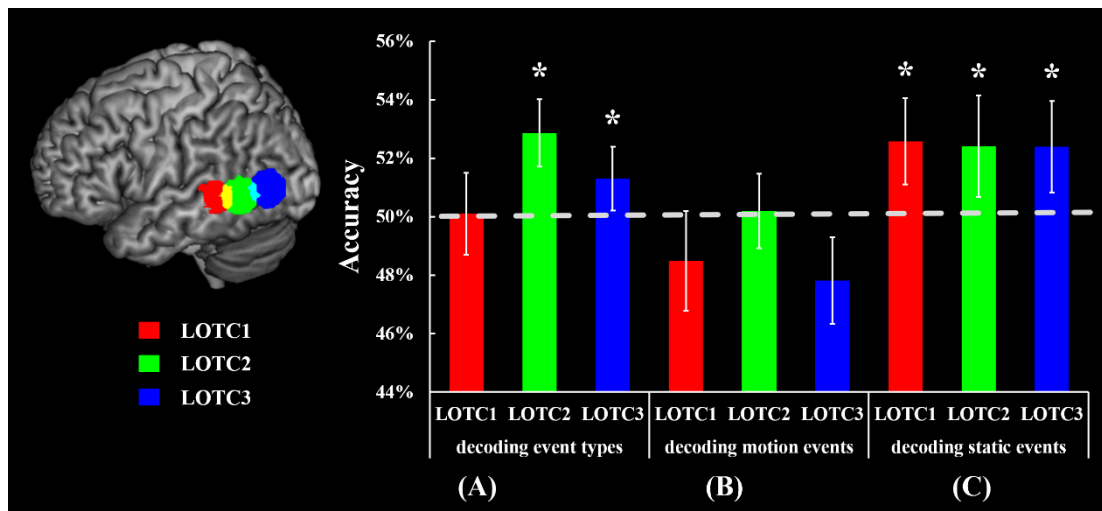
Figure 7. Decoding accuracies of LOTC1, LOTC2 and LOTC3 in different decoding models. Bars show one standard error of the mean.

3.4.2.3 PPI analysis

To investigate the functional connectivity of LOTC with other parts of the brain, PPI analyses were conducted using LOTC1, LOTC2 and LOTC3 as seed regions. Analyses tested for change in connectivity as a function of event type (motion vs. static). No regions showed significant increases in connectivity with LOTC for static relative to motion sentences. For motion events minus static events, however, significant effects were observed for the LOTC2 and LOTC3 seeds, as shown in Figure 8.
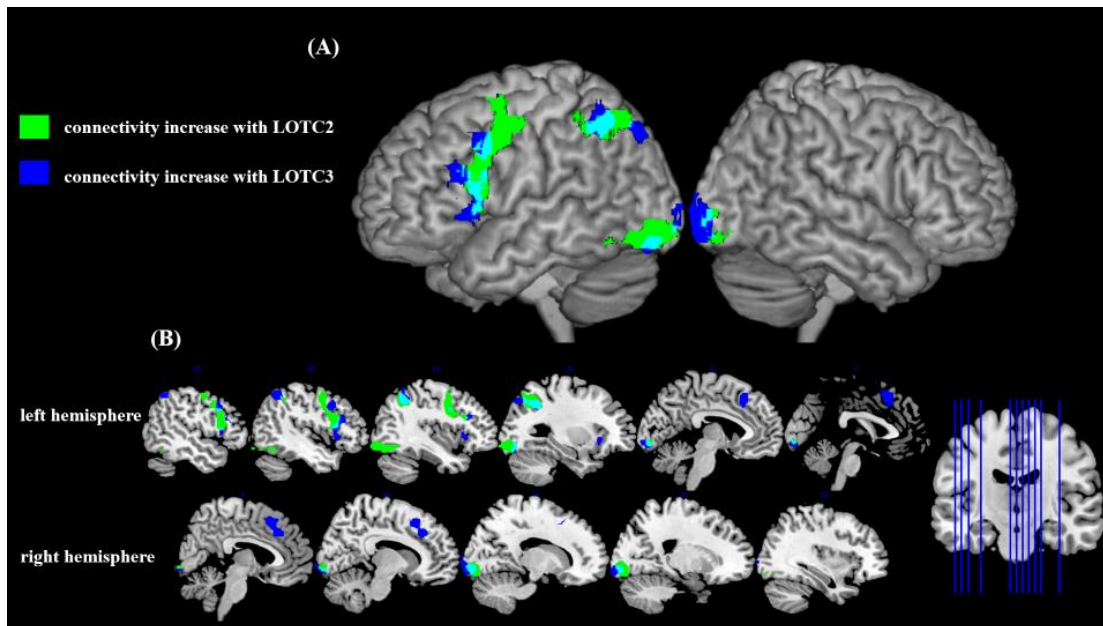
Figure 8. Regions showing increased connectivity with LOTC seeds for motion sentences vs. static sentences. (A) Surface render (cluster corrected p<0.05); (B) Slices (cluster corrected p<0.05)

A similar set of regions was revealed for both LOTC2 and LOTC3, including left precentral gyrus and lateral prefrontal cortex, left intraparietal sulcus, the presupplementary motor area and the lateral occipital cortex bilaterally. These areas all form part of a "multiple demand" network that shows increased engagement in response to cognitive challenges across multiple domains (Fedorenko et al., 2013). No regions showed significant connectivity changes for the LOTC1 seed.

3.5 Discussion

LOTC has been implicated in conceptual processing of events involving motion but the precise nature and location of these semantic motion effects remains unclear. In this study, we used multiple neuroimaging analyses to examine LOTC's role in motion concept representation. Participants made semantic decisions to sentences describing events that did or did not involve physical motion. MVPA revealed that activation patterns in LOTC discriminated between motion and static events. Significant decoding was observed in the middle and posterior parts of LOTC, although only the middle portion of the region showed an activation increase for motion sentences in univariate analyses. Moreover, PPI analyses indicated that the more posterior parts of LOTC increased their functional connectivity with the multiple

demand network when participants processed motion sentences. Taken together, these results suggest that the more posterior parts of LOTC, very close to motion perception cortex, are most selectively involved in comprehending events involving motion, while the anterior part contributes to semantic processing in a more general fashion.

MVPA searchlight analyses across the whole brain indicated that activation patterns in left LOTC were most able to discriminate descriptions of static events from those that describe motion. This is consistent with the general view that this area of the cortex plays a particular role in comprehension, as well as direct perception, of motion events. Within LOTC, above-chance discrimination was observed in its middle and posterior areas, LOTC2 and LOTC3, with better decoding accuracy in LOTC2. In contrast, univariate contrasts of motion > static only found a significant effect in the middle part of LOTC. This difference may reflect the greater sensitivity of MVPA methods to subtle distinctions between conditions, which are not present in mean activation magnitude (Weaverdyck et al., 2020). Generally, the significant MVPA effects in LOTC suggest that its middle and posterior regions are sensitive to differences between motion and static events in language, including the posterior part that overlaps with motion perception cortex (V5).

PPI analyses also support the idea that posterior parts of LOTC are engaged when people process verbal descriptions of motion events. We used PPI to examine whether the functional connectivity of LOTC with other regions changed as a function of conceptual motion content. When processing motion events, the posterior LOTC2 and LOTC3 areas increased their connectivity with precentral gyrus, supplementary motor area (SMA), IPL and early visual cortex. These regions form the multiple demand (MD) network which participates in domain-general cognitive control (De Baene et al., 2012; Koechlin et al., 2003; Kouneiher et al., 2009). This network has been implicated in controlled processing in domains such as semantic cognition (Jackson, 2021; Whitney et al., 2012), decision making (Coutlee & Huettel, 2012; Vickery & Jiang, 2009) and action coordination (Ridderinkhof et al., 2004; Rizzolatti et al., 2006). Here, we found that when participants made semantic decisions about motion events, these cognitive control areas showed increased interaction with the more posterior parts of LOTC. This could indicate that motion information encoded in

LOTC was recruited as part of decision-making processes involved in the semantic judgements. In addition, the stronger connectivity between LOTC regions and early visual cortex and precentral gyrus might be caused not only by general cognitive control, but also by the mental imagery of motions. Both early visual cortex and precentral gyrus were parts of an action network, engaging motor planning and imagery (Hanakawa et al., 2008; Hétu et al., 2013; Kosslyn & Thompson, 2003; Monaco et al., 2020; Szameitat et al., 2007). Compared to static events describing abstract actions (process, think), the motion events included verbs (jump over, hit) which were more likely to trigger motor imagination, leading to more connectivity between LOTC regions and early visual cortex and precentral gyrus.

The above results provide a more comprehensive view of LOTC involvement in processing motion concepts, on which previous studies hold different theories. Some researchers believe that motion concept representation requires re-enactment of perceptual experiences and the V5 would directly engage in this process (Hauk et al., 2004; Kiefer et al., 2012; Pulvermüller, 2005; Saygin et al., 2010). Others hold a weaker embodiment view, arguing that regions directly involved in perception do not necessarily engage in semantic processing, but areas close to them are recruited (Barsalou, 2003; Bedny et al., 2008; Kable et al., 2002; Martin & Chao, 2001). For understanding motion concepts, studies using univariate contrasts have found mixed evidence, with some reporting V5 involvement (Assmus et al., 2007; Glenberg & Kaschak, 2002; Revill et al., 2008; Rueschemeyer et al., 2010; Saygin et al., 2010) while others do not (Bedny et al., 2008; Gennari et al., 2007; Noppeney et al., 2005). In our study, we did not find any effect in LOTC3 in the univariate analyses but the more sensitive MVPA analyses did reveal motion effects. This discrepancy might be caused by different principles of the two analyses. Univariate analysis examines whether the averaged signal across voxels differs significantly between experimental conditions, But MVPA is sensitive to activation pattern differences across voxels (Haxby et al., 2014; Haynes & Rees, 2006). In LOTC3, motion and static events showed activation pattern differences but no significant activation level differences. The decoding results suggest that motion perception regions are functionally involved in semantic processing; the lack of activation level differences might reflect lack of power. The LOTC2, as a region anterior to V5, also showed motion sensitivity in a range of analyses (univariate ROI analyses, MVPA and PPI), consistent with the

weak embodiment view that areas anterior to V5 are sensitive to conceptual motion. Compared with middle and posterior parts of LOTC, the most anterior part, LOTC1, was not selective in its profile (no univariate motion effects, no PPI effects and no above-chance MVPA decoding) and we therefore conclude that the most anterior parts of LOTC play a more general role in semantic cognition. By combining univariate, MVPA and PPI analysis, the functions of different LOTC regions were examined. The LOTC2 and LOTC3 coded existence of motions, while LOTC1 engaged in more general semantic processing.

Overall, our results support general embodiment accounts of semantic processing, which implicate perceptual cortex and neighboring regions in processing related concepts. More importantly, the PPI analyses show how the various parts of LOTC coordinate with domain-general brain networks to process motion concepts. This complex interaction can be reflected more clearly in a study using a variety of analytic techniques, thus in future explorations, it is important to apply different analyses to develop a full picture.

MVPA models discriminating between the two motion events and the two static events revealed some unexpected results. The decoding model for the static events showed the expected pattern, with above-chance decoding in semantic regions such as prefrontal cortex, IFG and the anterior and posterior temporal lobes. However, when trained to discriminate between the two motion events, no regions showed above-chance performance and no effects were observed in LOTC (in searchlight or ROI analyses). The motion events describing two different motions: 'jump over' and 'hit', which might lead to imageries of different kinematics. As a motion perception area, LOTC was expected to code the two motion concepts with different activation patterns. But the MVPA analysis showed although neural signals across the brain and in LOTC distinguished between motion and static sentences, they could not reliably discriminate between two different types of motion events.

For the static events decoding model, the generally high classification across many brain regions might relate to the subjects of the events, rather than the actions involved. The temporoparietal junction region, lateral temporal cortex and posterior cingulate gyrus showed strong effects in discriminating between static events, and these areas are all parts of default mode network (DMN), which is engaged in processing socially

relevant information and plays a key role for understanding others' mental states (Li et al., 2014; Mars et al., 2012). One static event involved comprehending a person's mental state and the other did not (computer processed file/student considered question), and DMN regions are likely to have responded differently to the human-relevant and object-relevant events for this reason.

The poor performance of LOTC in motion events decoding model was not predicted by embodied cognition theories, which would expect different patterns when different types of motion are described. One possible reason for this null result is the degree of perceptual simulation required by the task. Previous MVPA studies that have successfully decoded specific types of motion using neural responses in lateral posterior temporal cortex have elicited responses using videos of actions (Wurm et al., 2016; Wurm & Caramazza, 2019) or have asked people to make explicit action judgements about sentences (Wurm & Caramazza, 2019). In contrast, in the present study we used the relatively shallow task of asking participants to judge whether a written sentence was meaningful. The motion types might be decoded better if participants were required to deeply visualize different motions. However, this conclusion is speculative and further studies with more and deeper target stimuli are needed to investigate effects of different motion types in LOTC.

This study has a few limitations. Our two-category classification design required us to use a small number of events with simple sentence structure (agent-verb-patient). Future studies could use more events with different structures in their training sets, testing the degree to which our results generalize across conceptual and linguistic space. This is a particularly important point considering the limited ability of activation patterns to discriminate between the two motion events included in the present study. Another possible limitation was that we did not know how deeply participants processed the sentences. The task goal may change people's comprehension strategies, modulating the degree of embodiment and accompanying brain activity (for discussion, see Binder & Desai, 2011; Barsalou et al. 2008). For example, when people read novels, a detailed description of the environment and events could encourage people to enact detailed simulations of the content. In contrast, deciding whether a sentence is meaningful (like our experimental task) might be accomplished with less resort to mental imagery and simulation. The

results of motion events decoding indicated that perceptual brain regions might not encode specific conceptual differences in certain semantic tasks. Although re-enactment of embodied experience can be a strategy in semantic processing, the embodied reasoning with perception regions may not be necessary in tasks which do not require deep comprehension of concepts. Further research could ask participants to imagine the scene described by the sentences, to explore whether the LOTC's function in motion concept representation would be affected by this factor.

In conclusion, using a range of analyses, this study found that middle and posterior parts of LOTC responded differently to motion and static events, including regions associated with perceptual processing of motion. We suggest that, future explorations combining activation-based, connectivity and pattern analysis techniques will be valuable in gaining further understanding of LOTC's role in motion concept representation.

Chapter 4: Taxonomic and thematic relations rely on different types of semantic features: Evidence from an fMRI meta-analysis and a semantic priming study

The contents of this chapter have been published in the following paper:

Zhang, Y., Mirman, D., & Hoffman, P. (2023). Taxonomic and thematic relations rely on different types of semantic features: Evidence from an fMRI meta-analysis and a semantic priming study. Brain and Language, 242, 105287.

4.1 Abstract

Taxonomic and thematic relations are major components of semantic representation, but their neurocognitive underpinnings are still debated. We hypothesised that taxonomic relations preferentially activate parts of anterior temporal lobe (ATL) because they rely more on colour and shape features, while thematic relations preferentially activate temporoparietal cortex (TPC) because they rely more on action and location knowledge. We first conducted activation likelihood estimation (ALE) meta-analysis to assess evidence for neural specialisation in the existing fMRI literature (Study 1), then used a primed semantic judgement task to examine if the two relations are primed by different feature types (Study 2). We find that taxonomic relations show minimal feature-based specialisation but preferentially activate the lingual gyrus. Thematic relations are more dependent on action and location features and preferentially engage TPC. The meta-analysis also showed that lateral ATL is preferentially engaged by Thematic relations, which may reflect their greater reliance on verbal associations.

4.2 Introduction

Many verbal and non-verbal behaviours require us to process taxonomic and thematic relationships. Taxonomic relations (or categorical relations) occur when two concepts belong to the same category (e.g., 'dog' and 'wolf' are both canines). Taxonomically related concepts typically share multiple features in colour, shape and

other sensorimotor characteristics (Dilkina & Lambon Ralph, 2013). In contrast, thematic relations (or associative relations) occur when two concepts frequently co-occur in events or situations (e.g., 'dog' and 'bone'), focusing on the interaction or association between concepts (Mirman et al., 2017). These two relation types are fundamental building blocks in semantic representation. Thus, unravelling how the human semantic system codes these distinct forms of conceptual relations, and which brain regions support them, is a major challenge.

Many behavioural experiments have indicated that taxonomic and thematic relations are acquired in different ways and rely on different cognitive processes. Some researchers have suggested that formal education enhances taxonomic cognition (Ince & Christman, 2002; Nation & Snowling, 1999; Whitmore et al., 2004). Conversely, specific domain expertise can disproportionately benefit thematic cognition (Coley, 2012; Crutch & Warrington, 2011; Medin et al., 2006). Other studies have investigated timing effects in processing each relationship type. One eye-tracking study has shown that when participants select pictures to match target words, they fixate on thematically-related pictures earlier than taxonomically-related ones (Kalénine, Mirman, Middleton, et al., 2012). Finally, Landrigan and Mirman (2018) reported that there is a processing cost when switching between taxonomic and thematic relatedness judgements. This suggests that the two relationship types rely on different cognitive systems.

In addition to performance differences in healthy individuals, neuropsychological studies, reviewed by Mirman et al. (2017), have provided evidence for the neural dissociation of taxonomic and thematic systems. In one of the first such studies, Semenza et al. (1980) found that people with Broca's aphasia made errors in thematic judgements but performed within the normal range on taxonomic trials, while those with Wernicke's aphasia showed the opposite pattern. Vivas et al. (2016) also reported that, people with non-fluent aphasia had poorer performance when choosing thematically-related pictures in a triad task, while people with fluent aphasia showed more difficulty in organizing pictures based on taxonomic relations. An eye-tracking study by Kalénine, Mirman and Buxbaum (2012) observed that people with left-hemisphere stroke produced earlier fixations to thematically related objects (e.g., broom-dustpan) and later fixations to functionally similar objects (e.g.,

broom–sponge). Dissociations have also been found in neurodegenerative conditions: it has been reported that people with semantic dementia have relatively more preserved thematic knowledge than taxonomic knowledge, when compared with people with Alzheimer's disease (Merck et al., 2019).

A number of studies have more directly investigated the brain regions supporting taxonomic and thematic processing. Some researchers have suggested that the semantic system might be supported by 2 distinct hubs in the left hemisphere: one located in the anterior temporal lobe (ATL) which is specialised for taxonomic processing, and one in temporo-paretial cortex (TPC) for thematic processing (Jefferies et al., 2020; Mirman et al., 2017; Schwartz et al., 2011; Thye et al., 2021). This is often referred to as the "dual-hub" hypothesis. TPC refers to a large swathe of posterior temporal and inferior parietal cortex. As reviewed by Mirman et al. (2017), this region has been reported as a crucial area for thematic processing in a variety of studies. Within TPC, subregions have different specializations for processing and integrating action and spatial-temporal information, which are major contents of thematic relations. The pMTG is important for coding action and motion concepts (Bedny et al., 2008; Gennari et al., 2007; Noppeney et al., 2005). The SMG is identified in a range of processes relating to action understanding, spatial working memory, spatial attention and spatial-temporal cognition (Assmus et al., 2005; Assmus et al., 2003; Moscovitch et al., 1995; Przybylski & Króliczak, 2017; Randerath et al., 2010; Silk et al., 2010; Tunik et al., 2007). The angular gyrus plays an important role in integrating spatial-temporal features (Ben-Zvi et al., 2015; Bonnici et al., 2016; Richter et al., 2016; Yazar et al., 2014, 2017), and combining semantics of verbs and nouns (Boylan et al., 2015). And many fMRI studies did find these regions engaged in thematic relations judgements. For example, fMRI studies using triads tasks (e.g., is dog more related to bone or feather?) have observed stronger activation in left posterior temporal cortex, superior temporal gyrus and angular gyrus for thematic relations (Jackson et al., 2015; Kalénine et al., 2009), especially for tool or action-related thematic judgements (Davey et al., 2016). Xu et al. (2018) also found thematic effects in SMG when taxonomic differences was controlled.

Besides, the other functions of pMTG and AG should also be considered. pMTG preference for thematic relations might also be relevant to semantic control. Thematic relations might require a higher level of semantic control compared to taxonomic relations, due to the need to actively search for the specific context in which the items co-occur (Thompson et al., 2017). Given that pMTG is a part of semantic control network which may respond more for higher demanding semantic tasks (Davey et al., 2015; Jackson, 2021; Noonan, Jefferies, Corbett, & Ralph, 2010; Whitney et al., 2011, 2012), the pMTG effects for thematic relations might be partially caused by retrieving and manipulating semantic information in certain contexts. Conversely, AG effects for thematic relation might partially reflect lower difficulty. AG deactivated stronger for more difficult tasks (e.g., Humphreys et al., 2015; Humphreys et al., 2021). Considering taxonomic relations usually require more reaction time than thematic relations (e.g., Abel et al., 2009; G. I. De Zubicaray et al., 2013; Kotz et al., 2002; Sachs, Weis, Krings, et al., 2008; Sass et al., 2009), the difficulty difference might also lead to more AG activation for thematic relations.

In contrast, greater ATL involvement has been associated with taxonomic relations (Geng & Schnur, 2016; Lewis et al., 2015; Schwartz et al., 2011). In other fMRI studies, however, the expected dissociation between ATL and TPC was not found or was reversed. Some studies have reported more activation in temporal-parietal areas when participants process taxonomic, rather than thematic, relations (Kuchinke et al., 2009; Lee et al., 2014; Sachs, Weis, Zellagui, et al., 2008). Others have found that, compared with taxonomic processing, thematic relations elicited more activation in parts of the ATL, such as anterior superior temporal gyrus (Lewis et al., 2019; Sass et al., 2009) and anterior middle temporal gyrus (G. I. De Zubicaray et al., 2013; Lewis et al., 2019). To summarize, although a substantial literature has shown that taxonomic and thematic relations rely on different cognitive and neural systems, their neuroanatomical correlates remain unclear.

Why would these two relation types rely on different brain regions, as the dual-hub hypothesis predicts? Mirman et al. (2017) proposed that different kinds of features may contribute differentially to taxonomic vs. thematic relations. They suggested that taxonomic relations rely more on static visual features, especially colour and shape, as taxonomically similar objects often have a similar appearance (Dilkina & Lambon

Ralph, 2013). Conversely, thematic relations may rely more on information about the actions and locations associated with objects, since thematic links depend on objects' interactions in particular events or contexts (Davey et al., 2016; Kalénine & Buxbaum, 2016; Tsagkaridis et al., 2014). We will refer to this idea as the *feature reliance* hypothesis. Mirman et al. (2017) suggested that these different sensitivities to different feature types could lead to differences in neural activation patterns. Specifically, as ATL and TPC are anatomically linked with different modality-specific brain regions, they might develop preferences for processing information from different modalities. The ventral ATL is linked with the 'what' visual pathway, a series of regions crucial for higher-order object processing and the integration of colour and shape features (Baron et al., 2010; Coutanche & Thompson-Schill, 2015; Kravitz et al., 2013). In contrast, TPC contains regions specialized for processing spatial information (Husain & Nachev, 2007; Wager & Smith, 2003; Yantis & Serences, 2003) and action/motion semantics (Andersen & Cui, 2009; Buxbaum & Kalénine, 2010; Watson & Chatterjee, 2011), as part of the 'where'/'how' visual pathway. Thus, ATL might develop as a hub for taxonomic relations since it is more sensitive to static object features like shape and colour, and TPC might become a hub for thematic relations since it is more relevant in processing information about object interactions, like action and location information.

The feature reliance hypothesis provides a plausible mechanism by which taxonomic vs. thematic neural specialization could develop. However, empirical support for this idea is lacking at present. To address this, we tested the neural predictions of the feature reliance hypothesis with a meta-analysis study and the cognitive predictions with a second, behavioural study. We first conducted an activation likelihood estimation (ALE) meta-analysis of fMRI studies that compared 332 participants' activation in taxonomic vs. thematic conditions. By aggregating activation peaks across studies, we were able to test whether thematic processing is reliably associated with TPC activation and taxonomic with ATL activation, and whether any other brain regions consistently show differences between relation types. Having investigated the neuroanatomical correlates of the two relation types, in Study 2 we used a novel behavioural task to evaluate the feature reliance hypothesis. We used a modality-priming paradigm to test whether the engagement of colour and shape

processing facilitates the retrieval of taxonomic relations, while action and location processing facilitates thematic relations.

4.3 Study 1

The feature reliance hypothesis predicts that ATL is strongly activated by taxonomic relations, since it is connected to inferior temporal regions representing colour and shape, while TPC is differentially activated by thematic relations since it contains regions that represent action and location knowledge. However, existing fMRI studies have presented a mixed picture as to whether this is the case. Therefore, to assess quantitively the evidence from the existing fMRI literature, we conducted an ALE meta-analysis which included all available contrasts of taxonomic and thematic relations from published fMRI studies.

4.3.1 Method

4.3.1.1 Study selection

We searched for relevant studies published between 2000 and 2021. The search was conducted using Google Scholar for papers including the following terms: 'fMRI', 'neuroimaging', 'taxonomic', 'taxonomy', 'thematic', 'categorical', 'associative'. The reference list of a systematic review was also searched for relevant studies (Mirman et al., 2017). We found 40 studies at this stage. These studies were then screened for inclusion in the meta-analysis.

