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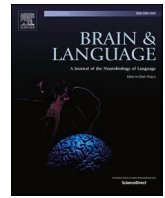
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# Taxonomic and thematic relations rely on different types of semantic features: Evidence from an fMRI meta-analysis and a semantic priming study

Yueyang Zhang, Daniel Mirman, Paul Hoffman\*

School of Philosophy, Psychology & Language Sciences, University of Edinburgh, UK

## 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.

## 1. 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 color, 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 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

\* Corresponding author at: School of Philosophy, Psychology & Language Sciences, University of Edinburgh, 7 George Square, Edinburgh, EH8 9JZ, UK.  
E-mail address: [p.hoffman@ed.ac.uk](mailto:p.hoffman@ed.ac.uk) (P. Hoffman).

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-parietal 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 using a range of different techniques. Much of the evidence has come from fMRI studies. 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). 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 (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.

## 2. 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 quantitatively 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.

### 2.1. Method

#### 2.1.1. 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,

**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.

Study	First Author	Year	Participants	Mean Age	Task	Number of peaks		Mean reaction time (ms)	
						TX > THM	THM > TX	TX	THM
1	Kotz (Kotz, Cappa, von Cramon, & Friederici, 2002)	2002	13	23.5	primed lexical decision	3	0	869	839
2	Sachs (Sachs, Weis, Zellagui, et al., 2008)	2008	16	27	primed lexical decision	1	0	646	627
3	Sachs (Sachs, Weis, Krings, Huber, & Kircher, 2008)	2008	14	28	triads task	3	0	1191;1186	1154;1189
4	Abel (Abel et al., 2009)	2009	19	26	picture-word-interference	3	2	909	814
5	Kalénine (Kalénine et al., 2009)	2009	45	22	triads task (picture)	3	10	1478	1512
6	Kuchinke (Kuchinke, van der Meer, & Krueger, 2009)	2009	15	27.2	relatedness judgement task	4	8	NA	NA
7	Sass (Sass, Sachs, Krach, & Kircher, 2009)	2009	16	26	primed lexical decision	0	1	742.47	710.85
8	Sachs (Sachs et al., 2011)	2011	16	27	primed lexical decision	1	0	670.23	669.56
9	De Zubicaray (De Zubicaray, Hansen, & McMahon, 2013)	2013	20	21.5	picture-word-interference	0	3	833	787
10	De Zubicaray (De Zubicaray, Johnson, Howard, & McMahon, 2014)	2014	28	22.93	picture naming	1	1	NA	NA
11	Lee (Lee, Pruce, & Newman, 2014)	2014	18	27.5	primed lexical decision	0	16	NA	NA
12	Jackson (Jackson, Hoffman, Pobric, & Lambon Ralph, 2015)	2015	25	25.48	triads task	2	2	1783.69	1653.68
13	Davey (Davey et al., 2016)	2016	20	24.8	triads task	0	31	2088	1655
14	Kumar (Kumar, 2018)	2018	18	28.3	primed relatedness judgement task	5	0	643.11	658.52
15	Lewis (Lewis, Poeppel, & Murphy, 2019)	2019	18	27	relatedness judgement task	0	6	982	1002
16	Zhang (Zhang et al., 2021)	2021	31	20.6	relatedness judgement task	7	23	NA	NA
<b>Means</b>									
<b>Sums</b>					25.3			1168.46	1105.97
			332			33	103		

albeit with reduced sensitivity to weaker effects.

### 2.1.2. 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<sup>3</sup>). 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).