Inclusion criteria were as follows:

1. The study used functional neuroimaging to investigate processing of taxonomic versus thematic relations.

2. Task paradigm. The experiment explicitly or implicitly required processing of both taxonomic and thematic relations. Tasks included matching-to-sample, primed lexical decision, primed picture naming and relatedness judgements (see Table 1). The match-to-sample and relatedness judgement tasks required explicit judgements of similarity or association between concept pairs. Primed studies involved implicit activation of taxonomic or thematic relations, since pairs of primes and targets were manipulated to be associatively or

categorically similar with each other. Some studies focused on particular aspects of taxonomic or thematic relations (e.g. some only compared thematic action relationships with taxonomic relations). We included these to maximize the power of the meta-analysis.

3. Participants. The study recruited healthy adults as participants.

4. Analyses. The study reported peak activation co-ordinates for a whole-brain contrast of taxonomic vs. thematic conditions.

With these criteria, 16 fMRI studies (332 participants in total) were included for meta-analyses (see Table 1). Studies were most commonly excluded for following reasons: some only presented the activation maps but did not report peak coordinates for the relevant contrasts, some only compared taxonomic versus rest and/or thematic versus rest, but did not compare taxonomic and thematic conditions directly, and some mixed taxonomic and thematic relations in their experimental conditions. The number of studies included was slightly below the minimum of 17 studies recommended for a well-powered ALE meta-analysis (Eickhoff et al., 2016). It did, however, allow us to conduct an initial assessment of the results of the currently available neuroimaging studies on this topic, albeit with reduced sensitivity to weaker effects.

4.3.1.2 ALE analysis

Activation Likelihood Estimation (ALE) analyses were conducted with GingerALE 3.0.2 (Eickhoff et al., 2012; Eickhoff et al., 2009). Using activation peaks from contrasts of interest (extracted from multiple studies), this tool computes the spatial distribution of the peaks and generates likelihood maps for activation in each voxel. Voxel-wise statistical tests are then used to identify regions that are reliably activated across the set of studies. We used ALE analyses to investigate which areas reliably responded more for taxonomic than thematic relations (TX>THM), and which responded more for thematic than taxonomic relations (THM>TX). For all analyses, peaks reported in Talairach space were converted to MNI space using the tal2icbm_spm transform (Lancaster et al., 2007).

Two sets of analyses were conducted, both comprising ALE analyses of TX>THM and THM>TX. Our main analyses used a family-wise error cluster-corrected threshold of $p<0.05$ (with a cluster-forming threshold of $p<0.01$). We used the non-additive version of the ALE algorithm from Turkeltaub et al. (2012), which limits the influence of a single study reporting multiple peaks very close to one another. Analysis thresholds were set using a permutation-based method for cluster-level inference (Eickhoff et al., 2009). All thresholds were computed using 5000 random permutations of the dataset. Given the relatively small number of studies available for analysis, we conducted a second pair of analyses to check whether there were additional clusters within ATL and TPC that did not survive correction for multiple comparisons. These used a more stringent voxel-level threshold ($p<0.001$) but did not correct for multiple comparisons (minimum cluster size = 100 mm^3). Because this analysis uses a more liberal threshold, we only interpret results in areas previously hypothesized to show effects (ATL for TX>THM and TPC for THM>TX).

Study	First Author	Year	Participants	Mean Age	Task	Number of peaks		Mean reaction time (ms)	
						TX>THM	THM>TX	TX	THM
1	Kotz	2002	13	23.5	primed lexcial decision	3	0	869	839
2	Sachs	2008	16	27	primed lexcial decision	1	0	646	627
3	Sachs	2008	14	28	triads task	3	0	1191;1186	1154;1189
4	Abel	2009	19	26	picture-word-interference	3	2	909	814
5	Kalénine	2009	45	22	triads task (picture)	3	10	1478	1512
6	Kuchinke	2009	15	27.2	relatedness judgement task	4	8	NA	NA

7	Sass	2009	16	26	primed lexcial decision	0	1	742.47	710.85
8	Sachs	2011	16	27	primed lexcial decision	1	0	670.23	669.56
9	De Zubicaray	2013	20	21.5	picture-word-interference	0	3	833	787
10	De Zubicaray	2014	28	22.93	picture naming	1	1	NA	NA
11	Lee	2014	18	27.5	primed lexcial decision	0	16	NA	NA
12	Jackson	2015	25	25.48	triads task	2	2	1783.69	1653.68
13	Davey	2016	20	24.8	triads task	0	31	2088	1655
14	Kumar	2018	18	28.3	primed relatedness judgement task	5	0	643.11	658.52
15	Lewis	2019	18	27	relatedness judgement task	0	6	982	1002

16	Zhang	2021	31	20.6	relatedness judgement task	7	23	NA	NA
Means				25.3				1168.46	1105.97
Sums			332			33	103		

Table 1. Details of studies included in meta-analyses. 'TX>THM', taxonomic versus thematic relation; 'THM>TX, thematic versus taxonomic relation. In the 'Mean Reaction Time (ms)' column, 'NA' is for those studies did not report reaction times for the relevant conditions.
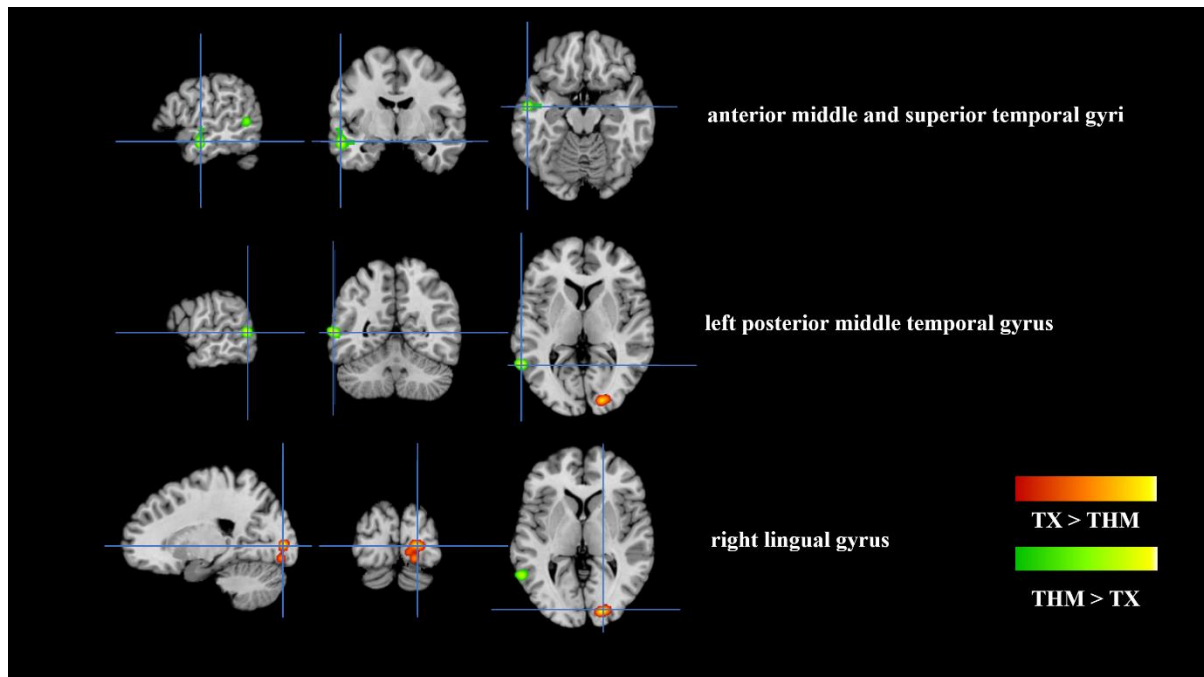
4.3.2 Results

Figure 1. Activation likelihood maps for taxonomic versus thematic relation (orange) and thematic versus taxonomic relation (green).   Images are thresholded at cluster-corrected p <0.05.

The THM>TX contrast revealed two clusters, both in the left hemisphere (Figure 1). One was centred on the posterior middle temporal gyrus, consistent with the view that TPC regions contribute preferentially to thematic processing. The second was in the lateral ATL, within middle and superior temporal gyri. The TX>THM contrast identified one cluster in right lingual gyrus. Peak effect co-ordinates are reported in Table 2.

Cluster	Anatomical region	Volume(mm^3)	BA	x	y	z	ALE Value
THM>TX							
1	Left Temporal Lobe	1856					
	Middle Temporal Gyrus		21	-56	-8	-18	0.016253173

	Region	Volume	BA	x	y	z	ALE value
	Sub-Gyral		21	-44	-8	-18	0.008369234
	Middle Temporal Gyrus		21	-58	-10	-6	0.007896487
2	Left Temporal Lobe	1680					
	Middle Temporal Gyrus		21	-62	-54	4	0.018458404
	Sub-Gyral		37	-52	-50	-4	0.009418378
TX>THM							
1	Right Occipital Lobe	3064					
	Lingual Gyrus		17	20	-90	2	0.012012509
	Lingual Gyrus		18	12	-92	-6	0.009581443
	Lingual Gyrus		18	18	-88	-12	0.009257395

Table 2. ALE clusters for activation of TX>THM and THM>TX across all studies

Note: BA, Brodmann Area.
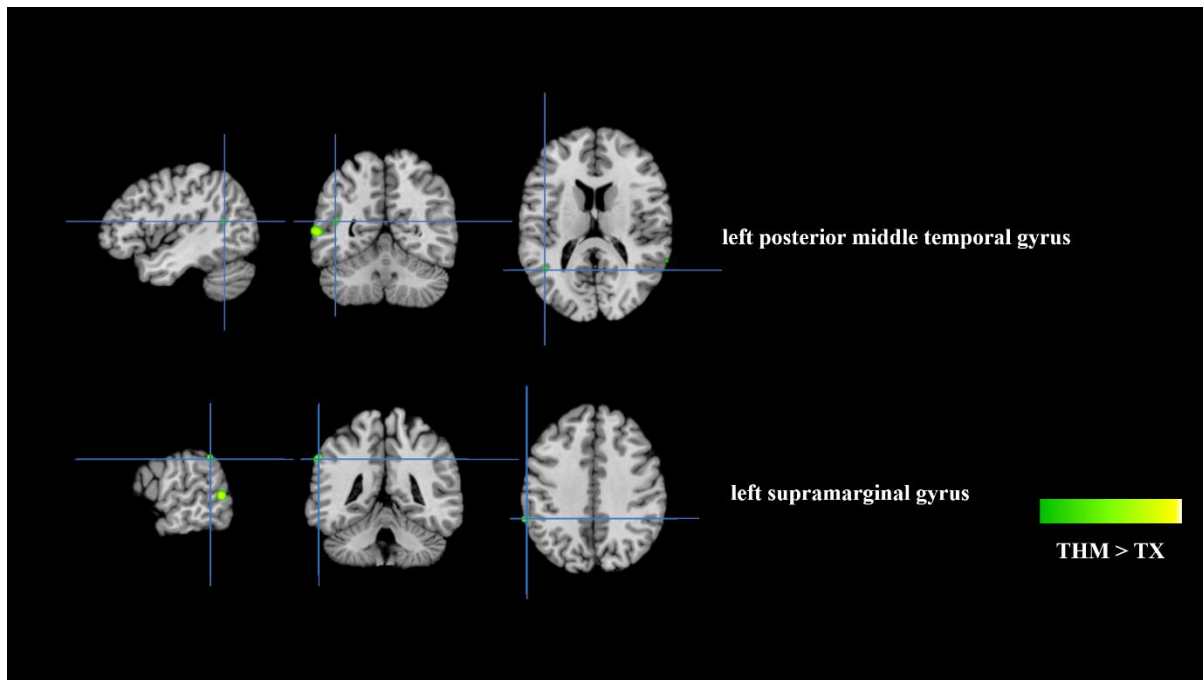
Figure 2. The activation likelihood of new clusters of thematic versus taxonomic relation (green). Images are thresholded at p<0.001 without correction for multiple comparisons.

The main analysis revealed that the THM>TX activated regions within TPC, albeit limited to pMTG and supramarginal gyrus (SMG), but provided no evidence for TX>THM effects in the ATL. Thus, ALE analyses without cluster correction ($p<0.001$ uncorrected) were conducted to investigate whether these effects were present at a more liberal statistical threshold. The definitions of ATL and TPC are based on the cluster labels in GingerALE 3.0.2 (Eickhoff et al., 2012; Eickhoff et al., 2009). For TPC, we considered peaks posterior to y = -40 labelled as angular gyrus (AG), supramarginal gyrus (SMG), middle temporal gyrus (MTG) or superior temporal gyrus (STG). For ATL, we considered peaks anterior to y = -30 labelled as MTG, STG, inferior temporal gyrus (ITG), fusiform or parahippocampal gyrus. A minimum cluster size of 100 mm^3 was applied to the results. For the THM>TX contrast, another 2 clusters in left pMTG and left SMG were found (Figure 2), which was consistent with the dual-hub view. The TX>THM contrast did not reveal any activation in ATL, even at this more liberal threshold. Other small clusters outside of ATL and TPC were also found but as this was an uncorrected analysis and we did not have specific predictions

about areas outside of ATL and TPC, we do not consider these results further.

4.3.3 Discussion

We used ALE meta-analysis of 16 functional neuroimaging studies to investigate the potential neural disassociation between taxonomic and thematic relations. Although the available evidence base is limited, this analysis still allows us to draw some initial conclusions about neural specialization for each of these relations. The contrast of THM>TX reported significant activation likelihood in left pMTG and left SMG, which is consistent with the dual-hub and feature reliance hypotheses. However, the TX>THM contrast did not show effects in left ATL; in fact, a portion of lateral ATL showed significant activation likelihood for THM>TX. The TX>THM contrast only revealed effects in right lingual gyrus.

For THM>TX, significant activation likelihood was found in pMTG (see Figure 1, corrected results) and SMG (see Figure 2, uncorrected results). The pMTG has been found crucial for representing motion, action or tool-related concepts (Buxbaum et al., 2014; Kalénine et al., 2010; Tarhan et al., 2015; Watson et al., 2013). The SMG, as a part of inferior parietal cortex, is important for planning and executing tool-related actions (Przybylski & Króliczak, 2017; Randerath et al., 2010; Tunik et al., 2007) and is also involved in processing spatial language (Struiksma et al., 2011), spatial memory (Moscovitch et al., 1995; Silk et al., 2010) and integrating spatial and temporal information (Assmus et al., 2003). Damage to SMG is also associated with impairment in comprehending spatial relations between objects (Amorapanth et al., 2012; Amorapanth et al., 2010; Tranel & Kemmerer, 2004). Thus, the meta-analysis result of TXM>TX is consistent with the feature reliance hypothesis, since thematic relations appear to preferentially activate regions involved in processing action and location information. In addition, pMTG is a part of the semantic control network (Jackson, 2021; Noonan, Jefferies, Corbett, & Ralph, 2010) which plays a crucial role in executively demanding semantic cognition (Davey et al., 2015; Whitney et al., 2011, 2012). Thompson et al. (2017) suggested that thematic relations require more semantic control than taxonomic relations, because they require participants to search for the particular context in which the items co-occur. Thus, the pMTG effects may also reflect semantic control processes, in addition to regions specialised for action and motion processing. The difficulty deactivation effects in AG should also be

considered in explaining the THM > TX results. The AG was found to deactivate more strongly for more difficult tasks (e.g., Humphreys et al., 2015; Humphreys et al., 2021). Considering many studies in the meta-analysis reported longer reaction time for taxonomic relations (e.g., Abel et al., 2009; G. I. De Zubicaray et al., 2013; Kotz et al., 2002; Sachs, Weis, Krings, et al., 2008; Sass et al., 2009), taxonomic judgements tend to be more difficult than thematic relations. This difficulty difference might lead to more AG activation for thematic relation than taxonomic relations. However, these effects were not found in the meta-analysis results.

The TX>THM contrast revealed reliable activation in the right lingual gyrus, potentially due to its role in visual processing. The lingual gyrus is involved in processing visual features like shape, colour and texture (Cant & Goodale, 2007; Chao & Martin, 1999; Humphreys & Riddoch, 2006; Marques et al., 2008); thus, this effect might indicate the importance of visual features for determining taxonomic relations, as predicted by the feature reliance hypothesis. There are two possible mechanisms for this effect. In line with embodied cognition theories (e.g., Barsalou, 2008a), processing taxonomic relations might engage simulations of their visual properties, re-activating perceptual regions involved in processing visual inputs. The second possibility is that lingual gyrus activation reflects more detailed visual processing of the presented stimuli. Some of the studies included in the meta-analysis used pictures to elicit taxonomic and thematic processing (Abel et al., 2009; De Zubicaray et al., 2014; G. I. De Zubicaray et al., 2013; Kalénine et al., 2009). If taxonomically-related concepts tend to be more visually similar to one another, taxonomic trials might require more detailed visual analysis of the presented pictures.

Surprisingly, the meta-analysis provided no evidence that ATL is consistently more engaged by taxonomic relations, even at a liberal threshold. In fact, the anterior middle temporal gyrus showed the opposite effect, with significant activation likelihood for the THM>TX contrast. We consider possible explanations for this result in the General Discussion.

4.4 Study 2

Study 1 provided some support for the feature reliance hypothesis at a neural level, since thematic relations preferentially activated TPC regions implicated in action and

location processing, while taxonomic relations to greater activation in visual processing regions. In Study 2, we examined the feature reliance hypothesis at a behavioural level. To test the hypothesis that thematic and taxonomic judgements rely differentially on action/location vs. colour/shape knowledge, we investigated costs in reaction time when people switch between different types of semantic judgement. It is well-established that there is a reaction time cost in making judgements when people are required to switch between different processes or types of representation (Monsell, 2003; Spence et al., 2001). In particular, studies have reported a processing cost in semantic judgements when participants switch between knowledge experienced in different sensory-motor modalities (Marques, 2006; Pecher et al., 2003, 2004; Scerrati et al., 2015; Spence et al., 2001). For example, Marques (2006) found people were faster to make a judgement about an auditory property (e.g., a dog can bark) if this was preceded by another auditory judgement (a bee can buzz), compared with if it was preceded by a visual judgment (a horse can have spots). These findings suggest that making a semantic judgement is faster if the relevant type of knowledge has recently been activated. Landrigan and Mirman (2018) have shown that a cost also occurs when people switch between judging taxonomic and thematic relationships, suggesting that these rely on different processes or representations. However, the nature of this difference has not been investigated. We reasoned that if taxonomic processing relies more on colour and shape attributes, while thematic processing relies more on action and location knowledge, then switching costs should be largest when thematic judgements follow processing of colour and shape, while taxonomic judgements should be slower after participants process action and location knowledge. These predictions can alternatively be framed in terms of priming: making an action/location judgement should prime people to make thematic judgements more efficiently, while a shape/colour decision should act as a more effective prime for taxonomic judgements.

4.4.1 Method

4.4.1.1 Participants

We recruited 212 native English speakers from a pool of psychology undergraduate students participating for course credit and from Prolific (141 females, 71 males). Participants were aged between 18 and 40 (Mean = 21.74, SD = 5.6). After excluding

participants who did not achieve 80% accuracy, 202 participants' data were used for analyses. All reported results are based on the full sample of 202. This study was approved by the PPLS research ethics committee of University of Edinburgh.

4.4.1.2 Design and Materials

Participants made semantic judgements to trials arranged in pairs (see Figure 3 for examples). Each pair consisted of a prime judgement that probed knowledge for an object in a particular sensory-motor modality, followed by a target judgement that probed either a taxonomic or a thematic relationship for different objects.

Each prime included a sentence stem, like 'apple can be' or 'chalk found in', and two feature options, like 'red' and 'blue' or 'classroom' and 'toilet'. There were 4 kinds of primes, which probed knowledge of objects' colour, shape, related action, or typical location. As we predicted similar effects for colour and shape and for action and location, we combined these into two conditions in our main analyses (i.e., colour/shape vs. action/location).

Target trials also included a sentence stem containing a reference word, like 'coffee goes with'. The two options consisted of a taxonomically or thematically related word (*wine/cup*), and an unrelated distractor (*fence*). Reference words and related options were selected from a norming study (Landrigan & Mirman, 2016) in which word pairs were rated on a 7-point scale for taxonomic similarity (whether they have similar features or belong to same category) and thematic relatedness (whether they have contiguity, usually occur in same scenario or event). Table 3 shows the mean ratings of taxonomic and thematic pairs. Pairs with high differences in ratings were selected on the following basis: (1) the absolute difference between taxonomic and thematic rating was larger than 1.15; (2) for taxonomic pairs, their thematic rating was lower than 3.5, for thematic pairs, their taxonomic rating was lower than 3.5. Independent-samples t-tests confirmed that there were significant differences in taxonomic ratings and thematic ratings of taxonomic pairs (t(198)=24.18, p<0.001) and thematic pairs (t(198)=-105.75, p<0.001).

	Taxonomic Rating	Thematic Rating	Rating Difference

Taxonomic Pairs	4.60(±0.58)	2.84(±0.43)	1.75(±0.44)
Thematic Pairs	1.85(±0.27)	6.10(±0.30)	4.26(±0.23)

Table 3. Mean and standard deviation of taxonomic rating, thematic rating, rating difference for taxonomic pairs and thematic pairs

There were 8 practice trials and 192 trials for the main experiment. Each trial consisted of a prime and a target. For the main experiment, 48 primes were created for each of the 4 feature types. For the 192 targets, half contained taxonomic pairs and the other half contained thematic pairs. Each participant was presented with all of the targets in a random order, each preceded by one of the four types of prime. To counterbalance the assignment of primes to targets, participants were divided into four groups. Each group received a different prime, of a different type, for each target. The primes were assigned such that all participants saw each prime and target once and each prime primed a taxonomic judgement for half of the participants and a thematic judgement for the other half. The stimuli of primes and targets can be found in supplementary material (see Appendices Supplementary material of chapter 4: Supplementary Table 1, Supplementary Table 2).

All materials and data can be accessed on OSF:
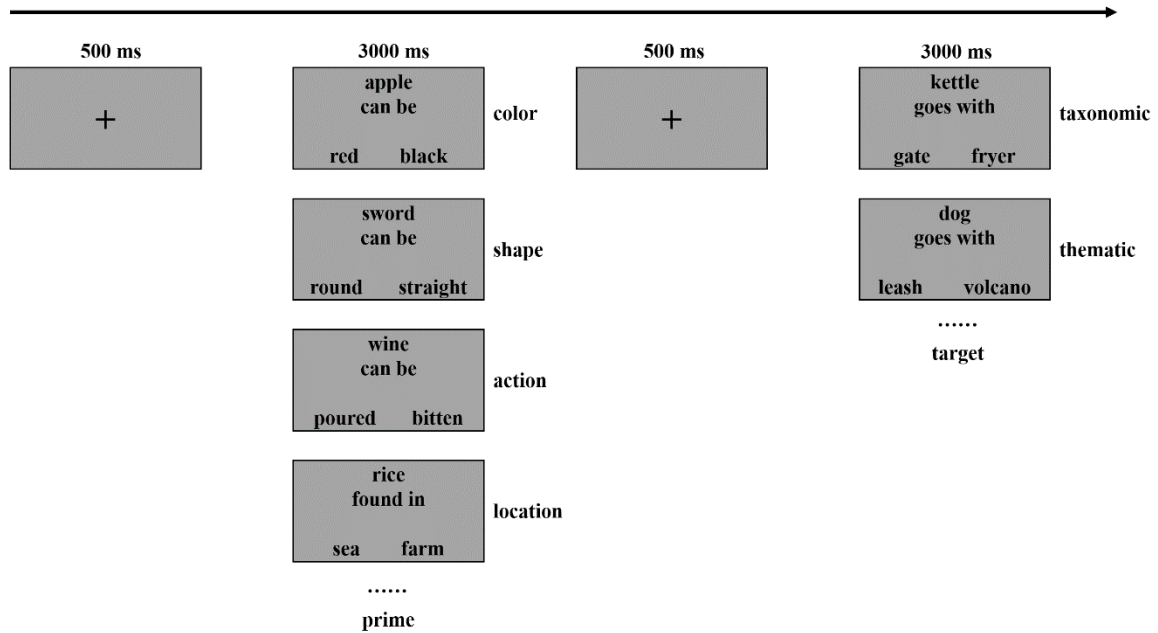
https://osf.io/mrvns/?view_only=4fa15d4f4d4d4595968227363929ca84 .

Figure 3. Procedure of the semantic task

4.4.1.3 Procedure

The experiment was created on the Testable experimental platform (https://www.testable.org/). Participants were instructed to choose the more reasonable word from the two options to complete the sentence, and that there would be 2 kinds of sentence: one describing features of objects; one describing relationships (meaningful connection or similarity) between objects. Participants pressed 'f' for the left option or 'j' for the right option. Correct responses appeared on left and right equally often. The stimuli of each trial were presented in the following sequence (see Figure 3): (1) a fixation cross in the middle of screen for 500ms; (2) prime judgement for a maximum of 3000ms; (3) a fixation cross in the middle of screen for 500ms; (4) target judgement for a maximum of 3000ms. For both primes and targets, if participants made a wrong decision or did not choose any option within 3000ms, then a feedback screen showing 'wrong' or 'too slow' would be displayed for 2000ms. The whole experiment took 20-30 minutes, including one practice session and 4 blocks of the main experiment. Participants were allowed to rest between every 2 blocks.

4.4.1.4 Analysis

The following steps were performed prior to statistical analysis. First, participants who did not achieve 80% accuracy overall were excluded from analyses. Second, for each trial, if its prime or target part were responded to in less than 500ms, it was considered as an outlier and removed (121 trials, 0.3% of all trials). Third, after checking accuracies of each prime and target stimuli in the group, we found 7 prime stimuli for shape features which were responded to with mean accuracy lower than 70%. The low accuracy on these trials suggests that they did not reliably elicit modality-specific knowledge in the way we intended, thus all trials using these primes were removed (753 trials, 1.9% of all trials). No other primes had accuracies of less than 70%. Finally, our analysis of targets excluded trials where participants did not respond correctly to the prime (3217 trials, 8.3% of all trials).

Linear mixed effects (LME) models were used to analyse reaction time data and generalized binomial LME models for accuracy. Our main LME model was fitted to the reaction time data for targets, on the trials where participants responded correctly to both prime and target. For this model, prime type (colour/shape vs. action/location), target type (taxonomic vs. thematic), and their interaction were included as fixed effects. The position of the correct option on the screen (left vs. right) and reaction time to the prime were included as control variables. We controlled for prime reaction time as reaction times in cognitive tasks are frequently influenced by the reaction time on the preceding trial. In other words, when participants make a decision quickly, they are more likely to respond quickly on the next trial (for discussion, see Baayen & Milin, 2010). As our prime reaction times varied as a function of prime type (see Results), it was important to control for this potential influence on the target. By doing so, we ensure that observed effects of prime type are independent of processing speed. Finally, participant, target identity and prime identity were all included as random effects, with random slopes specified according to a maximal model (Barr et al., 2013).

Post-hoc analyses were also conducted to check prime types' effects on reaction time of taxonomic and thematic relations separately. Finally, we checked how the prime type affected accuracy of taxonomic and thematic judgements. For these models, the fixed effects, control variables and random effects were as for the main model predicting reaction times.

4.5 Results

We first computed the accuracies and mean reaction times for primes (Table 4). Mixed effect models showed that action/location primes had significantly higher accuracy than colour/shape primes ($z=5.596$, $p<0.001$), but there was no significant difference between their reaction times ($t(3289.95)=-1.219$, $p=0.22$). The accuracies and mean reaction time for targets are also shown in Table 4.

Target	Prime	Accuracy		Reaction Time (ms)		
		Prime	Target (primed correctly)	Prime	Target (primed correctly)	Combined target (colour/shape; action/location)
Taxonomic	Colour	95%	92%	1225±176	1463 ±204	1473±206
	Shape	85%	93%	1521±186	1483 ±229	
	Action	95%	92%	1289±169	1450 ±204	1461±205
	Location	92%	92%	1332±179	1473 ±225	
Thematic	Colour	95%	96%	1227±171	1333 ±206	1341±198
	Shape	85%	96%	1517±186	1349 ±207	
	Action	95%	95%	1292±167	1312 ±188	1313±186
	Location	92%	95%	1329±187	1313 ±198	

Table 4. Mean reaction times and accuracies of all conditions of primes and target judgements.

Fixed effects		b	S.E.	df	t	p
Intercept		1379.679	13.743	324.132	100.391	<.001*
Prime Type (AL>CS)		-5.021	2.594	123.933	-1.935	.0552
Target Type (THM>TX)		-64.830	3.251	640.518	-19.944	<.001*
Prime Type * Target Type		-4.436	2.119	207.681	-2.093	**.0375***
Prime RT		67.629	2.075	30176.198	32.588	<.001*
Target Cor Pos		-30.427	3.322	7055.922	-9.158	<.001*

Table 5. Linear mixed-effect model estimates of fixed effects on target reaction times.

Note: AL, action/location; CS, colour/shape; THM, thematic; TX, taxonomic; Prime Type * Target Type, the interaction of prime type and target type; Prime RT, reaction time of prime; Target Cor Pos, the position of the correct option. df was estimated by Satterthwaite approximation from the LmerTest package.

Table 5 shows estimates for the model predicting target reaction time. There was a main effect of target type, whereby participants made thematic judgements faster than taxonomic judgements ($t(640.518)$ = -19.944, $p<0.001$). Most importantly, the interaction between prime type and target type was also significant ($t(207.681)$ = -2.093, $p=0.0375$). Model estimates for the effects of prime type and target type are shown in Figure 4. Post-hoc tests examined the effect of prime type on taxonomic and thematic relations separately. As shown in Table 6, prime type had a highly significant effect on thematic trials: as predicted, responses were faster following action/location primes. In contrast, there was no effect of prime type on taxonomic judgments.
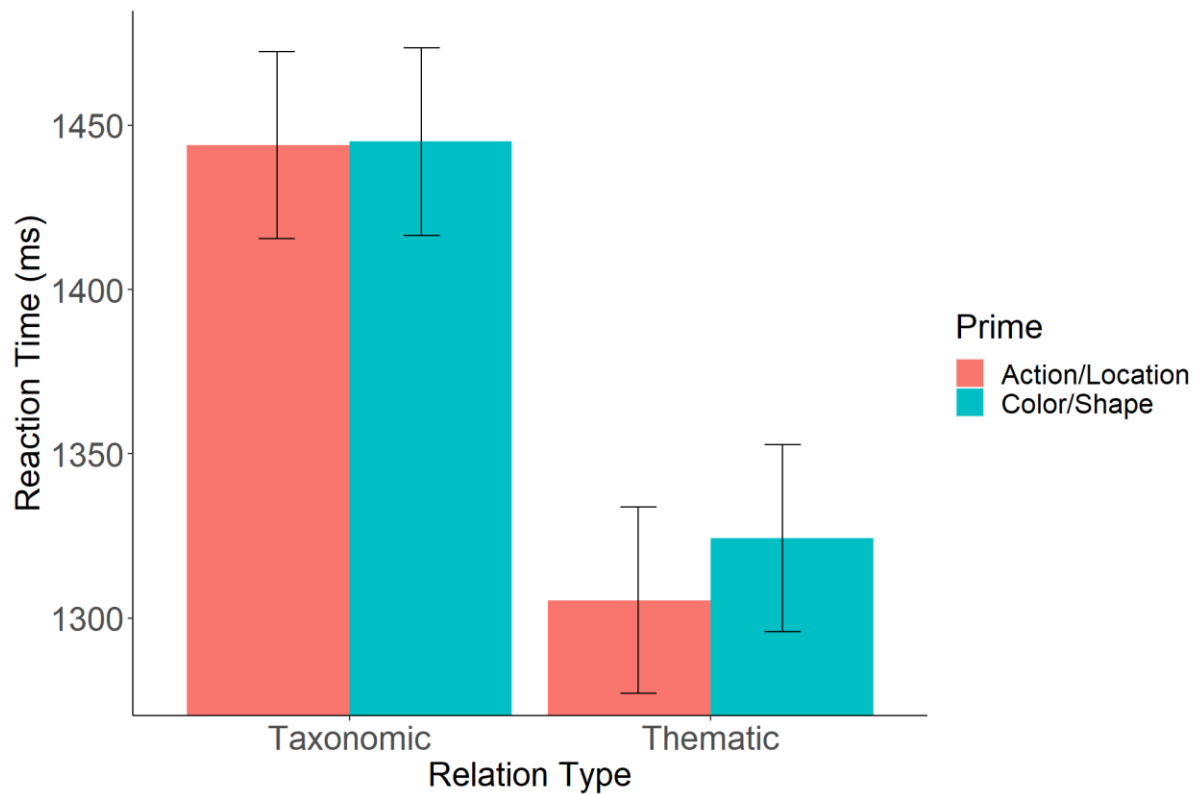
Figure 4. Model estimates for the effects of prime type on reaction time of taxonomic and thematic relations

TargetType	Fixed effects	b	S.E.	df	t	p
	Intercept	1450.602	17.428	194.692	83.233	<.001*
	Prime Type (AL>CS)	-0.087	3.652	80.870	-0.024	0.981
Taxonomic	Prime RT	71.295	3.033	14784.413	23.502	<.001*
	Target Cor Pos	-1.641	6.723	1402.623	-0.244	0.807
	Intercept	1308.120	15.016	227.270	87.113	<.001*
Thematic	Prime Type (AL>CS)	-10.549	3.116	81.821	-3.386	**.001***

		63.521	2.842	14338.929	22.351	<.001*
Prime RT						
Target Pos	**Cor**	-47.199	6.765	544.918	-6.976	<.001*

Table 6. Linear mixed-effect model estimates in separate models for taxonomic and thematic trials.

Note: AL, action/location; CS, colour/shape; Prime RT, reaction time of prime; Target Cor Pos, the position of the correct option. df was estimated by Satterthwaite approximation from the LmerTest package.

Finally, we investigated how prime type affected target accuracy. As shown in Table 7, participants were more accurate to respond on thematic trials but no other effects were significant.

Fixed effects		b	S.E.	Z	p
Intercept		3.019	0.077	39.110	<.001*
Prime Type (AL>CS)		-0.045	0.025	-1.794	0.0729
Target Type (THM>TX)		0.359	0.034	10.463	<.001*
Prime Type * Target Type		-0.013	0.024	-0.532	0.5950
Prime RT		-0.008	0.024	-0.330	0.7415
Target Cor Pos		0.019	0.037	0.510	0.6104

Table 7. Linear mixed-effect model estimates of fixed effects on target accuracies

*Note: AL, action/location; CS, colour/shape; THM, thematic; TX, taxonomic; Prime Type * Target Type, the interaction of prime type and target type; Prime RT, reaction time of prime; Target Cor Pos, the position of the correct option for target part in each*

trial.

4.6 Discussion

By using a primed semantic decision task, this behavioural experiment investigated the priming effects of accessing different types of semantic knowledge (colour, shape, action, location) on taxonomic and thematic judgements. Generally, thematic judgements required less processing time than taxonomic judgements (Table 4). Importantly, priming different types of knowledge had differential effects on thematic and taxonomic relations. Thematic judgements were more facilitated by action/location primes than by colour/shape primes. But for taxonomic judgements, colour/shape judgements did not show a significantly different priming effect to action/location judgements (Figure 4, Table 6).

Our results suggest that thematic judgements rely on access to knowledge about action and location to a greater extent than to knowledge about colour and shape. This is consistent with how previous studies have defined thematic relations as associations based on frequent co-occurrence in events or situations (Estes et al., 2012), including relations that are tied to specific roles in events or schemas (Goldwater et al., 2011; Jones & Love, 2007; Markman & Stilwell, 2001). Some researchers have also linked thematic semantics with knowledge of object-use actions (Davey et al., 2016; Kalénine & Buxbaum, 2016; Tsagkaridis et al., 2014). However, our data do not support the idea that taxonomic judgements rely preferentially on colour and shape knowledge. We consider possible reasons for this in the General Discussion.

4.7 General Discussion

Knowledge for taxonomic and thematic relations are thought to be supported by distinct neural systems, but the neural substrates of these systems and the root causes for neural specialisation remain unclear. In the present study, we tested one potential account of these effects: that taxonomic vs. thematic relations are determined by different types of semantic features (the feature reliance hypothesis). We first conducted neuroimaging meta-analyses contrasting taxonomic and thematic relation processing. These demonstrated that TPC subregions involved in action and

location processing, specifically the left pMTG and SMG, are reliably more engaged by thematic relations.

For taxonomic relations, the only region to show significant activation likelihood was an area of right occipital lobe. Second, in a behavioural experiment, we investigated how different domains of semantic knowledge prime the two relation types. This study showed that priming participants to think about actions or locations facilitates thematic relation processing (compared to priming shape or colour domains). However, no difference between prime types was found for taxonomic relations. Taken together, this evidence suggests thematic relations are particularly reliant on knowledge about objects' associated actions and locations, and that thematic relations preferentially engage temporo-parietal cortex. However, there was no evidence that taxonomic relations are linked specifically with shape and colour features, nor that they preferentially engage left ATL. In fact, a lateral portion of ATL showed the opposite effect. We considered reasons for this in the following discussion.

For the contrast of thematic over taxonomic relations, our meta-analysis showed effects in TPC regions. Left pMTG had significantly more activation likelihood for thematic relation. A cluster in left SMG also showed more thematic effects with a more lenient, uncorrected threshold. These effects are consistent with the proposal that action and location associations are particularly important in determining thematic relations. As subregions of TPC, pMTG and SMG are implicated in representing action- and motion-relevant concepts and in spatial cognition (Assmus et al., 2005; Assmus et al., 2003; Bedny et al., 2008; Gennari et al., 2007; Moscovitch et al., 1995; Noppeney et al., 2005; Przybylski & Króliczak, 2017; Randerath et al., 2010; Silk et al., 2010; Tunik et al., 2007). The pMTG is crucial for processing action or motion concepts, especially manipulation of familiar objects (Buxbaum & Kalénine, 2010; Watson & Chatterjee, 2011), or tool-related verbs (Tyler et al., 2003). Compared to object concepts, action and event concepts elicit more activation in left posterior middle and superior temporal gyri (Bedny et al., 2014; Kable et al., 2005; Kable et al., 2002; Watson et al., 2013). Lesion studies also showed the association between posterior temporal lobe and understanding gestures and object-use actions (Buxbaum et al., 2014; Kalénine et al., 2010; Tarhan

et al., 2015). In addition, our meta-analysis reported more activation likelihood in SMG for thematic relations. As a part of inferior parietal lobe, SMG is linked with a range of processes relating to action and spatial cognition (Assmus et al., 2005; Assmus et al., 2003; Moscovitch et al., 1995; Przybylski & Króliczak, 2017; Randerath et al., 2010; Silk et al., 2010; Tunik et al., 2007). Therefore, a variety of functional specializations within the pMTG and SMG suit the processing of thematic relations, in line with the idea that action and spatial representations are particularly important for computing thematic relations. The behavioural study supports this interpretation, since thematic decisions were faster after participants accessed action/location knowledge than after they accessed colour/shape knowledge.

In addition, pMTG is a key part of the semantic control network (Jackson, 2021; Noonan, Jefferies, Corbett, & Ralph, 2010). Inhibitory TMS applied to pMTG transiently disrupts semantic processing, particularly in conditions that need high levels of cognitive control (Davey et al., 2015; Whitney et al., 2011, 2012), suggesting that this region plays a crucial role in executively demanding semantic cognition. It has been proposed that thematic relations require more semantic control than taxonomic relations, because they require participants to search for the particular context in which the items co-occur (Thompson et al., 2017). Thus, our results may reflect recruitment of semantic control processes served by pMTG, in addition to regions specialised for action and motion processing. A recent meta-analysis indicates that these functions engage neighbouring and partially overlapping regions of posterior temporal cortex (Hodgson et al., 2022).

For taxonomic relations, our meta-analysis reported significant activation likelihood in right lingual gyrus. Although this is not the predicted ATL semantic hub, this effect is consistent with the feature reliance hypothesis (i.e., that taxonomic relations are determined preferentially by static visual features). Areas in the lingual gyrus process visual features like shape and colour (Cant and Goodale, 2007; Chao and Martin, 1999; Humphreys and Riddoch, 2006; Marques et al., 2008). Thus, activation in this region might reflect mental imagery or retrieval of objects' visual features, which may be required disproportionately when determining taxonomic relationships. Right lingual gyrus activation has been observed during imagery of faces, scenes (de Gelder et al., 2015), letters (Kosslyn et al., 1993) and spatial positions (Boccia et al., 2015), as well

as when people make judgements about objects' colours from their names (Hsu et al., 2011). Multivariate fMRI analyses have also shown that when people read object names, activation patterns in the lingual gyrus code information about their real-world size (Borghesani et al., 2016).

However, in our behavioural study, colour and shape judgements did not show priming effects for taxonomic judgements when compared with action and location judgements (Figure 4, Table 6), which was not consistent with the results of meta-analysis. One explanation is that taxonomic relations rely on multiple dimensions of information rather than selectively on colour and shape knowledge. A range of properties could be shared within taxonomic categories, including smell, taste, motion, habitat, usage scenarios or associated actions, in addition to colour and shape. For example, compared with watermelon, orange and lime might be more taxonomically related for people, even though watermelon and lime are more similar in colour. There is some empirical evidence for this view. Using feature listing data, Dilkina and Lambon Ralph (2013) found that taxonomic structure was most strongly predicted by perceptual similarity (such as shape, size, colour, and parts), but was also related to concepts' encyclopaedic features, which partly organised concepts based on commonality in location, and functional properties. Thus, taxonomic judgements might not have a strong reliance for shape/colour features, but instead require a whole range of information in multiple dimensions. However, the lingual gyrus effects in meta-analysis showed that occipital regions preferred taxonomic, suggesting a greater reliance on visual features. And that this requires further investigation to rule out possible explanations (e.g., difference in visual complexity between taxonomic and thematic trials).

Our meta-analysis also found unexpected results in the left ATL. The dual-hub hypothesis claims that taxonomic relations rely particularly on the ATL. The feature reliance hypothesis could explain this specialization since ventral parts of the ATL (especially the anterior fusiform gyrus) receive strong inputs from the ventral visual stream that process objects' visual properties (Bajada et al., 2015). But in the meta-analysis, there was no evidence that ATL regions show greater activation for taxonomic than for thematic relations. One possible reason for this is a lack of power. The meta-analysis included a limited number of studies, and the number of peaks was

much lower in the TX>THM contrast than the THM>TX. In addition, fMRI signal in ventral ATL is often poor as this region is affected by susceptibility artefacts that distort and degrade the BOLD signal (Ojemann et al., 1997; Visser et al., 2010). Alternatively, it could be that ventral ATL is equally engaged by both relations. According to hub-and-spoke theory, the ATL, particularly its ventral parts, encodes multimodal conceptual representations of concepts and integrates information from various modality-specialized regions across the cortex (Lambon Ralph et al., 2017). These representations might be equally important for computing taxonomic and thematic relations between concepts.

Our meta-analysis found that anterior parts of MTG and STG were more engaged by thematic relations. Recent evidence suggests there are graded specializations within the ATL and that the dorsolateral areas (particularly STG) are relatively specialized for processing verbal semantic knowledge (Hung et al., 2020; Lambon Lambon Ralph et al., 2017; Rice, Hoffman, et al., 2015). This may indicate a reliance of thematic relations on verbal processing. Thematic relations tend to benefit from linguistic associations and knowledge: when objects go together in the real world, their names are frequently used together in language (Dilkina & Lambon Ralph, 2013). In contrast, such verbal associations are often avoided when selecting taxonomically-related stimuli (e.g., Jackson et al., 2015). The reliance of thematic relations on linguistic knowledge is also evident behaviourally: a study of bilingual children found that they were much more likely to make thematic judgements than taxonomic ones when the stimuli words came from their first language rather than second language (Li et al., 2011). Thus, one possible explanation is that thematic relations rely to a greater extent on verbal associative knowledge, which could account for greater activation in dorsolateral ATL. If true, this would have two consequences for understanding the taxonomic-thematic distinction. First, verbal associations should be considered as another type of knowledge on which the two relations differentially rely. Second, it would suggest that the characterization of ATL as a general hub for taxonomic relations is too simplistic. Instead, different regions within ATL may show different forms of specialization, in line with graded specialization in this area for visual vs. verbal forms of knowledge (Lambon Ralph et al., 2017).

Finally, existing studies of taxonomic and thematic relations usually only consider concrete concepts, thus our feature reliance hypothesis is intended to apply to these concepts and we used only relatively concrete words in Study 2. The status of taxonomic and thematic relations in abstract concepts remains unclear, though some work suggests that their roles in representing abstract words differ from the concrete domain. Crutch et al. (2009) have proposed that abstract words are principally organised by their thematic relations with one another, while taxonomic similarity is the key organising principle for concrete words. Skipper-Kallal et al. (2015) also suggested that TPC is a key region for both thematic relations and for abstract concepts. Further studies are needed to explore how abstract thematic and taxonomic relations might differ in feature reliance, and how these effects are expressed in the brain.

4.8 Conclusion

Across two studies, we tested the hypothesis that different semantic features preferentially contribute to taxonomic and thematic relations, accounting for neural specialisation for these two relation types. A neuroimaging meta-analysis supported the association between thematic relations and TPC regions involved in action and spatial processing, but showed no evidence that taxonomic relations rely preferentially on ATL regions. A behavioural priming experiment found that attending to action and location knowledge facilitates thematic judgements, but that priming colour and shape knowledge does not facilitate taxonomic judgements. These results support the idea that thematic relations are differentially reliant on action and location features, and might rely particularly on TPC since this region is crucial for representing action and spatial information. Conversely, the evidence for taxonomic relations relying on visual feature knowledge was more mixed and it is possible that taxonomic relations rely on multiple types of features in various modalities, rather than specifically on visual features. Finally, greater activation of lateral ATL regions for thematic processing may indicate that thematic relations rely more on verbal associations. Taken together, these results help us to understand how particular semantic features contribute differently to taxonomic and thematic relations.

Chapter 5: Representation of event and object concepts in ventral anterior temporal lobe and angular gyrus

5.1 Abstract

Semantic knowledge includes understanding of objects and their features and also understanding of the characteristics of events. The hub-and-spoke theory holds that these conceptual representations rely on multiple information sources that are integrated in a central hub in the ventral anterior temporal lobes (vATL). Dual-hub theory expands this framework with the claim that the vATL hub is specialized for object representation, while a second hub in angular gyrus (AG) is specialized for event representation. To test these ideas, we used RSA, univariate and PPI analyses of fMRI data collected while participants processed object and event concepts (e.g., 'an apple', 'a wedding') presented as images and written words. RSA showed that AG encoded event concept similarity more than object similarity, although the left AG also encoded object similarity. Bilateral vATLs encoded both object and event concept structure, and left vATL exhibited stronger coding for events. PPI analysis revealed greater connectivity between left vATL and right pMTG, and between right AG and bilateral ITG and middle occipital gyrus, for event concepts compared to object concepts. These findings support the specialization of AG for event semantics, though with some involvement in object coding, but do not support vATL specialization for object concepts.

5.2 Introduction

Humans can recognise and reason about single objects, and we can also understand events as coherent conceptual units -- complex, context-bound interactions between objects that unfold over time. Object similarity can be captured by shared features, whereas events involve multiple objects' interactions, temporal sequences and causal relationships (Altmann & Ekves, 2019). A core function of the semantic system is to represent similarities between these abstract conceptual units. For example, apples are more similar to tomatoes than to hammers, and weddings are more similar to parties than to fights. The neural coding of object similarity has been studied in depth (Bi et al., 2016; Chen et al., 2016; Devereux et al., 2013; Hutchison et al., 2014; Kaneshiro et al., 2015; Xu et al., 2018). Event structure coding is also investigated by some studies (Baldassano et al., 2017; Bedny et al., 2014; Morton et al., 2020). However, object representation and event representation are rarely compared directly, meaning that differences in their neural bases remain unclear. Thus, in the present study, we used representational similarity analysis (RSA), univariate fMRI analyses, and functional connectivity analyses to directly compare how the semantic structures of objects and events are represented in the brain.

Vision is crucial for identifying objects and events, thus specializations for object and event understanding could be driven by the organization of the visual system into dorsal and ventral pathways (Mirman et al., 2017). The dorsal pathway usually refers to the processing stream that lies between early visual cortex and frontal-parietal regions specialized for action, and which courses through temporal-parietal cortex (Kravitz et al., 2013; Mishkin et al., 1983). The dorsal stream is identified as a 'where/how' pathway, supporting visually-guided action, motion and spatial cognition (Andersen & Cui, 2009; Buxbaum & Kalénine, 2010; Husain & Nachev, 2007; Wager & Smith, 2003; Watson & Chatterjee, 2011). The dorsal stream may be particularly important for event representation, as this requires processing of objects' interactions and their spatiotemporal relations. Conversely, the ventral pathway lies between early visual cortex and the ventral anterior temporal lobe (vATL), and courses through the inferior parts of the temporal lobe (Kravitz et al., 2013; Mishkin et al., 1983). This stream is characterised as a 'what' pathway, specialised for

identifying and categorizing objects. In line with this view, ventral pathway regions are engaged in processing and integrating perceptual features like colour, size, and brightness (Baron et al., 2010; Coutanche & Thompson-Schill, 2015; Martin et al., 2018). Regions in this pathway show category-selective effects for different object categories like tools, animals and human faces (Bi et al., 2016; Hutchison et al., 2014).

As the junction of the ventral pathway with other processing streams, vATL is thought to act as a transmodal semantic hub that combines visual features with multimodal information sources to generate conceptual representations (for review, see Lambon Ralph et al., 2017). The ATLs are strongly associated with integrating object features across sensory modalities (Coutanche & Thompson-Schill, 2015; Rogers & McClelland, 2004), and are engaged in semantic processing irrespective of input modality (e.g., words, pictures and sounds) (Binney et al., 2010; Marinkovic et al., 2003; Vandenberghe et al., 1996; Visser & Lambon Ralph, 2011) and across a range of conceptual categories (Conca et al., 2021; Hoffman et al., 2015; Rice et al., 2018; Wang et al., 2019).

Studies using multivariate pattern analysis indicate that ATL regions code semantic relationships between objects (Chen et al., 2016; Fairhall & Caramazza, 2013; Peelen & Caramazza, 2012; Rogers et al., 2021). For example, in an iEEG study using a picture-naming task, Chen et al. (2016) observed that vATL activity patterns were predicted by semantic similarity between objects, even after controlling for visual and phonological features of the stimuli. The medial part of vATL, the perirhinal cortex, has been implicated specifically in recognizing objects and in differentiating between objects that have many overlapping semantic features (for review, see Clarke & Tyler, 2015). Perirhinal cortex activation increases when participants recognize semantically more-confusable objects (Clarke & Tyler, 2014; Tyler et al., 2013) and damage to this region results in deficits for naming semantically more-confusable objects (Wright et al., 2015). RSA analyses of fMRI data indicate that more similar objects elicit more similar patterns of activation in the perirhinal cortex (Bruffaerts et al., 2013; Devereux et al., 2018; Liuzzi et al., 2015; Naspi et al., 2021). For example, Liuzzi et al. (2015) presented people with written object names, and found that in left perirhinal cortex, activation pattern similarity was

predicted by semantic similarity between objects (measured in terms of their property overlap). Besides, the ventrolateral part of vATL, fusiform gyrus (FG) is also crucial in semantic representation. In a functional positron emission tomography (PET) study, Mion et al. (2010) reported that the fusiform gyrus (FG) played a crucial role in semantic disruptions observed in individuals with semantic dementia (SD). Ding et al. (2016)further revealed that the gray matter volumes of the left FG was significantly correlated with the semantic scores of SD patients. The left FG, especially its anterior part, has been considered as an amodal region in semantic representation (Binney et al., 2010; Lambon Ralph, 2014). Given that the FG is adjacent to multiple modality-specific regions, such as auditory, visual and emotional systems (Rice, Lambon Ralph, et al., 2015), the FG may be responsible for amodal semantic representation of single objects (Binney et al., 2012). Much evidence using a variety of techniques has shown the important roles of left FG in semantic processing, including meta-analyses (Binder et al., 2009; Visser et al., 2010), neuroimaging studies (Visser et al., 2012; Visser & Lambon Ralph, 2011), cortical stimulation (Shimotake et al., 2015a) and neuropsychological studies (Wright et al., 2015). However, while it is now well-established that regions within vATL code semantic similarity between objects, it remains unclear whether this region also codes semantic similarities between events. Studies of event semantics have instead focused on regions within the temporoparietal cortex (TPC).

An association between TPC and event representation has been suggested by many researchers (for review, see Binder & Desai, 2011; Mirman et al., 2017). Event representations require frequent processing of interactions or contextual associations (e.g., action, spatial, temporal information). This kind of processing may be well-suited to TPC regions, which participate in, and receive inputs from, the dorsal visual stream. TPC regions have been implicated in the semantics of action and in representing thematic relationships between concepts. Posterior temporal lobe is involved in understanding action concepts (Bedny et al., 2014; Kable et al., 2005; Kable et al., 2002) and motion concepts (Bedny et al., 2008; Gennari et al., 2007; Noppeney et al., 2005; Watson et al., 2013; Zhang et al., 2022). The posterior parietal cortex is involved in action planning (for reviews, see Andersen & Cui, 2009; Buxbaum & Kalénine, 2010). Parietal regions within TPC are also important for integrating spatially distributed objects into a single coherent percept (Huberle &

Karnath, 2012; Lestou et al., 2014) and for making temporal order judgements (Davis et al., 2009). These roles in supporting the dynamic aspects of semantics make TPC particularly suited to representing interactions between objects. Indeed, based on neuropsychological and neuroimaging evidence, the dual-hub theory of semantic representation proposes that TPC is specialised for coding thematic/event-based semantic relations (e.g., dog-bone) and the ATL for taxonomic/similarity-based semantic relations (e.g., dog-cat) (Mirman et al., 2017; Schwartz et al., 2011). A recent fMRI meta-analysis provided support for this idea by revealing that TPC regions are reliably more activated by thematic than taxonomic relations (Zhang et al., 2023).

Within TPC, the angular gyrus (AG) in particular has been identified as a critical area for multiple functions relevant to event representation: autobiographical memory and episodic memory (Bonnici et al., 2018; Russell et al., 2019), retrieval of multimodal spatiotemporal memories (Ben-Zvi et al., 2015; Bonnici et al., 2016; Richter et al., 2016; Yazar et al., 2014, 2017), and combinatorial semantics (e.g., computing the meanings of noun+noun and verb+noun phrases) (Boylan et al., 2015; Price et al., 2015). AG has also been proposed as an amodal region integrating multimodal information and storing increasingly abstract representations of entity and event knowledge (Binder & Desai, 2011). They suggested that the level of activation in the AG reflected the amount of semantic information that could be retrieved from a given input (Binder et al., 2009; Binder et al., 2005; Graves et al., 2010; Humphries et al., 2007). They note that, compared with vATL receiving heavy input from the ventral visual stream, AG is bounded by dorsal stream that play a central role in spatial and action cognition (Kravitz et al., 2011), indicating that the AG may play a unique role in the representation of event concepts. More broadly, AG is a key part of the default mode network (DMN), which is implicated in coding situation models of ongoing events and segmenting experiences into separate events (Baldassano et al., 2017; Morales et al., 2022; Ranganath & Ritchey, 2012; Swallow et al., 2011; Yeshurun et al., 2021; Zacks et al., 2010). DMN appears to act as a dynamic network that combines incoming external information with internal information from prior experiences to create detailed, context-specific representations of situations as they develop over time (for review, see Ranganath & Ritchey, 2012; Yeshurun et al., 2021). In line with these functions, DMN is sensitive to event boundaries in a

continuous experience: stronger responses in DMN are observed when participants watch event changes in movies or listen to event changes in narratives (Baldassano et al., 2017; Swallow et al., 2011; Zacks et al., 2010). These various lines of evidence implicate AG in event processing, supporting the idea that this region may act as a semantic hub for event knowledge. If this is the case, it should represent semantic similarities between abstract event concepts (e.g., wedding-party), and it should code event similarities more strongly than object similarities. These predictions have not previously been tested directly.

In summary, vATL has emerged as a representational hub for various aspects of semantic knowledge and is known to play an important role in coding similarity-based relationships between individual concepts. It is not clear whether this role extends to coding semantic relationships between more complex event concepts. In contrast, AG has been proposed to be a semantic hub that specialises for representing event-based knowledge, by integrating contextual information, interactions, and associations between objects. However, while numerous studies have investigated how this region responds to processing temporally-extended events (e.g., movies or narratives; Baldassano et al., 2017; Bonnici et al., 2016; Swallow et al., 2011; Zacks et al., 2010), it is less clear to what extent this region represents more abstract event concepts, or whether it represents these in preference to object concepts. More generally, the regions involved in representing semantic relations for objects and events have rarely been directly compared.

To address these questions, we used fMRI to scan participants when they were presented with event and object concepts (as written words and still images), then conducted RSA to test whether neural patterns reflected semantic similarity within either set of concepts. We particularly focused on representation similarity effects in vATL and AG, since these have been proposed as core semantic hubs for objects and events respectively. We analysed left and right vATLs and AGs. Many studies have assumed semantic representations are left-lateralised and have not tested effects in right-hemisphere regions. Here we included both hemispheres, to determine whether effects are specific to the left hemisphere. In addition, univariate analysis was conducted to test general activation differences to event and object concepts. Finally, psychophysiological interaction (PPI) analyses were performed to

explore whether, when processing event and object concepts, semantic hubs have different connective patterns with other areas.

5.3 Method

5.3.1 Participants

We recruited 43 healthy participants (31 females, 12 males; mean age = 23.07 years, s.d. = 3.23 years, range = 19–32). All participants were right-handed native English speakers, and no-one reported history of dyslexia or other neurological disorders. The study was approved by University of Edinburgh School of Philosophy, Psychology & Language Sciences Research Ethics Committee.

5.3.2 Materials

We presented participants with 60 different concepts, each of which was represented by four different pictures (240 pictures in total; see Figure 1A for examples). 30 of these were event concepts, while the other 30 were object concepts. The list of all concepts can be found in Supplementary Materials (see Appendices Supplemental material of chapter 5: Supplementary Table 1). Object concepts referred to individual entities, and we sampled from a variety of categories: animals (e.g., a dog), food (an apple), manipulable tools (a hammer), vehicles (a car), buildings (a castle), body parts (an arm) and human entities (a woman). Event concepts referred to situations in which multiple people or entities interact, including a range of social (e.g., a party), cultural (an opera), professional (a diagnosis) and everyday events (a picnic). In the experiment, each concept was presented 4 times, with the concept name shown each time with a different picture. We used images to elicit richer representations of the underlying concepts. In addition, by showing broader contexts and interactions, event pictures encouraged participants to process the situational aspects of these concepts. In contrast, object pictures included no background or interactions, encouraging people to process each object as an individual entity. In RSA analyses, we used the average neural responses across all 4 presentations of each concept. This ensured that the neural pattern for each concept represented general knowledge of the concept, rather than idiosyncratic features of one particular image.

Object and event stimuli differed in several ways, reflecting intrinsic differences between object and event concepts. Compared with object pictures, event pictures were more visually complex because they showed scenes containing multiple people and objects. We also computed word frequency and concreteness for each concept name. Concreteness values were obtained from Brysbaert et al. (2014) and frequency values from Van Heuven et al. (2014). There was no significant difference between object and event concepts in frequency (t(58) = -0.04, p =0.97), but object concepts were more concrete than event concepts (t(58) = -9.95, p < 0.001). This was expected given that events are more complex and abstract than objects.

Given these differences, the main RSA analyses were conducted separately within each of the 2 sets of concepts. For completeness, we also present univariate activation contrasts of the two conditions but we note that effects in these contrasts could arise from differences at various levels of processing (i.e., lower-level visual perceptual processes as well as semantic processing).

For RSA, we constructed four 30*30 representational dissimilarity matrices (RDMs) that captured the similarity structures within events and within objects (see Figure 1C). For each set of concepts, we calculated a semantic RDM and a visual RDM. The semantic RDM was based on vector-based representations of word meaning, generated by training the word2vec neural network with the 100-billion word Google news corpus (Mikolov et al., 2013). We defined dissimilarity between two concepts as one minus the cosine between their word2vec vectors. Although a number of vector-based models of word meaning are available, we used word2vec because these vectors show the best fit to human semantic relatedness judgements (Pereira et al., 2016). The visual RDM controlled for the low-level visual characteristics of the images we presented. A visual representation of each image was calculated by entering images into the Hmax computational model of vision and extracting the output on the C1 layer of the model, which represents low-level visual attributes (Serre et al., 2007). Visual dissimilarity between images was defined as one minus the Pearson's correlation between their C1 outputs (for a similar approach, see Naspi et al., 2021). To determine the visual dissimilarity between concepts, we averaged the pairwise dissimilarities between the images representing each concept.

5.3.3 Experimental procedure

Participants viewed the concepts in a single scanning run of approximately 24 minutes, after completing two runs of unrelated tasks described later. The timeline for a single trial is shown in Figure 1B. Each trial consisted of a picture presented in the middle of screen for 2.5s with the concept name shown below. Participants were asked to think about the concept demonstrated by the picture and described by the word. To ensure that participants paid attention to the concepts, on 25% of trials the concept was followed by a catch question, which asked if the concept is related to another word. For example, for the concept 'a diagnosis', the catch question was 'Is it associated with doctor?'. Each concept was followed by a catch question on one of its four presentations. The correct answers for half of these catch questions were 'Yes', for the other half they were 'No'. All trials were presented with a mean interstimulus interval of 2.5 s, jittered between 1s and 4s. Trials were presented in 4 blocks, each containing one instance of each concept. The order of stimuli within each block was randomised separately for each participant.
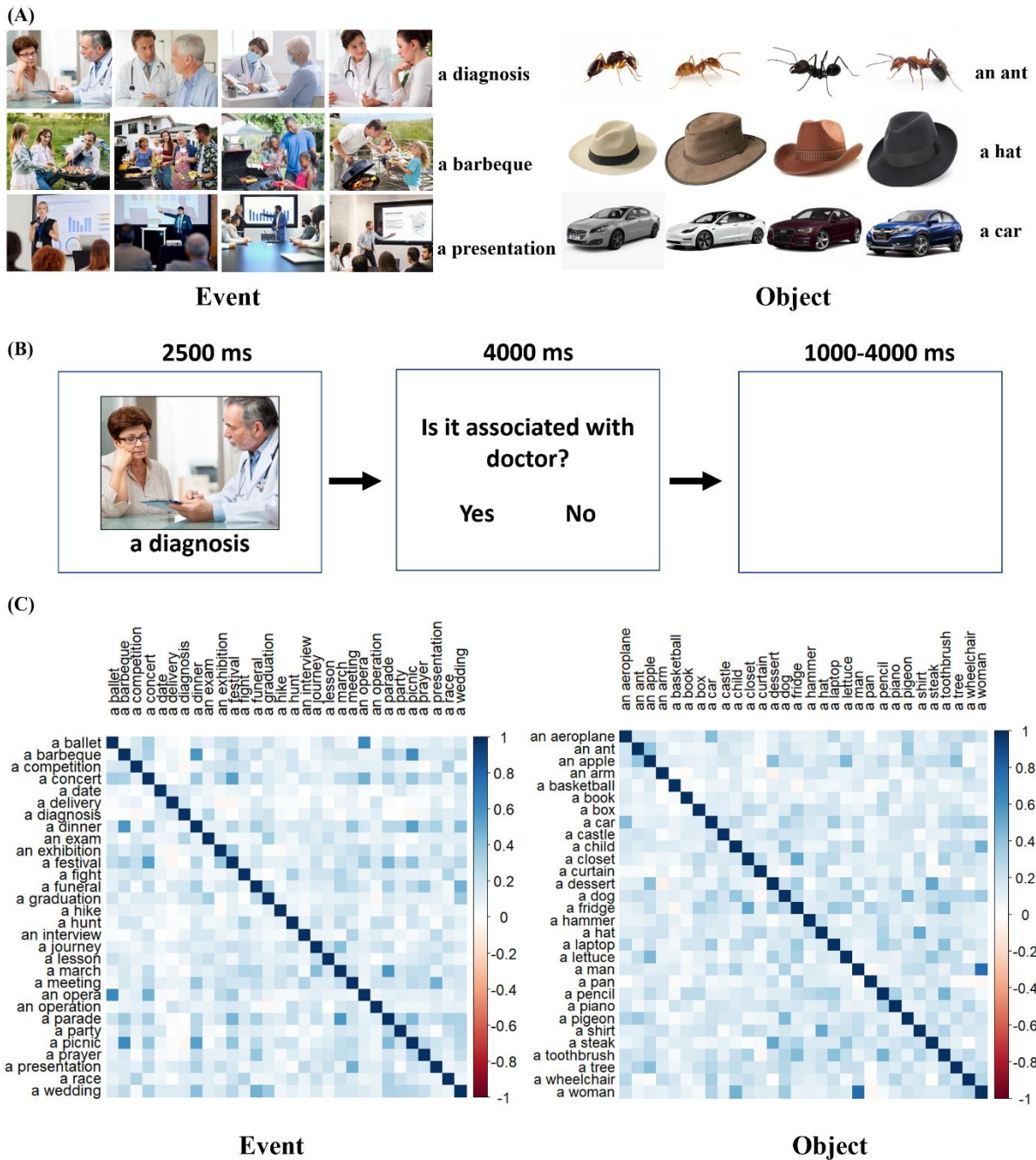
Figure 1. Experimental design.(A) Examples of object and event stimuli. (B) Experimental procedure, showing one trial followed by a catch question. (C) Semantic similarities for event concepts (left) and object concepts (right).

5.3.4 Image acquisition and processing

Images were acquired on a 3T Siemens Prisma scanner with a 32-channel head coil. For the functional images, the multi-echo EPI sequence included 46 slices covering the whole brain with echo time (TE) at 13 msec, 31 msec and 50 msec, repetition

time (TR) = 1.7 sec, flip angle = 73, 80 * 80 matrix, reconstructed in-plane resolution = 3 mm * 3 mm, slice thickness = 3.0 mm (no slice gap) and multiband factor = 2. A single run of 858 volumes was acquired. A high-resolution T1-weighted structural image was also acquired for each participant using an MP-RAGE sequence with 1 mm isotropic voxels, TR = 2.5 sec, TE = 4.4 msec. To minimize the impact of head movements and signal drop out in the ventral temporal regions (Kundu et al., 2017), the study employed a whole-brain multi-echo acquisition protocol, in which data were simultaneously acquired at 3 TEs. Data from the three-echo series were weighted and combined, and the resulting time-series were denoised using independent components analysis (ICA).

Images were pre-processed and analysed using SPM12 and the TE-Dependent Analysis Toolbox (Tedana) (Kundu et al., 2013; Kundu, Inati, Evans, Luh, & Bandettini, 2012). Estimates of head motion were obtained using the first BOLD echo series. Slice-timing correction was carried out and images were then realigned using the previously obtained motion estimates. Tedana was used to combine the three-echo series into a single-time series and to divide the data into components classified as either BOLD-signal or noise-related based on their patterns of signal decay over increasing TEs (Kundu et al., 2017). Components classified as noise were discarded. After that, images were unwrapped with a B0 field-map to correct for irregularities in the scanner's magnetic field. Finally, functional images were spatially normalised to MNI space using SPM's DARTEL tool (Ashburner, 2007), and were smoothed with a kernel of 8 mm FWHM for univariate and PPI analysis and 4 mm FWHM for RSA analysis. Data in our study were treated with a high-pass filter with a cut-off of 180s. Covariates consisted of six motion parameters and their first-order derivatives.

For univariate and PPI analysis, a general linear model (GLM) was used that included 3 regressors for event concepts, object concepts, and catch trials. For RSA, to obtain better estimates of activation patterns of each concept, we used the least squares separate (LSS) approach (Mumford et al., 2012). We ran a separate GLM for each concept, where the 4 trials of that concept were modelled as the regressor of interest and all other trials were combined into a single nuisance regressor (with a

further regressor modelling catch questions). This process yielded one activation map for each concept, which were used to compute neural RDMs.

5.3.5 Regions of Interest

We defined 4 regions of interest (ROIs): left ventral anterior temporal lobe (left vATL), left angular gyrus (left AG), right ventral anterior temporal lobe (right vATL), right angular gyrus (right AG). Each ROI was defined as a 10mm radius sphere centred on specific MNI co-ordinates, which were selected in a two-stage process.

In the first stage, we constructed anatomical masks covering the vATLs and AGs. Masks of vATLs were made in a similar way to Hoffman and Lambon Ralph (2018). We first created masks of the temporal regions: inferior temporal gyrus, fusiform gyrus, superior temporal gyrus, and middle temporal gyrus. These were created by including all voxels with a greater than 50% probability of being located within these areas in the LONI Probabilistic Brain Atlas (LPBA40) (Shattuck et al., 2008). These regions span the full length of the temporal lobe. As there are no anatomical landmarks that demarcate the ATL from the posterior temporal lobe, we had to decide which voxels to include. Following Hoffman and Lambon Ralph (2018), we divided the temporal lobe into 6 sections of roughly equal length along an anterior-to-posterior axis. These sections were numbered 0-5, with section 0 representing the most anterior section. The divisions were made approximately perpendicular to the long axis of the temporal lobe. Finally, we created left ATL and right ATL masks by combining sections 1 and 2 of temporal regions' masks in the left hemisphere and right hemisphere, separately. This includes ventral temporal cortex between y ≈ -2 and y ≈ -28, which is typically the main focus of semantic activation (e.g., Shimotake et al., 2015b).

For masks of AGs, we included all voxels with a greater than 30% probability of being located within this particular brain region as defined by the LPBA40 atlas (Shattuck et al., 2008).

Within these large anatomical masks, we then sought the voxels that were most responsive to semantic processing, using the activation peaks from an independent semantic > non-semantic contrast in the same participants. In the scanning runs

prior to the object/events task, participants completed a series of tasks which required them to match words based on similarities in colour, size, general meaning and letters (for further details, see Wu & Hoffman, 2023). The judgements of colour, size and general meaning all required access to semantic knowledge, while the letter similarity task did not. Based on these tasks, we made a semantic > non-semantic contrast at the group level and identified the peak co-ordinates within each anatomical mask. In the vATLs, the maximal response was in the left and right anterior fusiform region. The maximal AG response was in the ventral part of the AG mask, in the region of the temporoparietal junction. Each ROI was defined as a 10mm radius sphere centred on the peak semantic > non-semantic co-ordinates within each anatomical mask (see Figure 3). The centre coordinates were: left vATL [-36, -18, -30]; left AG [-51, -54, 15]; right vATL [33, -9, -39]; right AG [66, -45, 15]. These 4 ROIs were used in univariate, RSA, and PPI analyses.

5.3.6 Behavioural analysis

For the behavioral data, we built one linear mixed effect (LME) model to predict accuracy for responses to catch questions of event and object concepts, and another one to predict reaction times. The analyses were conducted with R-4.0.3, and 3 packages: 'lme4', 'effects' and 'afex'. In each LME model, concept type (event/object) was set as a fixed effect, and participant was set as the random effect with intercepts and random slopes for concept type.

5.3.7 Univariate analysis

To compare activation for event concept and object concept conditions, both whole-brain analysis and ROI analyses were conducted with SPM12. The whole-brain analysis was corrected for multiple comparisons ($p < 0.05$) at the cluster level using SPM's random field theory, with a cluster-forming threshold of $p < 0.005$. In ROI analyses, we extracted mean beta values in left vATL, left AG, right vATL, right AG in each condition, which represent activation relative to the implicit baseline (rest). Then a three-way repeated ANOVA analysis was done using R-4.2.2, to examine the effects of concept type (event/object), ROI (AG/vATL), hemisphere (left/right) and their interactions.

5.3.8 Representational similarity analysis (RSA)

We used RSA to examine which brain areas are sensitive to similarity in event and object concepts' semantic representations. CoSMoMVPA (Oosterhof et al., 2016) was used for these analyses.

To investigate effects across the brain, we used a searchlight analysis with a spherical searchlight with radius of 4 voxels. We extracted activation patterns for the 60 concepts, and computed pairwise dis-similarities (1 – Pearson correlation) between activation patterns for the event concepts and separately for the object concepts. Then the partial Spearman correlation between neural RDMs and semantic RDMs, controlling for effects of the visual RDMs, was computed. This process was repeated for all searchlights, resulting in two correlation maps, one for objects and one for events. These showed the degree to which neural similarities between concepts are predicted by their semantic similarity. We also computed a difference map by subtracting the 2 correlation maps, to check where neural patterns differed in their alignment with semantics for objects vs. events. Correlations were Fisher-z transformed for group-level analysis. We conducted ROI analysis in the same way but using neural patterns from the 4 spherical ROIs.

To test the significance of the semantic-neural correlations, we used a two-stage method to perform permutation tests (Stelzer et al., 2013). We first computed the correlation maps between semantic RDMs and neural RDMs 100 times for each participant, with random reshuffling of the labels in the semantic and visual RDMs each time. This process provided a distribution of expected correlations under the null hypothesis for each participant. Then we used a Monte Carlo approach to compute a null correlation distribution at the group level (over all participants). To do this, we randomly selected one null correlation map from each participant's null distribution and averaged these to generate a group mean. This process was repeated 10,000 times to generate a distribution of the expected group correlation under the null hypothesis. In searchlight analyses, we entered the observed and null correlation maps into the Monte Carlo cluster statistics function of CoSMoMVPA to generate a statistical map corrected for multiple comparisons using threshold-free cluster enhancement (Smith & Nichols, 2009). These maps were thresholded at corrected $p < 0.05$. For ROI analyses, we used the position of the observed group correlation in the null distribution to determine the p-value (e.g., if the observed

correlation was greater than 95% of correlations in the null distribution, the p-value would be 0.05).

5.3.9 Psychophysiological interaction (PPI) analysis

PPI analysis is a functional connectivity method for investigating task-specific changes in the relationship between different brain regions' activity (K. Friston et al., 1997). While functional connectivity analyses often consider the temporal correlations between different brain regions in all conditions (including the resting state), PPI concentrates on connectivity changes caused by experimental manipulations (Ashburner et al., 2014; Gitelman et al., 2003; O'Reilly et al., 2012). For this study, PPI analysis was conducted to examine which brain regions would show increased correlation with our ROIs when representing event concepts relative to object concepts, or vice versa. The PPI analysis for each seed region (left vATL, left AG, right vATL, right AG) was conducted using SPM12 and the gPPI toolbox (McLaren et al., 2012) with the following steps. First, the seed region was defined as described in the Region of Interest section above, and the BOLD signal time-series extracted using the first eigenvariate. Then, gPPI was used to create a GLM with the following regressors:

1. The signal in the seed region.

2. One regressor coding for each experimental effect of interest, including event concepts, object concepts and catch questions.

3. The interaction between the signal in the seed region and each experimental effect.

4. Head movement covariates as included in the main univariate analysis.

This model was used for testing differences between PPI regressors (i.e., changes in connectivity driven by concept type) in the whole brain. Results were corrected for multiple comparisons ($p < 0.05$) at the cluster using SPM's random field theory, with a cluster-forming threshold of $p < 0.005$.

5.4 Results

5.4.1 Behavioural data

LME models were used to test whether participants responded differently to catch questions about event and object concepts. There were no significant differences in accuracies between concept types (event M = 97.44%, SD = 0.04, object M = 96.98%, SD = 0.04, z (42) = 21.79, p = 0.29) and overall accuracy was very high, suggesting participants maintained attention through the experiment. Participants responded slightly faster to event questions (event M = 1.26 s, SD = 0.27 s, object M = 1.30 s, SD = 0.26 s, t (1815) = -2.152, p < 0.03).

5.4.2 Univariate fMRI analysis
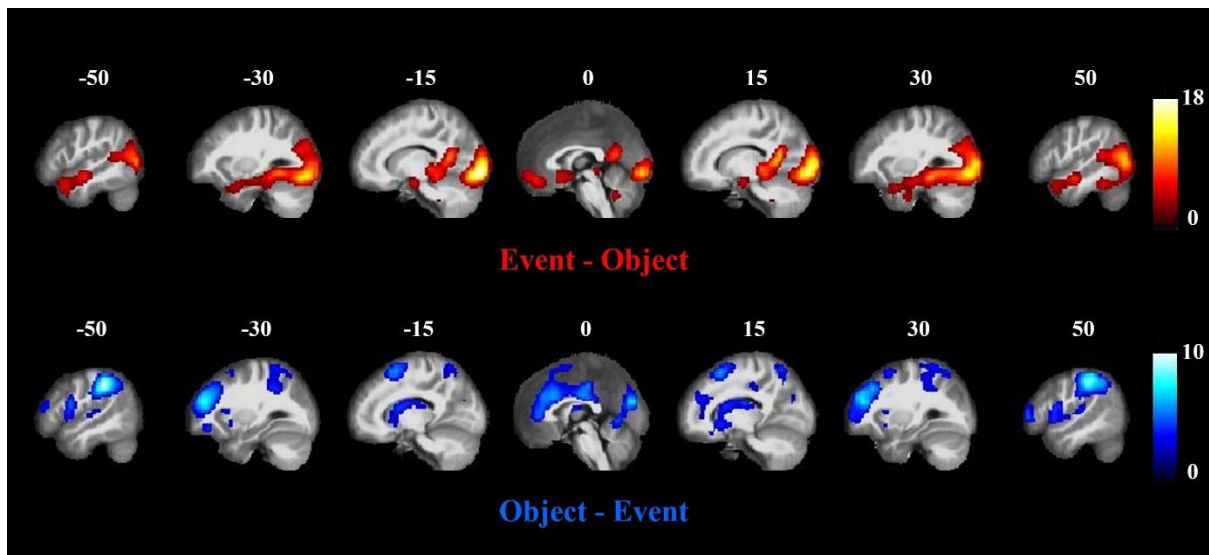
Figure 2. Univariate effects of event concepts versus object concepts, FWE corrected (p≤0.05)

We began by contrasting activation to events and objects. While these results showed which regions are differentially engaged by the conditions, it is important to note that there were substantial visual differences in the stimuli used in each condition. Thus, these results may reflect both semantic and visual differences between event and object trials. The whole-brain analysis contrasting event and object concepts is displayed in Figure 2. Event concepts elicited more activation than objects bilaterally in fusiform gyrus, middle occipital gyrus and lingual gyrus, as well as anterior and posterior parts of superior and middle temporal gyri, hippocampus

and parahippocampal regions, parts of the ventromedial prefrontal cortex and posterior cingulate. Higher activation in visual and scene-processing areas (e.g., parahippocampal gyrus and posterior cingulate) may reflect differences in the images used in the two conditions. Event images were more visually complex, contained a higher number of objects and included contextual elements not present in the object images (see Figure 1 for examples). Stronger responses to events in ventromedial prefrontal cortex and temporal pole could be due to the relevance of social interactions to events (Binney & Ramsey, 2020). Comparatively, object concepts elicited higher activation bilaterally in supramarginal gyrus (SMG), superior parietal cortex and parts of the dorsolateral prefrontal cortices.
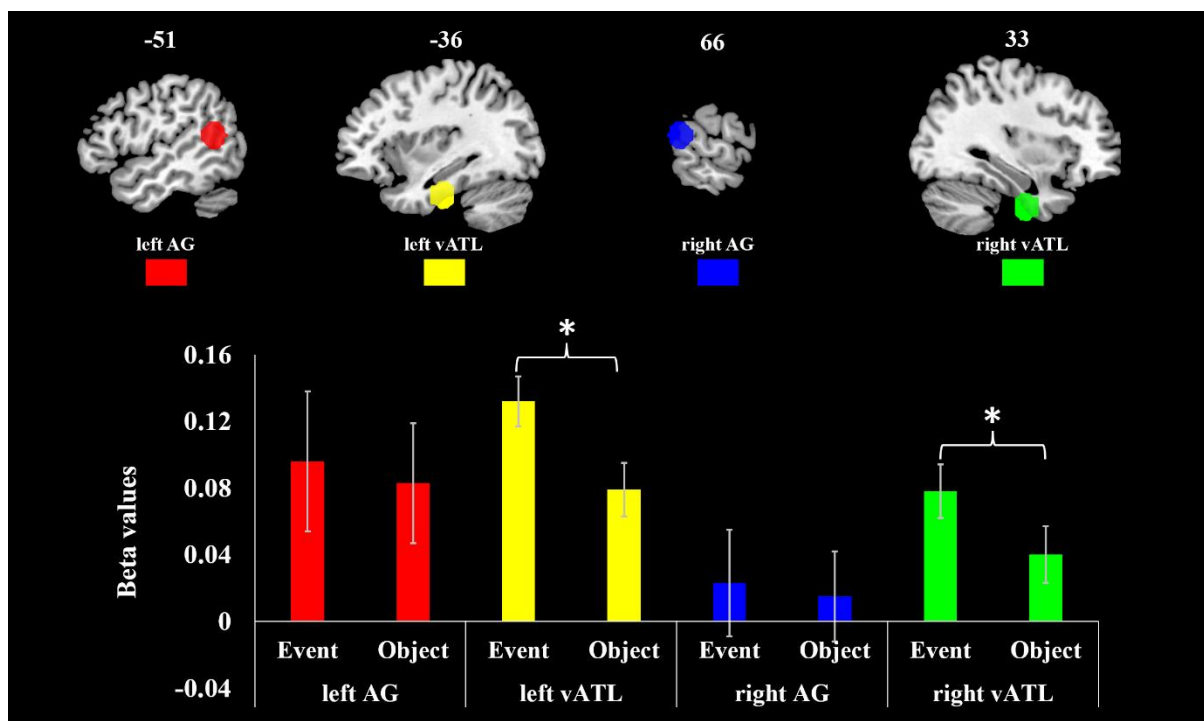

Figure 3. Activation to events and objects in ROIs. Bars show one standard error of the mean.

Figure 3 shows whether ROIs' activations were affected by 3 factors: concept type (event/object), ROI (vATL/AG), hemisphere (left/right). A three-way repeated ANOVA was used to examine these effects. For both event and object concepts, ROIs in left hemisphere showed significantly higher activation ($F(1, 42) = 15.88$, $p < 0.001$). Overall, events elicited more activation than objects, and an interaction between concept type and ROI was also found (Concept effect: $F(1, 42) = 4.436$, $p = 0.041$;

Concept x ROI: $F_{(1, 42)} = 5.483$, $p = 0.024$). No other effects were significant. Post-hoc tests were performed comparing events vs. objects in each ROI. Left vATL was activated more strongly by events ($F_{(1, 42)} = 30.741$, $p < 0.001$), as was right vATL ($F_{(1, 42)} = 11.322$, $p = 0.002$). There were no effects of concept type in left AG and right AG. According to dual-hub theory, vATL would be more engaged in processing objects, while AG is more engaged by event representation. The ROI analysis did not show this pattern. However, given the greater complexity of the event images, it is difficult to draw conclusions from these univariate analyses. For example, event images include multiple objects which could drive greater activation in object-specialised regions. To avoid this issue, we next conducted RSA within each concept type.
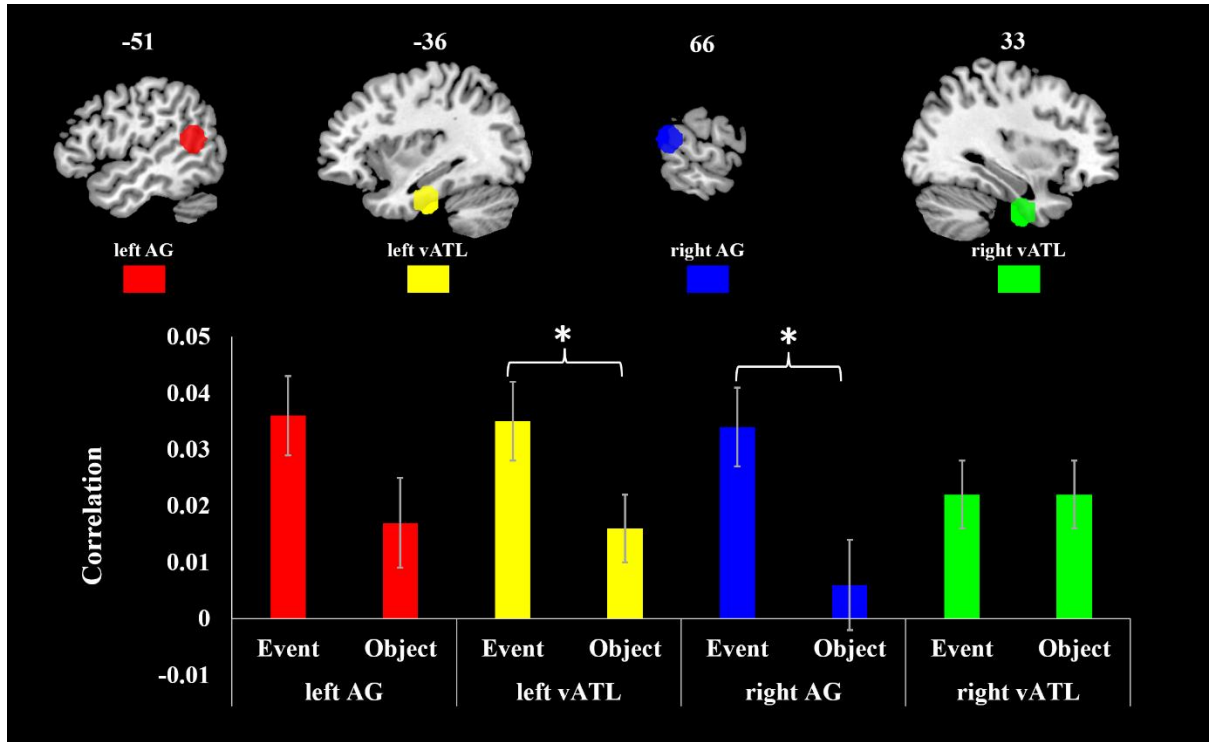
5.4.3 Representational Similarity analysis
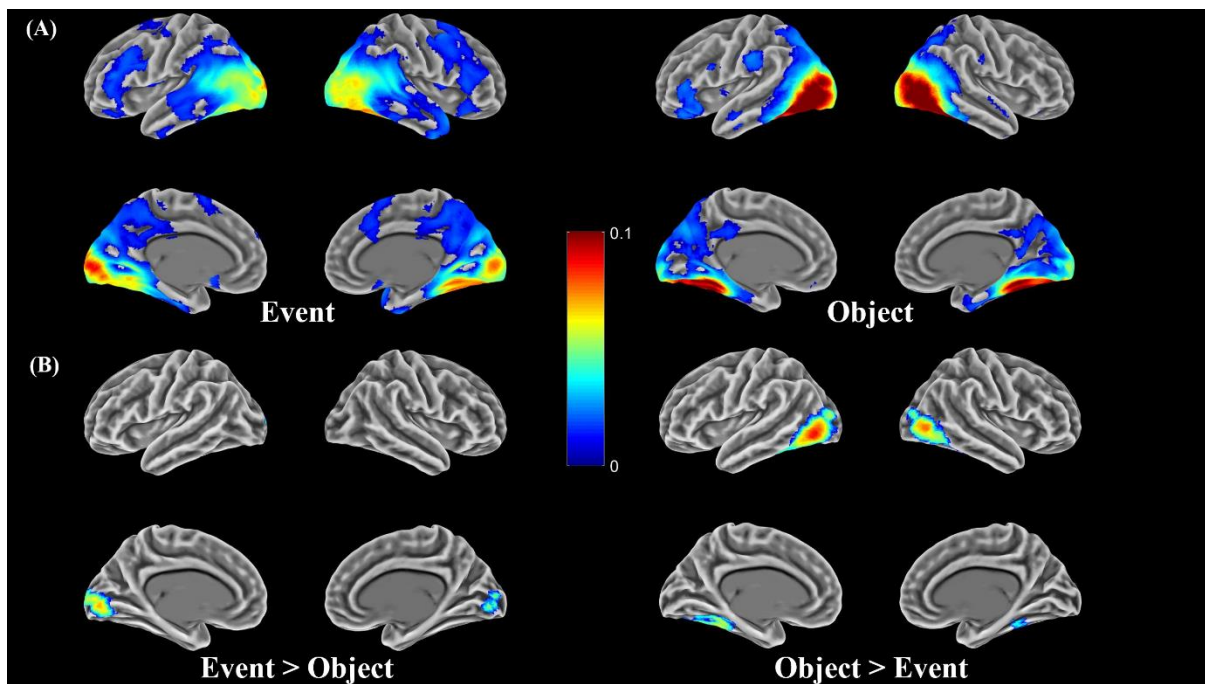
Figure 4. (A).Representational similarity maps for each concept type, showing regions where neural similarity is significantly correlated with semantic similarity (corrected p < 0.05); (B). The difference of representational similarities between event and object concepts (corrected p < 0.05). In (A) and (B), low-level visual features are controlled by covarying visual similarities measured with Hmax. Colour scale shows correlation strength.

The correlation maps, showing regions where neural RDMs were predicted by semantic RDMs, are displayed in Figure 4A. Generally, correlation effects were found in a similar set of bilateral regions for both events and objects. Specifically, the strongest effects were found in lateral occipital areas and parts of the ventral visual stream (ventral and medial temporal lobe), extending forward into vATL. We also observed effects spreading into TPC, especially for event concepts. The left inferior frontal area also showed correlations for both events and objects. Thus, neural activation patterns were correlated with semantic relationships not only in canonical semantic regions but also extensively in object and scene processing regions of the visual system. These effects indicate sensitivity to the semantic features of objects and events in these regions, since low-level visual similarity was controlled for in our analyses.

Figure 4B presents regions that showed a significant difference in correlation strength between the event and object analyses. Bilateral primary visual cortex showed stronger correlations for events relative to objects. Conversely, stronger correlations for objects were found in lateral occipital regions, which is consistent with evidence for category-selective responses in this region in object recognition (for review, see Bi et al., 2016; Carota et al., 2017; Chen et al., 2017; Wu et al., 2020; Wurm & Caramazza, 2022). No differences were found in our target regions of vATL and AG, so we turned to more sensitive ROI analyses to investigate effects in these regions.

Figure 5. Representational similarity effects in ROIs

The correlations between neural and semantic RDMs in the four ROIs are displayed in Figure 5. Permutation testing indicated that left vATL, right vATL and left AG showed significant correlation between neural RDMs and semantic RDMs for both event and object concepts (all $p < 0.0056$). Right AG only showed a significant correlation for event concepts ($p < 0.001$).

A three-way repeated ANOVA was conducted to examine whether correlations were affected by 3 factors: ROI (vATL/AG), hemisphere (left/right) and concept type (event/object). Overall, event concepts' RDM showed higher correlations with neural RDMs than objects' ($F(1, 42) = 9.467$, $p = 0.004$). No other main effects or interactions were significant at $p < 0.05$, though there was a suggestion of a weak three-way interaction ($F(1, 42) = 3.27$, $p = 0.078$). In post-hoc pairwise comparisons of events and objects in each ROI, left vATL and right AG had significantly higher correlations for event concepts (left vATL $F(42) = 5.106$, $p = 0.03$; right AG $F(42) = 10.951$, $p = 0.002$). Left AG also showed a stronger correlation for event concepts, but this difference was not statistically significant ($F(42) = 3.362$, $p = 0.074$). A two-way ANOVA (concept type*hemisphere) conducted on the AG data reported a main effect of concept type ($F(1, 42) = 9.379$, $p = 0.004$), but no interaction between

concept type and hemisphere (F (1, 42) = 0.509, p = 0.479). This result suggests left AG and right AG had similar effects of concept type.

In a post-hoc two-way ANOVAs in data split by hemisphere (concept type*ROI), both left and right hemispheres showed significantly higher correlations for event concepts (left hemisphere F (1, 42) = 7.112, p = 0.011; right hemisphere F (1, 42) = 4.875, p = 0.033), and only right hemisphere showed interaction between ROI and concept type (F (1, 42) = 6.962, p = 0.012). This result suggests left vATL and left AG had similar effects of concept type, whereas right AG showed a stronger representational similarity for events than for objects compared to right vATL.

To summarise, stronger correlations for events than objects were found in bilateral AG and in left vATL. The results in AGs are consistent with the dual-hub hypothesis, which proposes that AG is specialised for representing semantic properties of events. However, effects in the vATLs contradict the idea that this region is particularly sensitive to object semantics. Our results instead indicate that right vATL is equally sensitive to events and objects' semantics, while left vATL is more sensitive to events.

5.4.4 Psychophysiological interaction (PPI) analysis
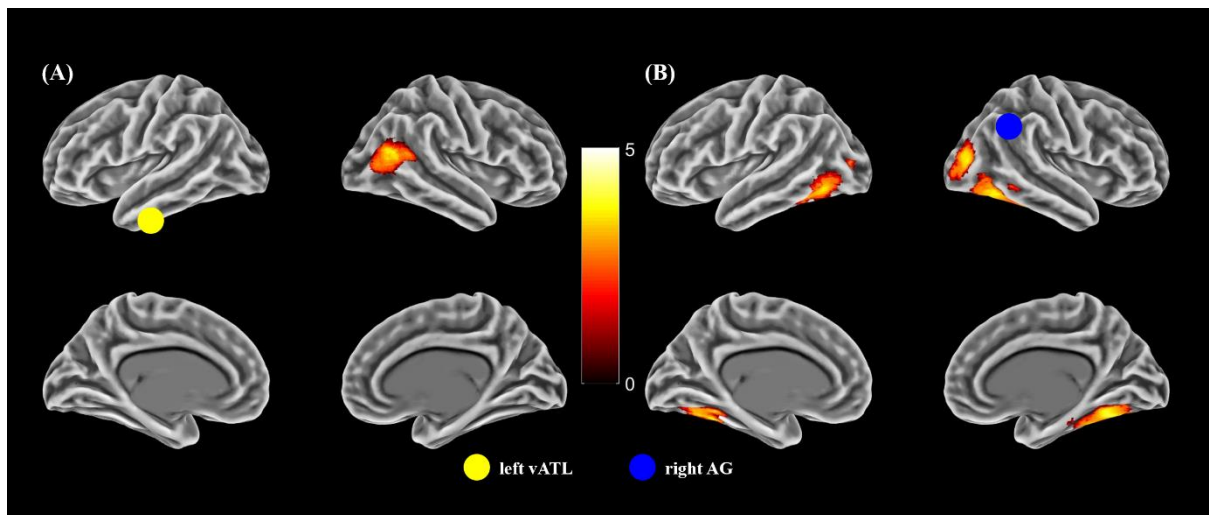
Figure 6. (A). For events > objects, regions showing increased connectivity with left vATL; (B). For events > objects, regions showing increased

connectivity with right AG. Surface render (cluster corrected p<0.05). Seed regions are shown as coloured circles

To investigate how vATL and AG interact with other brain regions in representing concepts, PPI analyses were conducted using left vATL, left AG, right vATL and right AG as seed regions. Analyses tested for change in connectivity as a function of concept type (event vs. object). When participants processed event concepts, left vATL had stronger connectivity with right posterior MTG (Figure 6A). Right vATL showed a similar pattern but the effect did not survive cluster correction (see Appendices Supplemental material of chapter 5: Supplementary Figure 1). Right AG showed stronger connectivity with bilateral fusiform gyrus and middle occipital gyrus (Figure 6B). Left AG showed no effects at cluster-corrected significance, though a more lenient uncorrected threshold showed increased connectivity with left fusiform gyrus, left ITG and right IFG for event concepts. Supplementary Figure 1 shows uncorrected events > objects effects for all four seed regions. No effects for objects > events were found at a cluster-corrected threshold and very few significant areas were found at an uncorrected threshold (see Appendices Supplemental material of chapter 5: Supplementary Figure 2).

5.5 Discussion

Both event and object knowledge are critical semantic abilities, but their neural correlates are unclear. Some researchers have suggested that vATL is specialized for object semantics and AG for event semantics (Binder & Desai, 2011; Mirman et al., 2017). To test this hypothesis, we used RSA to investigate the neural basis of representing event and object concepts. Left and right AG were found to encode semantic similarity among event concepts more strongly than similarity among object concepts, though left AG also coded objects' semantic similarity. Left and right vATLs both encoded semantic structure for object and event concepts, and left vATL showed stronger effects for events than objects. Univariate analyses also indicated more engagement of bilateral vATLs for event concepts. These findings support the idea that AG is more specialized for event semantics relative to object semantics. However, vATL specialization for object semantics is not supported by our results, suggesting that this region plays a more global role in semantic representation.

5.5.1 Sensitivity to object and event semantics in the vATLs and AGs

Many previous studies have found that activity patterns in vATL code semantic similarities among object concepts (e.g., Bruffaerts et al., 2013; Chen et al., 2016; Clarke & Tyler, 2014; Devereux et al., 2018; Liuzzi et al., 2015; Naspi et al., 2021; Tyler et al., 2013). Our data indicate that the same region is also sensitive to semantic relationships between event concepts.

For vATLs, RSA indicated that their activity patterns reflect the semantic structure of events as well as objects (Figure 4), and left vATL showed a stronger correlation for events than objects. The simplest explanation for this is that vATL represents not only object, but also objects' interactions and their context. The RSA finding is consistent with hub-and-spoke models of this region's function (Lambon Ralph et al., 2017; Patterson et al., 2007; Rice, Hoffman, et al., 2015), which propose that vATL forms conceptual representations by integrating information from a range of neural sources. Our results suggest that, in addition to integrating the features of individual objects, this region may also form representations of more complex event-related concepts. However, an alternative explanation is that vATL *is* specialised for object representation and that the effects we see are a by-product of processing the objects involved in the depicted event stimuli. If semantically similar events involve semantically-similar objects, then vATL effects for events may reflect the coding for objects involved in those events. For example, *picnic* and *barbeque* are semantically similar events but they also contain semantically similar objects (food, plates, knives etc). To test this possibility, one potential approach is to set a control with the representation of objects' combinations. Future studies can code each event's semantic vector as the combination of included objects' vectors, then use this as a control when computing correlation between neural RDM and events' sematic RDM.

The univariate analysis showed more vATL activation for event trials (Figure 2). A possible explanation is that event concepts are more complex than object concepts, and therefore require greater semantic processing. According to hub-and-spoke theory, vATL integrates different modalities' features into a concept, including not only visual features like colour or shape, but also objects' relevant actions or locations (Lambon Ralph et al., 2017; Peelen & Caramazza, 2012). Events contains multiple objects and people interacting in a specific environment. Thus, event

concepts might lead the vATL to encode multiple concepts' properties before settling on an overall representation of the event concept. The stronger vATL response for event concepts in univariate analysis might be caused by the heavier working load.

PPI analysis indicated that left vATL had stronger connectivity with right pMTG when processing event concepts (Figure 6A). Right pMTG has been implicated in coding causal relations between objects (Leshinskaya & Thompson-Schill, 2020), and in representing action concepts present in videos, still images and in language (Chen et al., 2020; Watson et al., 2013). The increased connectivity between vATL and pMTG may be a result of an enhanced contribution of relational and action-related information when understanding event concepts. This is in line with evidence that the vATL semantic hub alters its connectivity with more specialised spoke regions depending on the type of information that is relevant to the concepts being processed (Chiou & Ralph, 2019; Coutanche & Thompson-Schill, 2015).

For AG, RSA showed that activity patterns in both AG were correlated with events more strongly than for objects. Xu et al. (2018) also used RSA and found specialization of TPC for event-based relations among objects relative to category-based relations among the same objects. In contrast, the present study examined a single type of similarity (based on word2vec) and compared different types of concepts (events vs objects). Thus, the two studies provide converging complementary evidence of TPC (more specifically, AG) specialization for event semantics, consistent with region's involvement in event representation more generally. AG plays an important role in representing autobiographical and episodic memories of events (Bonnici et al., 2018; Russell et al., 2019), in spatial-temporal feature integration (Ben-Zvi et al., 2015; Bonnici et al., 2016; Richter et al., 2016; Yazar et al., 2014; 2017), and in combinatorial semantics (Boylan et al., 2015). Binder and Desai (2011) considered AG an amodal region integrating multimodal information, especially the action and spatial-temporal information. Anatomically, AG was adjacent to the dorsal visual stream, which including temporal regions processing action/motion concepts and parietal regions relevant to spatial cognition (Kravitz et al., 2011). The AG activation level was also related to the amount of semantic information in input (Binder et al., 2009; Binder et al., 2005; Graves et al., 2010; Humphries et al., 2007). This evidence suggested that AG may play an integrating role in representing event concepts. This hypothesis is consistent with

evidence showing involvement of the AG in retrieval of episodic memories and temporal and spatial information in stories (Ferstl et al., 2005; Ferstl & von Cramon, 2007). AG is also part of the broader DMN, which integrates information to form context-specific representations of evolving situations (for review, see Ranganath & Ritchey, 2012; Yeshurun et al., 2021), and is sensitive to event boundaries within a continuous experience (Baldassano et al., 2017; Swallow et al., 2011; Zacks et al., 2010). These functions of AG together suggest that it encodes dynamic and complex combinations of concepts and experiences, where people, objects, and actions are bound together in time and space (for related proposals, see Humphreys & Lambon Ralph, 2015; Humphreys et al., 2021).

In addition, AG effects for different task difficulties should also be considered. Studies found that AG deactivated more for difficult tasks than easier ones (Humphreys et al., 2015; Humphreys & Lambon Ralph, 2017; Humphreys et al., 2021). In the current study, the reaction time for event concepts was less than that for object concepts, indicating lower difficulty of understanding event concepts. This difficulty difference was also a potential factor leading to more AG activation in event condition.

The univariate analysis did not show significant activation differences in AG between events and objects. This is not consistent with the idea that AG is specialised for event semantics. Bedny et al. (2014) used a similar univariate analysis and found stronger response in TPC (primarily posterior MTG) for event nouns relative to object nouns. A key difference between the two studies is that, in the present study, pictures were presented along with the nouns. Indeed, there were uncontrolled differences between event and object images, making these results (and differences from the results of Bedny et al.) hard to interpret.

Many previous studies implicating AG in event representation have presented temporally extended stimuli like narratives (e.g., Bonnici et al., 2016) or movies (e.g., Baldassano et al., 2017; Swallow et al., 2011; Zacks et al., 2010), or have required continuous generation of words (e.g., Bonnici et al., 2018; Yazar et al., 2014). In contrast, our study has shown that simple representations of static, abstract events are sufficient to engage AG for semantic processing. Furthermore, while previous language-based studies have focused on the role of left AG in representing

thematic/event knowledge, here we found both left AG and right AG code event semantics (Figure 5). The bilateral effects might be due to our multimodal stimuli: while semantic activations are often left-lateralised for written word processing, more bilateral engagement is common for multimodal and non-verbal stimuli (Rice, Lambon Ralph, et al., 2015). Previous behavioural studies and lesion-symptom mapping studies indicated that left hemisphere injuries impaired verbal knowledge, while right hemisphere damage affected pictorial memory (Acres et al., 2009; Butler et al., 2009; Gainotti et al., 1994; Grossman & Wilson, 1987). Neuroimaging investigations further support this view, showing increased involvement of left temporal regions in processing verbal stimuli and right temporal cortex in understanding environmental sounds and images (Hocking & Price, 2009; Thierry et al., 2003; Thierry & Price, 2006).

In PPI analysis, right AG showed strong connectivity with bilateral ventral visual regions for event concepts (Figure 6B), which might be a consequence of this region extracting event-related information from the visual scenes we presented. An event image commonly incorporates a diverse set of agents and objects situated in a particular context. To represent an event as a cohesive concept, these individual items must be amalgamated, taking into account their identities, positions, orientations, and interactions. Increased connectivity between right AG and visual regions may reflect this process.

5.5.2 Effects in other regions

In addition to the effects in vATL and AG, our RSA analysis also found that patterns throughout large portions of lateral and ventral occipitotemporal cortex (OTC) were correlated with semantic structure for both objects and events. Within these areas, correlations were stronger for object concepts than event concepts (Figure 4B). The correlation effects in OTC are consistent with selectivity for specific object categories in these regions (for review, see Bi et al., 2016). Many studies have reported that when people view pictures or object names, clusters of voxels in OTC are selectively responsive to certain categories of objects, such as faces, bodies, tools, or places (Chao et al., 1999; Costantini et al., 2011; Fairhall et al., 2014; Fairhall & Caramazza, 2013; Goyal et al., 2006; Ishai et al., 2000; Noppeney et al., 2006; O'Craven & Kanwisher, 2000). In particular, lateral OTC is known to be more

strongly activated by small, manipulable objects (such as tools) and by body parts (Chao et al., 1999; Costantini et al., 2011; Noppeney et al., 2006). In ventral OTC, anterior medial regions (parahippocampal and medial fusiform) show preferences for inanimate items broadly related to navigation, including scenes, places, buildings, and large non-manipulable objects (Fairhall et al., 2014; Fairhall & Caramazza, 2013; Ishai et al., 2000; O'Craven & Kanwisher, 2000), while the posterior fusiform has a preference for animate items including faces and animals (Chao et al., 1999; Goyal et al., 2006; Ishai et al., 2000; O'Craven & Kanwisher, 2000). These category-selective responses explain why objects showed stronger semantic correlations with OTC patterns than events: objects from the same category were more semantically related, thus activated similar patches of cortex in OTC. Nevertheless, OTC patterns also showed correlations with event semantics. This could be because pictures of similar events tend to contain objects from similar categories, as discussed earlier.

Event concepts showed stronger correlations than object concepts in primary visual cortex. There are a few possible explanations for this effect. One intriguing possibility is that, when presented with static event images, participants were primed to mentally anticipate the movements of the objects or people depicted in those images. Primary visual cortex (V1) has been associated with motion-inducing illusion and predicting visual stimuli in many studies (Alink et al., 2010; Ekman et al., 2017; Gavornik & Bear, 2014; Kok et al., 2014; Muckli et al., 2005; Sterzer et al., 2006). V1 activation can be modulated by prediction of motion direction or onset (Alink et al., 2010) Muckli et al., 2005) and prior expectation of specific visual stimuli or visual sequences can evoke V1 responses similar to those evoked by viewing the actual stimuli or sequence (Ekman et al., 2017; Gavornik & Bear, 2014; Kok et al., 2014; Sterzer et al., 2006). For example, Ekman et al. (2017) found that after familiarizing participants with a spatial sequence, flashing only the starting point of the sequence triggered an activity wave in V1 that resembled the full stimulus sequence. Thus, the observed correlation effects in V1 might indicate the encoding of different predictions about potential motions in event images.

In conclusion, by testing the predictions of dual-hub theory with event and object concepts, our study found AG specialization for coding event semantics, but did not find vATL specialization for object semantics. Left vATL even coded similarity for

events more strongly than objects. These findings provide new data on the divisions of labour that exist within the semantic system.

Chapter 6: General discussion

In recent decades, neuroimaging and lesion studies have provided much evidence for embodied view of semantics, suggesting that sensory and motor experiences are important constituents of conceptual knowledge (for review, see Barsalou, 2008a). Modality-specific brain regions are involved in coding corresponding forms of semantic knowledge, such as sound, colour, action and motion. But accumulating evidence also supports the existence of high level convergence zones, suggesting a cross-modal semantic hub. Semantic dementia studies initiated the view that ATL integrates multiple modalities' semantics, acting as a general hub (Bozeat et al., 2000; Hodges & Patterson, 2007; Jefferies et al., 2009; Lambon Ralph & Patterson, 2008). This view was further supported by neuroimaging studies and developed into 'Hub-and-Spoke' theory: multimodal experiences provide ingredients for constructing concepts, which are mediated by ATL (for review, see Lambon Ralph et al., 2017; Patterson et al., 2007). Although the hub role of ATL has been suggested by many studies, some argued that ATL still has preferences in semantic tasks, and that TPC had different specialization and might contain another semantic hub (for review, see Mirman et al., 2017). This belief has been summarized as the 'dual-hub' view, which suggested ATL was more specialized for features like colour and shape since it was terminus of ventral visual stream, and TPC was more specialized for action and location due to its closer location to dorsal visual stream. And taxonomic relation relies more on ATL since colour and shape are its major contents, and thematic relation relies more on TPC since it mainly includes action and location information. In addition, ATL was indicated more specialized for coding objects' semantics, and AG in TPC, has been suggested as a convergence zone for representing sentence and event structures. This thesis used a combination of neuroimaging, meta-analysis and behavioural studies to investigate these issues.

To examine the role of perceptual brain regions in semantic representation, Chapter 3 focused specifically on the modality of motion. By conducting MVPA, univariate and PPI analysis, I explored how the different parts of LOTC, including both pMTG and V5, reacted to language descriptions of moving and static events. MVPA revealed strongest decoding effects in the posterior parts of LOTC for motion versus

static events, although only the middle portion of LOTC showed increased activation for motion sentences in univariate analyses. PPI analyses showed increased functional connectivity between posterior LOTC and the multiple demand network for motion events. These findings suggest that posterior LOTC, which overlaps with motion perceiving cortex, is selectively involved in comprehending motion events, while the anterior part contributes to more general semantic processing.

Chapter 4 investigated the relationships between taxonomic and thematic relations, different semantic feature types and neural activations. A neuroimaging meta-analyses (study 1) of studies contrasting taxonomic and thematic relations was first conducted. Thematic relations showed activation likelihood in action and location processing regions (left pMTG and SMG), while taxonomic relations only had significant activation likelihood in the right occipital lobe. Then a behavioural experiment (study 2) was used for further testing feature reliance for taxonomic and thematic relations. The experiment found priming participants with action or location domains facilitated thematic relation processing, but no difference was found for taxonomic relations. The findings of the two studies suggest thematic relations rely more on knowledge of actions and locations and preferentially engage TPC, while taxonomic relations are not specifically linked to shape and colour features and do not preferentially engage left ATL.

Chapter 5 explored roles of ventral ATL (vATL) and AG in representing event and object concepts, by combining RSA, univariate and PPI analysis. Bilateral AGs encoded semantic similarity of event concepts, although left AG also coded object similarity. Bilateral vATLs encoded semantic structures of object concepts, but also coded event similarity. Left vATL showed stronger coding for events than objects. Univariate analysis showed increased engagement of bilateral vATLs for event concepts. PPI analysis found left vATL showed stronger connections with right pMTG, and right AG showed more connections with bilateral ITG, and middle occipital gyrus, for event concepts compared to object concepts. Consistent with meta-analysis in Chapter 4, results in Chapter 5 support AG specialization for event semantics, but do not support vATL specialization for objects.

In this Discussion Chapter, I will first focus on the implications of my results for understanding how semantic knowledge relies on the three key regions: LOTC, ATL

and TPC. Then I will discuss limitations of my work and draw some broader conclusions.

6.1 Lateral occipitotemporal cortex (LOTC)

In the analyses in Chapter 3, the LOTC was divided into 3 subregions from anterior to posterior: LOTC1, 2 and 3. MVPA searchlight analysis revealed left LOTC's significant effects in discriminating static and motion event descriptions, supporting its involvement in comprehending language descriptions of motion. LOTC2 and LOTC3 exhibited above-chance discrimination in ROI analysis, with higher accuracies in pMTG (LOTC2). And univariate contrasts only showed significant effects in pMTG (LOTC2) for motion > static. In contrast to the posterior parts of LOTC, the most anterior part, LOTC1, demonstrated the lowest selectivity in its profile. It showed no effects in univariate, PPI, and MVPA decoding analysis. Based on these findings, the most anterior regions of LOTC might play a more general role in semantic cognition. This is consistent with the meta-analysis by Hodgson et al. (2022), which reported anterior LOTC activation likelihood for semantic control studies. The more posterior parts of LOTC appear to show a transition to more motion/action-selective regions, which is also consistent with Hodgson et al. (2022), who found semantic control regions were more anterior than "tools" and "biological motion" regions.

PPI analyses also indicated the engagement of posterior LOTC in processing verbal descriptions of motion events. Both LOTC2 and LOTC3 showed increased connectivity with parts of the multiple demand network during motion event processing. This network is known for its role in domain-general cognitive control (De Baene et al., 2012; Koechlin et al., 2003; Kouneiher et al., 2009), and plays a role in controlled processing for various domains, including semantic cognition, decision making, and action coordination (Coutlee & Huettel, 2012; Jackson, 2021; Ridderinkhof et al., 2004; Rizzolatti et al., 2006; Vickery & Jiang, 2009; Whitney et al., 2012). The PPI findings in Chapter 4 indicated that cognitive control areas interacted more with posterior LOTC during semantic decision-making tasks involving motion events, potentially suggesting the recruitment of motion information encoded in LOTC for decision-making processes. Moreover, the stronger connection between lateral visual cortex and LOTC might result from both cognitive control and

mental imagery of motion events. Motion event descriptions, unlike abstract actions, often include verbs that trigger dynamic image imagination, necessitating increased connectivity between the lateral visual cortex and motion perception-related areas.

Although LOTC has been widely implicated in processing motion concepts, the role of the most posterior part (V5) has been the focus of debates. Some researchers hold a strong re-enactment view, suggesting that direct engagement of V5 is necessary for motion concept representation, involving re-enactment of perceptual experiences (Hauk et al., 2004; Kiefer et al., 2012; Pulvermüller, 2005; Saygin et al., 2010). Others proposed a weaker embodiment view, suggesting recruitment of nearby regions rather than direct perceptual areas for semantic processing (Barsalou, 2003; Bedny et al., 2008; Kable et al., 2002; Martin & Chao, 2001). Some previous univariate analyses have supported V5 involvement (Assmus et al., 2007; Glenberg & Kaschak, 2002; Revill et al., 2008; Rueschemeyer et al., 2010; Saygin et al., 2010), while others did not (Bedny et al., 2008; Gennari et al., 2007; Noppeney et al., 2005). In Chapter 3, univariate analysis showed no effects in posterior LOTC, but the more sensitive MVPA approach revealed motion effects, indicating functional involvement of motion perception regions in semantic processing.

The results of Chapter 3 are consistent with general embodied accounts of semantics, but cannot be used as strong evidence for supporting re-enactment view or the weak embodiment view. Combining Chapter 3's multiple analyses, and the mixed findings from previous studies, there may be a more complex possibility: some factors affecting effect strength in LOTC have been ignored. For instance, the richness of representation. Some fMRI studies used MVPA to investigate LOTC decoding effects for action understanding at different concreteness levels (Wurm et al., 2016; Wurm & Lingnau, 2015). For the concrete level, they trained and tested a classifier to distinguish actions within each object category. For the abstract level, the classifier was trained to classify actions on one object but tested by discriminating actions performed on the other object. Although posterior LOTC (including V5) engaged in decoding actions in both concrete and abstract level, the concrete level demonstrated a larger area of decoding effects. These studies also used videos as stimuli, which provide a rich perceptual input to engage motion representations, more so than verbal descriptions. These studies illustrate how

specificity and richness of representation might affect engagement of V5 in understanding actions. This possibility could explain Chapter 3 results. The experimental task required deciding if a sentence is meaningful, a relatively superficial semantic decision that might not engage rich internal representations of the properties of the motion being described. This task was sufficient to engage V5 activation that discriminated the presence of motion in an event. However, this strength might not be enough for distinguishing between different motion types, or surviving in a less sensitive univariate analysis.

LOTC2 (pMTG), a region anterior to V5, demonstrated motion sensitivity in multiple analyses (univariate ROI, MVPA, and PPI). This aligns with the weak embodiment view that areas anterior to V5 are receptive to conceptual motion. Unlike V5, pMTG is not only engaged in processing motion images (Kable et al., 2002), but also consistently involved in motion words (Bedny et al., 2008; Gennari et al., 2007; Kable et al., 2002; Noppeney et al., 2005; Watson et al., 2013). The pMTG has been long associated with motion comprehension, due to its stronger response to moving tools than static ones (Beauchamp et al., 2002, 2003; Chao et al., 1999; Martin, 2001). The pMTG was also found activated more for verbs than nouns or other words (Bedny et al., 2008; Damasio et al., 2001; Kable et al., 2002; Perani et al., 1999; Tranel, Martin, et al., 2005). These are consistent with findings of Chapter 4. In the meta-analysis contrasting thematic relation and taxonomic relation (study 1 of Chapter 4), significant activation likelihood was found in left pMTG, which peaked at [-62 -54 4]. This is very close to the LOTC2 region in Chapter 3 (centred at [-54 -55 3]; cf. LOTC1 [-52 -40 2] and LOTC3 [-44 -72 5]). The behavioural experiment (study 2 of Chapter 4) also reported that action/location primes facilitated thematic judgements more than colour and shape primes, suggesting that thematic relations relied more on action/location knowledge. Combining meta-analysis and behavioural tests, Chapter 4 also supported the critical role of this specific part of pMTG in coding concepts of motion and observed actions and, by extension, thematic semantic relations.

As mentioned previously, task may play an important role in determining when motion effects are observed in LOTC. The task objective may influence comprehension strategies, affecting embodiment and associated brain activity

(Barsalou, 2008b; Binder & Desai, 2011). For instance, when reading novels, vivid descriptions may prompt individuals to engage in detailed mental simulations. Conversely, determining sentence meaningfulness (as the experiment in Chapter 3) may require less reliance on mental imagery and simulation. Future studies could investigate the impact of instructing participants to imagine the depicted scene, examining whether this factor alters the role of LOTC in representing motion concepts.

The task-dependence may also explain the inconsistency of neuroimaging results about taxonomic and thematic relations (Chapter 4). Some of the studies analysed required explicit semantic judgments (Jackson et al., 2015; Kalénine et al., 2009; Sachs, Weis, Krings, et al., 2008), while others relied on relationships being activated implicitly in priming paradigms (Chen et al., 2014; Kriukova et al., 2013; Sass et al., 2009; Wamain et al., 2015). These varying task demands may influence which regions are recruited in each relation type. These issues influenced the experimental design in Chapter 5, where a combination of pictures and words was used to encourage richer representation and deeper semantic processing.

6.2 Anterior temporal lobe (ATL)

The role of ATL was investigated in Chapter 4 and 5. Chapter 4 focused on ATL and taxonomic relations, and Chapter 5 concentrated more on vATL and object concept representation.

Hub-and-spoke theory proposes ATL as a general semantic hub (Lambon Ralph et al., 2017). But dual-hub theory predicts more ATL specializations for certain types of semantic knowledge. According to dual-hub hypothesis, taxonomic relations rely particularly on the ATL. Mirman et al. (2017) suggested that this might because ATL shows specialisation for colour and shape features. However, the priming study of Chapter 4 (study 2) found no evidence that taxonomic judgements are particularly reliant on colour and shape knowledge. And in addition to visual object properties, ATL shows activation for a wide range of other types of semantic information, like auditory features (Visser & Lambon Ralph, 2011) or social knowledge (Lars A Ross & Ingrid R Olson, 2010). Also, the meta-analysis in Chapter 4 did not find greater activation likelihood in ATL regions for taxonomic than for thematic relations. And

anterior MTG and STG in ATL, showed more activation likelihood for thematic relations versus taxonomic relations.

In previous studies, MVPA analyses have demonstrated that vATL regions encode semantic relationships between objects (Chen et al., 2016; Fairhall & Caramazza, 2013; Rogers et al., 2021). The perirhinal cortex, a medial part of vATL, is specifically involved in recognizing and distinguishing objects with overlapping semantic features (for review, see Clarke & Tyler, 2015). It has more similar activation patterns for more similar objects (Bruffaerts et al., 2013; Devereux et al., 2018; Liuzzi et al., 2015; Naspi et al., 2021), and responds more strongly for identifying semantically confusable objects (Clarke et al., 2013; Clarke & Tyler, 2014). Damage to perirhinal cortex leads to deficits in naming such objects (Wright et al., 2015). Thus, the vATL is known to encode the semantic similarity structure of objects. These findings about vATL coding object similarity structure suggested it might be particularly involved in taxonomic relations, which required frequent comparisons between objects.

However, the meta-analysis did not show ATL effects for taxonomic > thematic relations. A potential explanation is the insufficient power of the meta-analysis, which included a limited number of studies. Only 16 studies were included in the meta-analysis, and the number of peaks in the TX>THM contrast was even lower compared to THM>TX. Furthermore, the fMRI signal in vATL is often poor, since susceptibility artifacts may cause distortion and degradation of the BOLD signal (Ojemann et al., 1997; Visser et al., 2010).

Another possibility is that vATL represents diverse types of information and has no specialization to taxonomic or thematic relations. According to the hub-and-spoke theory, ATL, particularly its ventral components, encode multimodal conceptual representations and integrate information from diverse modality-specialized regions across the cortex (Lambon Ralph et al., 2017). These representations could be equally important for processing taxonomic and thematic relations between concepts (Jackson et al., 2015). This hypothesis is also consistent with results in Chapter 5: vATLs coded both events' similarity and objects' similarity.

Chapter 5 concentrated on examining the association between vATL and object representation. The main RSA analyses revealed that vATL activity patterns are correlated with semantic structures of both events and objects. Left vATL even exhibited a stronger correlation for events. One possibility is that vATL represents not just objects, but also their interactions and contextual information. Another explanation is that the correlation between vATL patterns and events' semantics only reflects vATL coding of objects, since understanding an event requires accessing knowledge about the objects involved. Although semantically similar events may involve semantically similar objects, it is unlikely that ATL coding for events solely reflects coding for objects in those similar events. This is because stronger correlations for event semantics were observed, which cannot be solely attributed to correlations with direct measures of object similarity.

Univariate analysis also revealed greater ATL activation for complex event concepts, potentially due to their heavier cognitive load and the integration of multiple objects' appearances, positions, movements, and causal relations. Hub-and-spoke theory suggests that ATL serves as a hub for integrating various modalities' features, including visual, action-related, and locational aspects (Lambon Ralph et al., 2017; Peelen & Caramazza, 2012). In controlled semantic cognition (CSC) theory (for review, see Lambon Ralph et al., 2017), ATL interacts with the semantic control network, supporting working memory and executive representations relevant to current language behaviours (Chiou et al., 2018), such as encoding temporal, situational, and contextual information. When processing events, ATL may facilitate the auto-associative retrieval of crucial object features, enabling adjustment of ongoing conceptual activations based on task and context demands (Jefferies et al., 2020; Teige et al., 2019). This could explain the stronger ATL response to event concepts observed in the univariate analysis, reflecting the heavier conceptual load imposed by events.

PPI analysis showed stronger left vATL – right pMTG connectivity for event concepts. Events may engage more motion processing for object manipulation. The right pMTG was found engaged in coding visually similar events (Leshinskaya & Thompson-Schill, 2020), and actions in videos (Chen et al., 2020). Hub-and-spoke theory indicates that ATL uses inputs from multimodal perception regions for

constructing concepts (Lambon Ralph et al., 2017). Thus, the coordination between left vATL and right pMTG might reflect that left vATL utilizes the action and motion information coded in right pMTG to represent event concepts.

In Chapter 5, both the cross-hemispheric connections and the RSA effects in right vATL suggested that the right hemisphere also made a big contribution to semantic processing. The multimodal stimuli might explain these bilateral effects: processing written word often shows left-lateralised engagement for semantics, but multimodal and non-verbal stimuli are more likely to elicit bilateral effects (Rice, Lambon Ralph, et al., 2015). Previous lesion studies and behavioural tests indicated that left hemisphere injuries impair verbal knowledge, while right hemisphere damage affect pictorial memory (Acres et al., 2009; Butler et al., 2009; Gainotti et al., 1994; Grossman & Wilson, 1987). Neuroimaging research has also reported greater left temporal activity for verbal processing and right temporal cortex engagement for comprehending environmental sounds and images (Hocking & Price, 2009; Thierry et al., 2003; Thierry & Price, 2006). Although bilateral engagements for conceptual representation have been reported in some studies (Bright et al., 2004; Ding et al., 2020; Lambon Ralph et al., 2017; Patterson et al., 2007; Tranel, Grabowski, et al., 2005; Vandenberghe et al., 1996; Visser et al., 2010; Visser & Lambon Ralph, 2011), the cross-hemispheric functional connection for semantics was not paid much attention. In Chapter 5, the connectivity between left vATL and right pMTG suggested that, heteromodal information might be transferred across hemispheres to inform semantic representation. This result also indicated the importance of cross-hemisphere interactions in semantic processing. Thus, to investigate semantic processing for more naturalistic stimuli (e.g., images), the right hemisphere's activation and hemispheres' connections deserves more exploration. Future studies should consider using more multimodal and non-verbal materials. Although these stimuli may cause confounds, they can provide insight to neural network of semantics in multiple sensory modalities.

In the meta-analysis of Chapter 4, anterior parts of the MTG and STG showed more activation likelihood for thematic relations than taxonomic relations. This might reflect different roles of ATL subregions. Recent findings indicate graded specializations within the ATL (Jackson et al., 2018; Lambon Ralph et al., 2017; Rice, Hoffman, et

al., 2015). Like vATL, anterior MTG also plays a significant role in multimodal semantic processing (Visser et al., 2012), responding to both verbal and non-verbal stimuli (Rice, Lambon Ralph, et al., 2015). But the anterior superior temporal gyrus (STG) exhibits relative specialization in processing verbal semantic knowledge (Hung et al., 2020). Thematic relations benefit from linguistic associations and knowledge, as frequently observed in the co-occurrence of object names in language when they are paired in the real world (Dilkina & Lambon Ralph, 2013). In contrast, such verbal associations are often avoided when selecting taxonomically-related stimuli (e.g. Jackson et al., 2015). The reliance of thematic relations on linguistic knowledge is also evident in behavior, as bilingual children tend to make more thematic judgments when presented with stimuli words from their first language rather than their second language (Li et al., 2011). Thus, one possible explanation is that thematic relations heavily depend on verbal associative knowledge, potentially accounting for the heightened activation in the lateral ATL. This possibility suggests that taxonomic and thematic relation may have different reliance on verbal associations, which could be tested in future works for a more comprehensive understanding of differences between taoxnomic and thematic relations. In addition, the hypothesis of verbal association also demonstrates the importance of not treating the ATL as a single functional unit: ATL might be an area with subregions of different specializations (Lambon Ralph et al., 2017), and future studies should consider of the importance of functional variations across this area.

6.3 Temporal parietal cortex (TPC)

The role of TPC was investigated in Chapter 4 and 5. Chapter 4 focused on TPC and thematic relations, and Chapter 5 concentrated more on AG and event concept representation.

Dual-hub view suggests thematic relations particularly rely on TPC, due to TPC specialization for the major features for thematic relations (e.g. action and location). This is consistent with the meta-analysis in Chapter 4: the left pMTG and supramarginal gyrus (SMG) showed greater activation likelihood for thematic relations than taxonomic relations.

However, similar to the fact that ATL subregions have different functions, TPC subregions also show different specializations. The LOTC, especially pMTG, shows specialisation for motion and action concepts (Buxbaum et al., 2014; Kalénine et al., 2010; Tarhan et al., 2015; Watson et al., 2013). SMG is associated with planning and executing tool-related actions (Przybylski & Króliczak, 2017; Randerath et al., 2010; Tunik et al., 2007). In contrast, AG shows a more heteromodal profile of engagement (Ben-Zvi et al., 2015; Bonnici et al., 2016; Richter et al., 2016; Yazar et al., 2014, 2017), leading some to propose that this regions acts as a semantic hub, specialised for representing temporally extended experiences like events or sentences (e.g., Baldassano et al., 2017; Bonnici et al., 2016; Swallow et al., 2011; Zacks et al., 2010) .

The meta-analysis showed thematic effects in TPC regions specialised for action/motion/tool-related knowledge, which was consistent with the priming study findings: action and location primes facilitate thematic judgements. These neural and behavioural finding converge on the idea that feature reliance is an important factor in determining neural specialisation for thematic relations.

However, the meta-analysis found no thematic effect in AG. One possibility is the low power caused by the relatively small number of studies in the analysis, which is not enough to detect the effect. Another possibility is AG might be more involved in higher-level integration of concepts within a particular context, rather than simple associations between two objects. Many studies found AG activation in spatial-temporal feature integration (Ben-Zvi et al., 2015; Bonnici et al., 2016; Richter et al., 2016; Yazar et al., 2014, 2017), and combinatorial semantics (Boylan et al., 2015). Brain stimulation studies found that free recall of autobiographical memories was impaired after disruption on angular gyrus, whereas recall of word-pair memories were unaffected (Bonnici et al., 2018; Thakral et al., 2017). Compared with word-pair memories, retrieval of autobiographical memories often involves subjective remembering a dynamic process, consist of a sequence of stimuli from multiple modalities and complex contexts (Moscovitch et al., 2016; Shimamura, 2011; St. Jacques, 2019). Thus, AG is suggested to be specialized to multimodal spatio-temporal information, but maybe not particularly sensitive to relations in a single

sensory modality (Ben-Zvi et al., 2015; Bonnici et al., 2016; Richter et al., 2016; Yazar et al., 2014, 2017).

Chapter 5 concentrated particularly on the AG region within TPC. AG showed stronger correlations for events than for objects. A similar effect was seen in both left and right AG, but only reached significance in the right AG. These findings support AG's relative specialization for encoding event semantics and align with its role in other studies related to event representation. AG is critical for functions like autobiographical and episodic memory (Bonnici et al., 2018; Russell et al., 2019), spatial-temporal integration (Ben-Zvi et al., 2015; Bonnici et al., 2016; Richter et al., 2016; Yazar et al., 2014, 2017), and semantic combination of nouns and verbs (Boylan et al., 2015). Besides, AG's involvement in the default mode network (DMN) points to a role in constructing context-specific representations (for review, see Ranganath & Ritchey, 2012; Yeshurun et al., 2021) and event boundaries within continuous experiences (Baldassano et al., 2017; Swallow et al., 2011; Zacks et al., 2010).

PPI analysis revealed increased connectivity between right AG and bilateral ventral visual regions for event concepts, possibly indicating the extraction of event-related information from visual scenes. AG's role in integrating contextual information, combined with the object category selectivity of LOTC and VOTC, may explain this increased connectivity, reflecting the process of unifying objects within a specific environment into a coherent event or contextual representation.

Previous studies often used temporally extended stimuli or language-based tasks to examine AG's function in event representation (e.g. Baldassano et al., 2017; Bonnici et al., 2016; Swallow et al., 2011; Zacks et al., 2010). However, Chapter 5 demonstrates that simple representations of static, abstract events are sufficient to engage AG in semantic processing. Additionally, both left AG and right AG contribute to coding event semantics, possibly because the left AG responds more to language stimuli and right AG responds more to visual stimuli.

The connection between AG and bilateral ventral visual regions, and the RSA effects in right AG, might be caused by multimodal stimuli of the experiment (word and picture). The meta-analysis of Rice, Lambon Ralph, et al. (2015) shows that written

words engage more left-lateralised semantic effects at a whole-brain level, and multimodal and non-verbal (images or sounds) stimuli elicit more bilateral effects. However, cross-hemispheric semantic connection received less attention in previous studies. The connectivity analyses of both right AG and left vATL in Chapter 5 revealed cross-hemisphere connections for semantics from multimodal stimuli, which future studies could investigate further. In addition, future studies can more carefully control modality of stimuli. For example, they can present concepts with only words, with only pictures, or combined words and pictures, to separately examine activation patterns in verbal, non-verbal and multimodal conditions. This may reveal more potential associations between bilateral effects and stimuli modalities, and gain deeper insight of right hemisphere involvement in semantic processing.

6.4 Limitations

All studies have to consider how to operationalise key concepts and choose a design that conforms to the practical constraints on the projects (e.g., time available for scanning). Here, I consider some potential limitations of the design choices in this thesis, and make suggestions for future research.

For Chapter 3, limitations are the small number of events and the simple sentence structure (agent-verb-patient) used. Future studies could use different event structures in their training sets to test the generalizability of these results across conceptual and linguistic domains. Another limitation is the uncertainty of the depth in semantic processing. People were only instructed to decide if a sentence is meaningful, which might be not enough for some participants to imagine events' details. To explore more of relationship between concreteness and embodied effects, future research could instruct participants to imagine the described scene and examine the potential impact on the role of the LOTC in motion concept representation.

For Chapter 4, potential limitations are the small number of studies included in meta-analysis, and concept type in behavioural experiment. The meta-analysis contained 16 studies, which were slightly below the recommended minimum of 17 for a well-powered ALE meta-analysis (Eickhoff et al., 2016). Some relevant studies were excluded for not listing peak coordinates for contrasting taxonomic and thematic

relations (e.g., Sachs et al., 2011). To allow meta-analyses and aggregation of evidence across studies, it is important that studies report peak coordinates, or share activation maps in future research. Thus in Chapter 4, the meta-analysis just provided an initial assessment of the results from existing neuroimaging studies on this topic, but with reduced sensitivity to weaker effects in vATL. This region often has poor fMRI signal, since it is affected by susceptibility artefacts that distort and degrade the BOLD signal (Ojemann et al., 1997; Visser et al., 2010). For the behavioural experiment, concrete concepts are used, as the feature reliance hypothesis specifically applies to concrete concepts. This is because existing studies of taxonomic and thematic relations usually only consider concrete concepts. However, the role of taxonomic and thematic relations in abstract concepts is still unclear. Some researchers suggest that abstract words are primarily organized based on thematic relations among themselves, while taxonomic similarity plays a crucial role in organizing concrete words (Crutch et al., 2009). Skipper-Kallal et al. (2015) also suggests that TPC is important for both thematic relations and abstract concepts. Further studies are needed to investigate the differences in feature reliance between abstract thematic and taxonomic relations, as well as how these effects are reflected in the brain.

For Chapter 5, one limitation may be the stimuli used to represent events. To instruct participants to represent each event as a concept, this study presented each event with a static picture. This enabled a good contrast of objects and events in concept level, but prevented study of dynamic processes and temporal sequences of actions in the event comprehension. And this may account for why left AG did not show significantly stronger correlation for events than objects.

6.5 Conclusions

This thesis aimed to investigate predictions of three overlapping but distinct theoretical frameworks for understanding semantic representation in the brain: the embodied semantics view, the hub-and-spoke theory and the dual-hub hypothesis. The evidence in the thesis provides partial support for each of these theories. However, hub-and-spoke theory can better explain the thesis' results, especially the unexpected parts.

The embodied semantics view suggests that concepts are grounded in sensory and motor experiences. Chapter 3 supports this general idea by showing that V5 and surrounding areas are engaged in discriminating motion and static events. However, the absence of V5 effects in decoding different motion types suggested that participants did not visualize all details of the various motions. This implies that semantic understanding may not always require a full simulation of perceptual experiences, if the task does not require (in experiment of chapter 3, participants only had to judge if a sentence is meaningful). Some extent of abstractness is allowed for representing amodal symbols, which is consistent with hub-and-spoke theory: modality-specific features are ingredients of a concept, but the concept itself can become an abstracted amodal symbol integrated in a hub.

The dual-hub theories suggested different specializations of ATL and TPC for different semantic relations and features, which were not completely consistent with the results in chapters 4 and 5. Chapter 4 found more pMTG and SMG activation likelihood and action/location priming effects for thematic relations, which is consistent with dual-hub hypothesis of TPC. However, hub-and-spoke theory also admits cortical specializations for different modalities' features. The pMTG effect could also be accounted by more semantic control in processing thematic relations. In addition, chapter 4 found no evidence for ATL specializations for taxonomic relations, which also supported the view that ATL engages for a range of semantic tasks and stimuli.

Hub-and-spoke theory proposes that ATL is a general semantic hub, with graded specializations in different subregions. Chapter 5 shows that vATL codes semantic similarity for a broad range of concepts, including both objects and events. This supports the idea that vATL engages for general semantic processing for multiple categories' concepts. Chapter 4 reports more superior ATL activation likelihood for thematic relations, which is consistent with the hypothesis that superior ATL is specialised for verbal information. Although AG activity had more correlation with event concepts, the effects of episodic memory and difficulty deactivation are still potential confounds to consider.

Chapters 4 and 5 provide evidence for the idea that the TPC region is generally important for thematic/event-related semantics but cannot support the existence of

another semantic hub like ATL. Future research is still needed, to understand how modality-specific information is coded in subregions of TPC, and where the information is integrated into higher-level contexts.

In a sum, this thesis investigated cortical specializations for different modalities' features, further consolidating the importance of embodied experience for semantic concepts. Results also indicated abstractness in semantic processing and the hub role of ATL. According to these findings, semantic representation recruits both distributed sensory-motor regions and hub areas for dealing with specific embodiment experiences and abstract language symbols. Studies in this thesis highlight the complex neural mechanisms in processing different types of semantic knowledge. Future work will give more specific mappings and decoding to the neural underpinnings and nature of semantics.

Appendices

Supplemental material of chapter 3

Supplementary Table 1: List of Stimuli

Sentence	Condition	Meaningfulness	Syntax Form	Lexical Form	Event
The bull leapt over the gate.	motion	meaningful	Active	1	Event 1
The gate was leapt over by the bull.	motion	meaningful	Passive	1	Event 1
The cow jumped over the fence.	motion	meaningful	Active	2	Event 1
The fence was jumped over by the cow.	motion	meaningful	Passive	2	Event 1
The lorry bumped the lamp post.	motion	meaningful	Active	1	Event 2
The lamp post was bumped by the lorry.	motion	meaningful	Passive	1	Event 2
The truck hit the street light.	motion	meaningful	Active	2	Event 2
The street light was hit by the truck.	motion	meaningful	Passive	2	Event 2
The computer processed the	static	meaningful	Active	1	Event

file.					3
The file was processed by the computer.	static	meaningful	Passive	1	Event 3
The laptop analysed the document.	static	meaningful	Active	2	Event 3
The document was analysed by the laptop.	static	meaningful	Passive	2	Event 3
The student considered the problem.	static	meaningful	Active	1	Event 4
The problem was considered by the student.	static	meaningful	Passive	1	Event 4
The pupil pondered the issue.	static	meaningful	Active	2	Event 4
The issue was pondered by the pupil.	static	meaningful	Passive	2	Event 4
The files pondered the truck	control	anomalous	Active	1+2	
The streetlight was jumped over by the computer	control	anomalous	Passive	1+2	
The problem hit the cow	control	anomalous	Active	1+2	
The document was considered by the lorry	control	anomalous	Passive	1+2	
The gate pondered the pupil	control	anomalous	Active	1+2	
The problem was hit by the cow	control	anomalous	Passive	1+2	
The computer jumped over the	control	anomalous	Active	1+2	

streetlight					
The fence was analysed by the cow	control	anomalous	Passive	1+2	
The issue bumped the bull	control	anomalous	Active	1+2	
The issue was bumped by the bull	control	anomalous	Passive	1+2	
The laptop leapt over the streetlight	control	anomalous	Active	1+2	
The gate was pondered by the pupil	control	anomalous	Passive	1+2	
The fence processed the student	control	anomalous	Active	1+2	
The truck was pondered by the files	control	anomalous	Passive	1+2	
The streetlight was leapt over by the laptop	control	anomalous	Passive	1+2	
The lorry was considered by the document	control	anomalous	Passive	1+2	

Supplementary Table 2: Mean properties for each event

Event	Condition	Concreteness	Frequency	Vision	Motion	Sound	Emotion
Event 1	Motion	3.02	5.875	5.359	5.532	3.566	2.207
Event 2	Motion	3.068	5.508	5.499	5.312	4.514	2.953
Event 3	Static	2.775	5.553	2.913	2.162	2.023	1.619
Event 4	Static	2.303	5.88	3.489	2.313	2.228	3.065
Mean Difference (Motion-Static)		0.505	-0.025	2.228	3.184	1.915	0.24
Motion Mean		3.04	5.69	5.43	5.42	4.04	2.58
Static Mean		2.54	5.72	3.2	2.24	2.13	2.34
T-value(Motion VS Static)		3.654**	-0.146	11.868***	17.763***	7.836***	0.67
df		13.27	11.77	13.23	9.66	7.99	12.23

** = $p < 0.01$; *** = $p < 0.001$.

Supplementary Table 3: Mean properties for each target sentence

Sentence	Condition	Conc	Freq	Vision	Motion	Sound	Emotion
The bull leapt over the gate	Motion	3.17	5.7	5.65	5.87	3.87	2.57
The gate was leapt over by the bull	Motion	2.78	5.92	4.96	4.91	3.48	2.35
The cow jumped over the fence	Motion	3.27	5.85	5.78	5.91	3.65	2.09
The fence was jumped over by the cow	Motion	2.86	6.03	5.04	5.43	3.26	1.83
The lorry bumped the lamp post	Motion	3.29	5.27	5.43	5.09	4.35	2.61
The lamp post was bumped by the lorry	Motion	2.81	5.64	4.87	4.78	3.74	2.43
The truck hit the streetlight	Motion	3.33	5.39	5.95	5.95	5.14	3.55
The streetlight was hit by the truck	Motion	2.84	5.73	5.74	5.43	4.83	3.22
The computer processed the file	Static	3.03	5.82	2.87	2.09	2.22	1.61
The file was processed by the	Static	2.62	6.04	3.04	2.52	2.04	1.61

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computer							
The laptop analyzed the document	Static	2.91	4.94	2.83	2.04	1.87	1.65
The document was analyzed by the laptop	Static	2.54	5.41	2.91	2	1.96	1.61
The pupil pondered the issue	Static	2.4	5.5	3.65	2.3	2.43	3.43
The issue was pondered by the student	Static	2.18	5.81	3.48	2.43	2.09	3.22
The student considered the problem	Static	2.43	6.03	3.52	2.43	2.26	3.3
The problem was considered by the student	Static	2.2	6.18	3.3	2.09	2.13	2.3
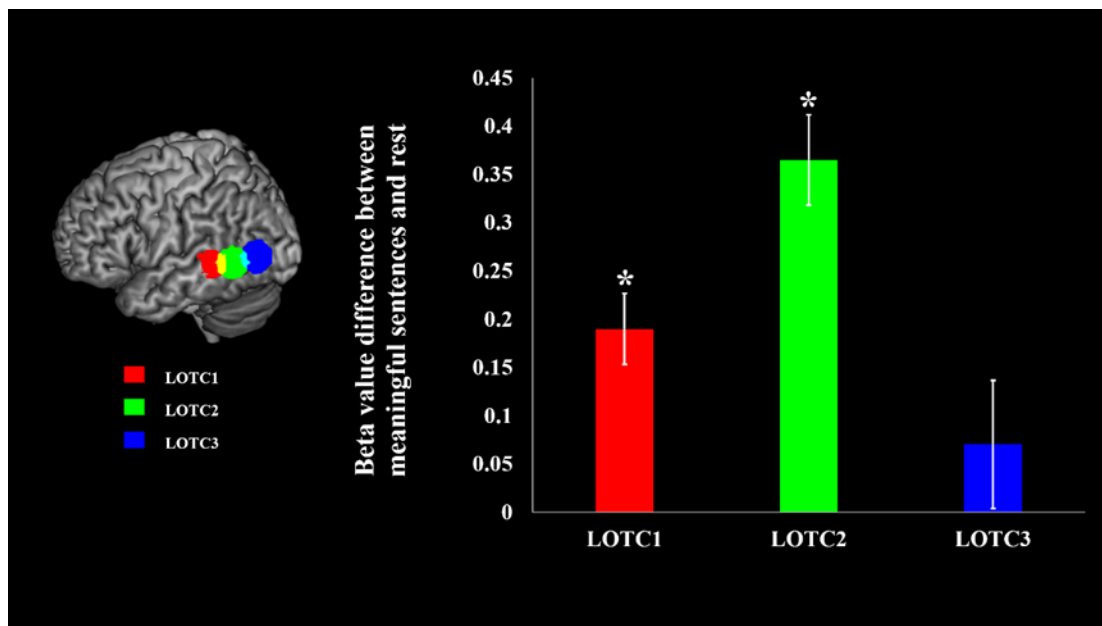
Supplementary Figure 1: The 3 ROIs' beta value differences between 'meaningful' and 'rest'

Supplemental material of chapter 4

Supplementary Table 1: Primes

prime key	option 1	option 2	prime type
apple can be	green	black	colour
banana can be	yellow	red	colour
sky can be	blue	green	colour
leaves can be	green	purple	colour
sea can be	blue	yellow	colour
butter can be	yellow	green	colour
spaghetti can be	yellow	blue	colour
carrot can be	orange	black	colour
grass can be	green	white	colour
eggplant can be	purple	red	colour
broccoli can be	green	red	colour
pineapple can be	yellow	black	colour
iron can be	yellow	silver	colour
chocolate can be	red	brown	colour
wine can be	blue	red	colour
sand can be	black	yellow	colour

chicken can be	green	white	colour
steak can be	blue	red	colour
spinach can be	blue	green	colour
tinfoil can be	green	silver	colour
ginger can be	blue	yellow	colour
onion can be	black	purple	colour
egg can be	blue	white	colour
moon can be	black	yellow	colour
sun can be	green	red	colour
apple can be	green	black	colour
banana can be	yellow	red	colour
sky can be	blue	green	colour
leaves can be	green	purple	colour
sea can be	blue	yellow	colour
butter can be	yellow	green	colour
spaghetti can be	yellow	blue	colour
carrot can be	orange	black	colour
grass can be	green	white	colour
eggplant can be	purple	red	colour
brocc can be	green	red	colour
pineapple can be	yellow	black	colour

iron can be	yellow	silver	colour
chocolate can be	red	brown	colour
wine can be	blue	red	colour
sand can be	black	yellow	colour
chicken can be	green	white	colour
steak can be	blue	red	colour
spinach can be	blue	green	colour
tinfoil can be	green	silver	colour
ginger can be	blue	yellow	colour
onion can be	black	purple	colour
egg can be	blue	white	colour
moon can be	black	yellow	colour
sun can be	green	red	colour
lettuce can be	green	black	colour
garlic can be	white	orange	colour
oil can be	yellow	white	colour
vinegar can be	black	green	colour
paprika can be	red	white	colour
salt can be	white	green	colour
strawberry can be	red	blue	colour
cheese can be	yellow	black	colour

mustard can be	yellow	purple	colour
pumpkin can be	orange	blue	colour
blood can be	red	purple	colour
crow can be	black	white	colour
sugar can be	blue	white	colour
cabbage can be	orange	purple	colour
mango can be	white	yellow	colour
tomato can be	white	red	colour
rice can be	blue	white	colour
lemon can be	white	yellow	colour
snow can be	green	white	colour
coffee can be	green	black	colour
flour can be	purple	white	colour
chip can be	black	yellow	colour
lime can be	purple	green	colour
fire can be	black	red	colour
bone can be	green	white	colour
lettuce can be	green	black	colour
garlic can be	white	orange	colour
oil can be	yellow	white	colour
vinegar can be	black	green	colour

paprika can be	red	white	colour
salt can be	white	green	colour
strawberry can be	red	blue	colour
cheese can be	yellow	black	colour
mustard can be	yellow	purple	colour
pumpkin can be	orange	blue	colour
blood can be	red	purple	colour
crow can be	black	white	colour
sugar can be	blue	white	colour
cabbage can be	orange	purple	colour
mango can be	white	yellow	colour
tomato can be	white	red	colour
rice can be	blue	white	colour
lemon can be	white	yellow	colour
snow can be	green	white	colour
coffee can be	green	black	colour
flour can be	purple	white	colour
chip can be	black	yellow	colour
lime can be	purple	green	colour
fire can be	black	red	colour
bone can be	green	white	colour

smartphone can be	rectangular	triangular	shape
brick can be	cuboid	oval	shape
funnel can be	conical	rectangular	shape
card can be	rectangular	round	shape
hook can be	curved	straight	shape
notebook can be	rectangular	round	shape
moon can be	round	square	shape
egg can be	oval	cuboid	shape
hair can be	wavy	cuboid	shape
hanger can be	triangular	oval	shape
pot can be	round	triangular	shape
laptop can be	rectangular	oval	shape
sausage can be	rectangular	cylindrical	shape
sword can be	round	straight	shape
box can be	triangular	cuboid	shape
onion can be	square	round	shape
hanger can be	round	rhombic	shape
bottle can be	triangular	columnar	shape
apple can be	rectangular	round	shape
sandwich can be	round	triangular	shape
wire can be	oval	thin	shape

wheel can be	rectangular	round	shape
plate can be	triangular	round	shape
signpost can be	cuboid	triangular	shape
sun can be	cuboid	round	shape
smartphone can be	rectangular	triangular	shape
brick can be	cuboid	oval	shape
funnel can be	conical	rectangular	shape
card can be	rectangular	round	shape
hook can be	curved	straight	shape
notebook can be	rectangular	round	shape
moon can be	round	square	shape
egg can be	oval	cuboid	shape
hair can be	wavy	cuboid	shape
hanger can be	triangular	oval	shape
pot can be	round	triangular	shape
laptop can be	rectangular	oval	shape
sausage can be	rectangular	cylindrical	shape
sword can be	round	straight	shape
box can be	triangular	cuboid	shape
onion can be	square	round	shape
hanger can be	round	rhombic	shape

bottle can be	triangular	columnar	shape
apple can be	rectangular	round	shape
sandwich can be	round	triangular	shape
wire can be	oval	thin	shape
wheel can be	rectangular	round	shape
plate can be	triangular	round	shape
signpost can be	cuboid	triangular	shape
sun can be	cuboid	round	shape
tomato can be	round	rectangular	shape
stick can be	slender	round	shape
cash can be	rectangular	triangular	shape
flute can be	tubular	cuboid	shape
coin can be	round	square	shape
pizza can be	wedge-shaped	square	shape
pumpkin can be	round	triangular	shape
cabbage can be	round	square	shape
pencil can be	thin	round	shape
suitcase can be	cuboid	round	shape
wardrobe can be	cuboid	oval	shape
roadblock can be	conical	round	shape

cucumber can be	conical	straight	shape
spaghetti can be	cuboid	thin	shape
battery can be	wedge-shaped	cylindrical	shape
lettuce can be	rectangular	round	shape
moon can be	straight	curved	shape
pen can be	curved	straight	shape
fridge can be	round	cuboid	shape
potato can be	slender	oval	shape
submarine can be	conical	tubular	shape
ruler can be	round	straight	shape
tin can be	round	cylindrical	shape
sickle can be	straight	curved	shape
earth can be	cuboid	round	shape
tomato can be	round	rectangular	shape
stick can be	slender	round	shape
cash can be	rectangular	triangular	shape
flute can be	tubular	cuboid	shape
coin can be	round	square	shape
pizza can be	wedge-shaped	square	shape

pumpkin can be	round	triangular	shape
cabbage can be	round	square	shape
pencil can be	thin	round	shape
suitcase can be	cuboid	round	shape
wardrobe can be	cuboid	oval	shape
roadblock can be	conical	round	shape
cucumber can be	conical	straight	shape
spaghetti can be	cuboid	thin	shape
battery can be	wedge-shaped	cylindrical	shape
lettuce can be	rectangular	round	shape
moon can be	straight	curved	shape
pen can be	curved	straight	shape
fridge can be	round	cuboid	shape
potato can be	slender	oval	shape
submarine can be	conical	tubular	shape
ruler can be	round	straight	shape
tin can be	round	cylindrical	shape
sickle can be	straight	curved	shape
earth can be	cuboid	round	shape
horse can be	ridden	spread	action

flag can be	waved	pressed	action
doorknob can be	turned	bitten	action
bread can be	eaten	worn	action
jam can be	spread	planted	action
tree can be	planted	fried	action
plaster can be	carved	drunk	action
egg can be	broken	ridden	action
steak can be	bitten	driven	action
tie can be	worn	eaten	action
water can be	drunk	sliced	action
painting can be	rolled	drunk	action
button can be	fried	pressed	action
paper can be	eaten	folded	action
blanket can be	eaten	rolled	action
dog can be	worn	walked	action
dress can be	carved	worn	action
pork can be	planted	chopped	action
shirt can be	drunk	washed	action
milk can be	bitten	drunk	action
flower can be	driven	planted	action
car can be	waved	driven	action

garlic can be	walked	chopped	action
floor can be	fried	swept	action
beard can be	ridden	shaved	action
horse can be	ridden	spread	action
flag can be	waved	pressed	action
doorknob can be	turned	bitten	action
bread can be	eaten	worn	action
jam can be	spread	planted	action
tree can be	planted	fried	action
plaster can be	carved	drunk	action
egg can be	broken	ridden	action
steak can be	bitten	driven	action
tie can be	worn	eaten	action
water can be	drunk	sliced	action
painting can be	rolled	drunk	action
button can be	fried	pressed	action
paper can be	eaten	folded	action
blanket can be	eaten	rolled	action
dog can be	worn	walked	action
dress can be	carved	worn	action
pork can be	planted	chopped	action

shirt can be	drunk	washed	action
milk can be	bitten	drunk	action
flower can be	driven	planted	action
car can be	waved	driven	action
garlic can be	walked	chopped	action
floor can be	fried	swept	action
beard can be	ridden	shaved	action
door can be	opened	sliced	action
bike can be	ridden	opened	action
wine can be	poured	bitten	action
sword can be	waved	drunk	action
banana can be	peeled	driven	action
football can be	kicked	sliced	action
sock can be	worn	eaten	action
bus can be	driven	poured	action
carrot can be	sliced	worn	action
clothes can be	folded	ridden	action
book can be	opened	eaten	action
bell can be	rung	driven	action
screwdriver can be	poured	turned	action
orange can be	worn	peeled	action

hat can be	drunk	worn	action
motorbike can be	drunk	ridden	action
cash can be	bitten	folded	action
words can be	opened	typed	action
dice can be	eaten	thrown	action
oil can be	worn	poured	action
steak can be	drunk	sliced	action
dumbell can be	sliced	lifted	action
butter can be	driven	spread	action
beer can be	sliced	drunk	action
hair can be	peeled	combed	action
door can be	opened	sliced	action
bike can be	ridden	opened	action
wine can be	poured	bitten	action
sword can be	waved	drunk	action
banana can be	peeled	driven	action
football can be	kicked	sliced	action
sock can be	worn	eaten	action
bus can be	driven	poured	action
carrot can be	sliced	worn	action
clothes can be	folded	ridden	action

book can be	opened	eaten	action
bell can be	rung	driven	action
screwdriver can be	poured	turned	action
orange can be	worn	peeled	action
hat can be	drunk	worn	action
motorbike can be	drunk	ridden	action
cash can be	bitten	folded	action
words can be	opened	typed	action
dice can be	eaten	thrown	action
oil can be	worn	poured	action
steak can be	drunk	sliced	action
dumbell can be	sliced	lifted	action
butter can be	driven	spread	action
beer can be	sliced	drunk	action
hair can be	peeled	combed	action
chalk found in	classroom	bed	location
locust found in	grass	water	location
monitor found in	study	roof	location
wolf found in	forest	sea	location
painting found in	wall	air	location
lizard found in	jungle	sky	location

fridge found in	kitchen	toliet	location
shark found in	sea	grassland	location
seagull found in	sky	underground	location
nurse found in	hospital	farm	location
sugar found in	kitchen	classroom	location
scorpion found in	desert	river	location
salt found in	sky	kitchen	location
crab found in	grassland	sea	location
kite found in	river	sky	location
chef found in	farm	restaurant	location
worker found in	jungle	factory	location
runner found in	factory	stadium	location
sheet found in	kitchen	bedroom	location
farmer found in	factory	farm	location
toothpaste found in	bedroom	bathroom	location
hob found in	study	kitchen	location
shower found in	kitchen	bathroom	location
blackboard found in	bedroom	classroom	location
soap found in	living room	toliet	location
chalk found in	classroom	bed	location
locust found in	grass	water	location

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monitor found in	study	roof	location
wolf found in	forest	sea	location
painting found in	wall	air	location
lizard found in	jungle	sky	location
fridge found in	kitchen	toliet	location
shark found in	sea	grassland	location
seagull found in	sky	underground	location
nurse found in	hospital	farm	location
sugar found in	kitchen	classroom	location
scorpion found in	desert	river	location
salt found in	sky	kitchen	location
crab found in	grassland	sea	location
kite found in	river	sky	location
chef found in	farm	restaurant	Location
worker found in	jungle	factory	Location
runner found in	factory	stadium	Location
sheet found in	kitchen	bedroom	Location
farmer found in	factory	farm	Location
toothpaste found in	bedroom	bathroom	Location
hob found in	study	kitchen	Location
shower found in	kitchen	bathroom	Location

blackboard found in	bedroom	classroom	Location
soap found in	living room	toliet	Location
cactus found in	desert	sea	Location
shell found in	sea	grassland	Location
pyramid found in	desert	canyon	Location
train found on	track	roof	Location
gorilla found in	forest	farm	Location
bed found in	hotel	classroom	Location
octopus found in	sea	forest	Location
antenna found on	roof	river	Location
tiger found in	zoo	canteen	Location
medicine found in	hospital	forest	Location
seagull found in	sky	desert	Location
camel found in	desert	jungle	Location
monkey found in	sea	jungle	Location
rice found in	sea	farm	Location
kangaroo found in	taxi	zoo	Location
sloth found on	river	tree	Location
burger found in	forest	restaurant	Location
fish found in	grass	river	Location
bus found in	space	station	Location

lion found in	farm	zoo	Location
lobster found in	desert	sea	Location
crododile found in	sky	river	Location
cheese found in	forest	supermarket	Location
fox found in	river	forest	Location
zebra found in	restaurant	grassland	Location
cactus found in	desert	sea	Location
shell found in	sea	grassland	Location
pyramid found in	desert	canyon	Location
train found on	track	roof	Location
gorilla found in	forest	farm	Location
bed found in	hotel	classroom	Location
octopus found in	sea	forest	Location
antenna found on	roof	river	Location
tiger found in	zoo	canteen	Location
medicine found in	hospital	forest	Location
seagull found in	sky	desert	Location
camel found in	desert	jungle	Location
monkey found in	sea	jungle	Location
rice found in	sea	farm	Location
kangaroo found in	taxi	zoo	Location

sloth found on	river	tree	Location
burger found in	forest	restaurant	Location
fish found in	grass	river	Location
bus found in	space	station	Location
lion found in	farm	zoo	Location
lobster found in	desert	sea	Location
crododile found in	sky	river	Location
cheese found in	forest	supermarket	Location
fox found in	river	forest	Location
zebra found in	restaurant	grassland	Location

Supplementary Table 2: Targets

target key	option 1	option 2	target type
Easter goes with	Thanksgiving	laptop	Taxonomic
coffee goes with	iron	wine	Taxonomic
breakfast goes with	dinner	pen	Taxonomic
python goes with	hanger	worm	Taxonomic
fireman goes with	teacher	curtain	Taxonomic

snake goes with	wardrobe	lobster	Taxonomic
train goes with	motorcycle	sheet	Taxonomic
cow goes with	board	bear	Taxonomic
boat goes with	train	jam	Taxonomic
dog goes with	sauce	fox	Taxonomic
spaceship goes with	convertible	bun	Taxonomic
radio goes with	vinegar	telephone	Taxonomic
goldfish goes with	haddock	pencil	Taxonomic
tummy goes with	sock	head	Taxonomic
helmet goes with	crown	cactus	Taxonomic
shovel goes with	game	spoon	Taxonomic
ambulance goes with	speedboat	juice	Taxonomic
train goes with	earthworm	submarine	Taxonomic
teacher goes with	nurse	monkfish	Taxonomic
dog goes with	keyboard	mule	Taxonomic
urn goes with	jug	lock	Taxonomic
cat goes with	blade	wolf	Taxonomic
waitress goes with	clerk	scorpion	Taxonomic
monkey goes with	hammer	bear	Taxonomic
car goes with	tractor	penguin	Taxonomic
helicopter goes with	arrow	truck	Taxonomic

ice goes with	jelly	bull	Taxonomic
rabbit goes with	skirt	beaver	Taxonomic
cow goes with	lamb	grape	Taxonomic
garden goes with	magma	pasture	Taxonomic
panda goes with	grizzly	ruler	Taxonomic
tuxedo goes with	language	uniform	Taxonomic
floss goes with	yarn	rock	Taxonomic
chips goes with	law	crouton	Taxonomic
peanut goes with	bean	dragon	Taxonomic
lecture goes with	octopus	song	Taxonomic
applesauce goes with	jelly	magic	Taxonomic
tractor goes with	toe	tank	Taxonomic
stewardess goes with	nurse	sword	Taxonomic
desert goes with	mask	meadow	Taxonomic
owl goes with	chicken	seaweed	Taxonomic
cradle goes with	lipstick	cot	Taxonomic
beaver goes with	seal	dwarf	Taxonomic
pig goes with	headset	donkey	Taxonomic
owl goes with	sparrow	coin	Taxonomic
crib goes with	cancer	hammock	Taxonomic
snack goes with	lunch	pants	Taxonomic

pencil goes with	elephant	stick	Taxonomic
doctor goes with	police	fence	Taxonomic
necklace goes with	butter	belt	Taxonomic
honey goes with	sap	violin	Taxonomic
waitress goes with	jellyfish	nurse	Taxonomic
squirrel goes with	rat	picture	Taxonomic
vase goes with	calculator	goblet	Taxonomic
hen goes with	robin	matrix	Taxonomic
forge goes with	lens	oven	Taxonomic
rat goes with	otter	magazine	Taxonomic
dolphin goes with	plate	pig	Taxonomic
mouse goes with	chipmunk	fan	Taxonomic
yacht goes with	pepper	automobile	Taxonomic
vase goes with	bucket	switch	Taxonomic
car goes with	stomach	wagon	Taxonomic
lager goes with	juice	shoes	Taxonomic
suit goes with	tower	robe	Taxonomic
surgeon goes with	dentist	string	Taxonomic
pram goes with	bean	surfboard	Taxonomic
syrup goes with	oil	trumpet	Taxonomic
belt goes with	spring	hat	Taxonomic

rabbit goes with	skunk	carpenter	Taxonomic
highway goes with	forest	alley	Taxonomic
airplane goes with	taxi	integer	Taxonomic
closet goes with	idea	vault	Taxonomic
jet goes with	ship	form	Taxonomic
butter goes with	bridge	yogurt	Taxonomic
dough goes with	clay	musician	Taxonomic
dragon goes with	cross	snake	Taxonomic
belly goes with	head	electricity	Taxonomic
tea goes with	community	wine	Taxonomic
pot goes with	pan	detective	Taxonomic
tea goes with	ankle	vodka	Taxonomic
monarch goes with	president	jar	Taxonomic
horse goes with	pajamas	elephant	Taxonomic
cola goes with	ale	fire	Taxonomic
lorry goes with	shrimp	limousine	Taxonomic
pig goes with	rooster	camp	Taxonomic
trainers goes with	bamboo	skates	Taxonomic
canteen goes with	vial	code	Taxonomic
church goes with	butterfly	store	Taxonomic
boxer goes with	gymnast	magnet	Taxonomic

kettle goes with	gate	fryer	Taxonomic
surgeon goes with	butcher	phone	Taxonomic
cave goes with	salad	valley	Taxonomic
fork goes with	rake	flour	Taxonomic
castle goes with	blanket	cottage	Taxonomic
leopard goes with	fox	opera	Taxonomic
brick goes with	rocket	boulder	Taxonomic
spaghetti goes with	rice	broadcast	Taxonomic
bus goes with	locust	buggy	Taxonomic
submarine goes with	raft	song	Taxonomic
sneeze goes with	pond	belch	Taxonomic
pillow goes with	head	plastic	Thematic
bread goes with	ray	bakery	Thematic
castle goes with	king	tomato	Thematic
apron goes with	wire	chef	Thematic
floss goes with	teeth	wood	Thematic
razor goes with	glass	beard	Thematic
helicopter goes with	pilot	turtle	Thematic
actress goes with	bean	play	Thematic
janitor goes with	mop	hen	Thematic
soup goes with	hill	spoon	Thematic

dolphin goes with	ocean	grass	Thematic
zoo goes with	jeans	lion	Thematic
pompom goes with	cheerleader	broccoli	Thematic
owl goes with	doll	nest	Thematic
airplane goes with	sky	rat	Thematic
marathon goes with	window	runner	Thematic
hotel goes with	guest	lion	Thematic
tea goes with	tape	mug	Thematic
gun goes with	bullet	cheese	Thematic
lecture goes with	claw	student	Thematic
beaver goes with	dam	air	Thematic
suit goes with	tomb	groom	Thematic
gum goes with	wrapper	horse	Thematic
coffee goes with	pen	mug	Thematic
desert goes with	camel	scissors	Thematic
jeweller goes with	spider	necklace	Thematic
ring goes with	fniger	submarine	Thematic
sardines goes with	crane	can	Thematic
veil goes with	bride	can	Thematic
mower goes with	salmon	grass	Thematic
horse goes with	saddle	mantis	Thematic

glasses goes with	garlic	eyes	Thematic
baby goes with	crib	flute	Thematic
boxer goes with	dust	gloves	Thematic
car goes with	mechanic	mountain	Thematic
juice goes with	flag	cup	Thematic
bandage goes with	wound	sea	Thematic
train goes with	salt	rail	Thematic
truck goes with	road	bread	Thematic
boat goes with	tissue	harbour	Thematic
whistle goes with	referee	steam	Thematic
menu goes with	cell	diner	Thematic
comb goes with	hair	signal	Thematic
squirrel goes with	cash	nut	Thematic
spaceship goes with	astronaut	deer	Thematic
stamp goes with	cotton	postcard	Thematic
colander goes with	pasta	mailbox	Thematic
oven goes with	hair	cake	Thematic
umbrella goes with	rain	message	Thematic
blender goes with	paper	smoothie	Thematic
pram goes with	baby	lizard	Thematic
canteen goes with	carbon	water	Thematic

airplane goes with	stewardess	classroom	Thematic
crib goes with	ant	toddler	Thematic
badge goes with	cop	button	Thematic
cow goes with	gun	milk	Thematic
stockings goes with	legs	oxygen	Thematic
elevator goes with	pork	passenger	Thematic
surgeon goes with	scalpel	charger	Thematic
badge goes with	wind	officer	Thematic
soldier goes with	rifle	lake	Thematic
sneeze goes with	diamond	nose	Thematic
cereal goes with	bowl	sand	Thematic
cradle goes with	tape	infant	Thematic
dog goes with	leash	volcano	Thematic
horse goes with	ship	cowboy	Thematic
waiter goes with	tip	pipe	Thematic
steak goes with	data	grill	Thematic
lotion goes with	skin	class	Thematic
rake goes with	cloud	leaves	Thematic
hair goes with	brush	wheel	Thematic
bird goes with	voice	egg	Thematic
clinic goes with	nurse	crow	Thematic

drawer goes with	python	socks	Thematic
trainers goes with	laces	document	Thematic
door goes with	poem	keys	Thematic
jet goes with	airport	pill	Thematic
waitress goes with	whale	dinner	Thematic
snake goes with	venom	screen	Thematic
airport goes with	bone	baggage	Thematic
spider goes with	web	flashlight	Thematic
script goes with	eagle	actor	Thematic
horse goes with	stable	battery	Thematic
nurse goes with	tree	medicine	Thematic
refrigerator goes with	food	soil	Thematic
graffiti goes with	river	wall	Thematic
laundry goes with	hamper	rabbit	Thematic
leopard goes with	virus	zoo	Thematic
teeth goes with	dentist	camel	Thematic
pig goes with	ghost	sty	Thematic
chimney goes with	smoke	shark	Thematic
alarm goes with	diploma	fire	Thematic
shop goes with	basket	meteor	Thematic
rat goes with	directory	maze	Thematic

puppy goes with	kennel	galaxy	Thematic
cat goes with	kettle	vet	Thematic
boat goes with	river	plaster	Thematic
vase goes with	calf	tulip	Thematic
suit goes with	tailor	crab	Thematic
jail goes with	crop	robber	Thematic

Supplemental material of chapter 5

Supplementary Table 1: Stimuli

Concept	Question	Correct Answer
a ballet	Is it associated with performer	YES
a barbeque	Is it associated with suitcase	NO
a competition	Is it associated with athlete	YES
a concert	Is it associated with bread	NO
a date	Is it associated with wall	NO
a delivery	Is it associated with customer	YES
a diagnosis	Is it associated with doctor	YES
a dinner	Is it associated with island	NO
an exam	Is it associated with student	YES
an exhibition	Is it associated with pill	NO
a festival	Is it associated with cactus	NO
a fight	Is it associated with boxing	YES
a funeral	Is it associated with coffin	YES
a graduation	Is it associated with donkey	NO
a hike	Is it associated with boots	YES

a hunt	Is it associated with oil	NO
an interview	Is it associated with reporter	YES
a journey	Is it associated with table	NO
a lesson	Is it associated with teacher	YES
a march	Is it associated with flower	NO
a meeting	Is it associated with discussion	YES
an opera	Is it associated with tomato	NO
an operation	Is it associated with hospital	YES
a parade	Is it associated with shelf	NO
a party	Is it associated with wine	YES
a picnic	Is it associated with rubber	NO
a prayer	Is it associated with religion	YES
a presentation	Is it associated with package	NO
a race	Is it associated with referee	YES
a wedding	Is it associated with rat	NO
an aeroplane	Is it associated with transport	YES
an ant	Is it associated with shark	NO
an apple	Is it associated with fruit	YES
an arm	Is it associated with lamp	NO
a basketball	Is it associated with sports	YES
a book	Is it associated with fish	NO

a box	Is it associated with water	NO
a car	Is it associated with road	YES
a castle	Is it associated with brick	YES
a child	Is it associated with atom	NO
a closet	Is it associated with pants	YES
a curtain	Is it associated with tissue	NO
a dessert	Is it associated with sugar	YES
a dog	Is it associated with star	NO
a shirt	Is it associated with clothing	YES
a fridge	Is it associated with scissors	NO
a hammer	Is it associated with nail	YES
a hat	Is it associated with boat	NO
a laptop	Is it associated with document	YES
a lettuce	Is it associated with police	NO
a man	Is it associated with carrot	NO
a pan	Is it associated with heat	YES
a pencil	Is it associated with eraser	YES
a woman	Is it associated with beard	NO
a pigeon	Is it associated with bird	YES
a steak	Is it associated with roof	NO
a toothbrush	Is it associated with bathroom	YES

a tree	Is it associated with coral	NO
a wheelchair	Is it associated with knife	NO
a piano	Is it associated with music	YES
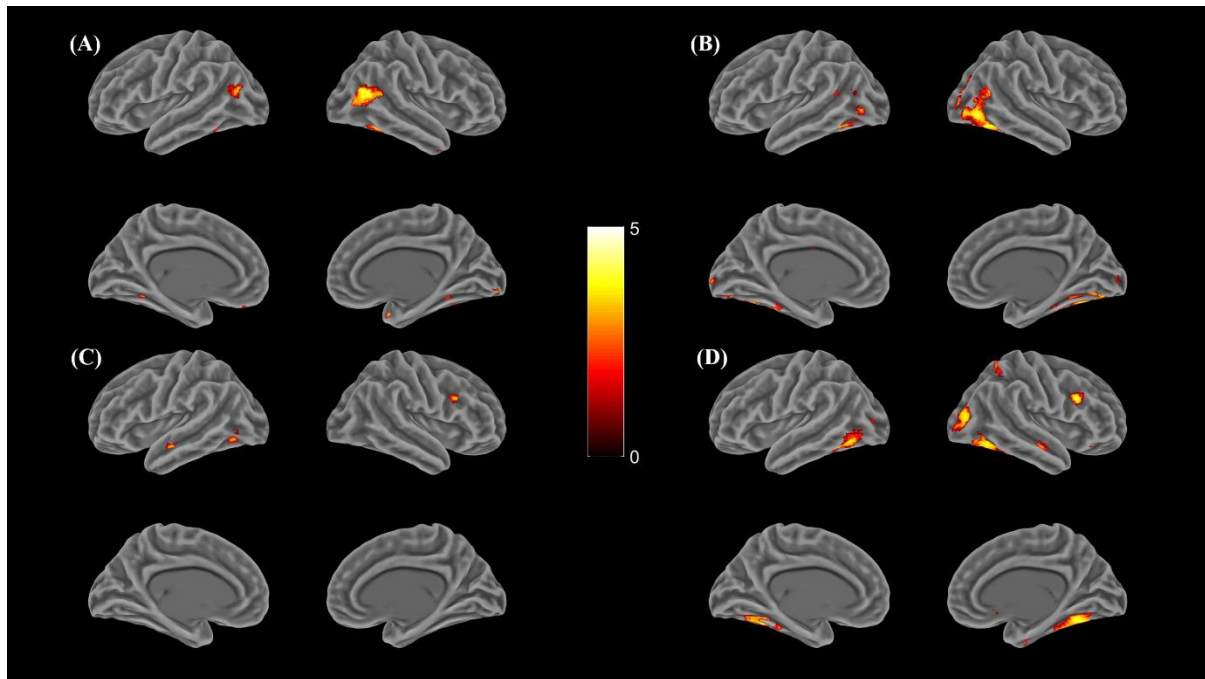
Supplementary Figure 1: For events > objects, regions showing increased connectivity with (A). Left vATL; (B). Right vATL; (C). Left AG; (D). Right AG. Surface render (p<0.005, no cluster correction)
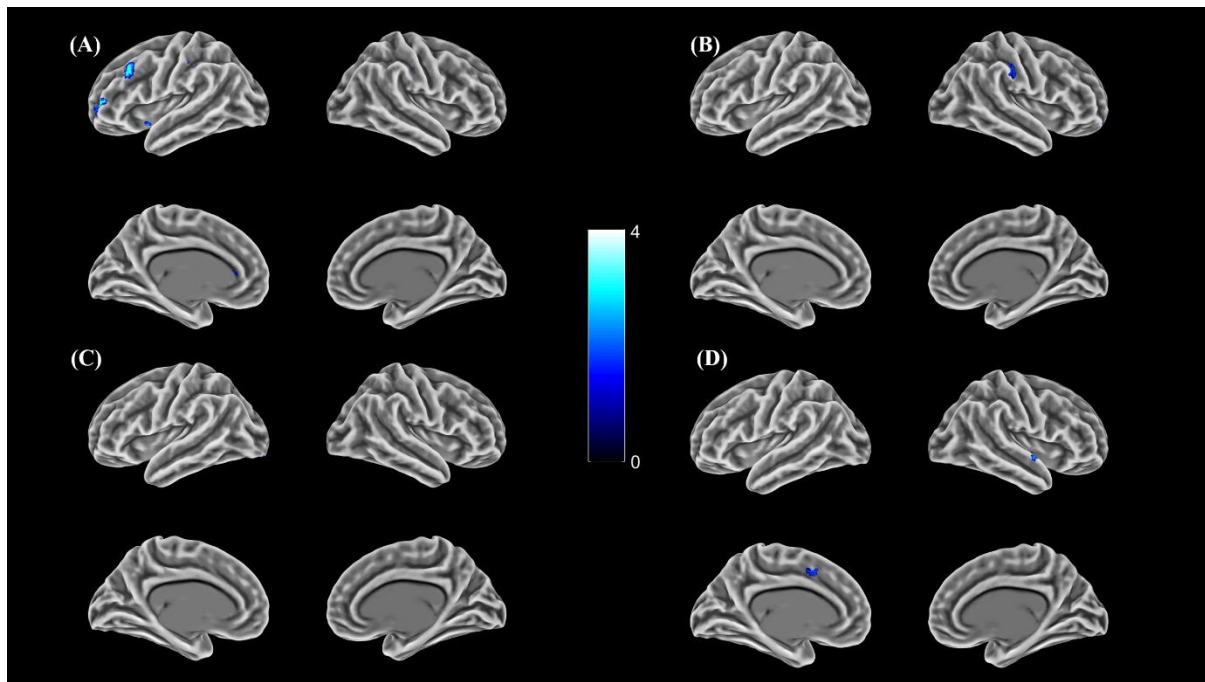
Supplementary Figure 2: For object > events, regions showing increased connectivity with (A). Left vATL; (B). Right vATL; (C). Left AG; (D). Right AG. Surface render (p<0.005, no cluster correction)

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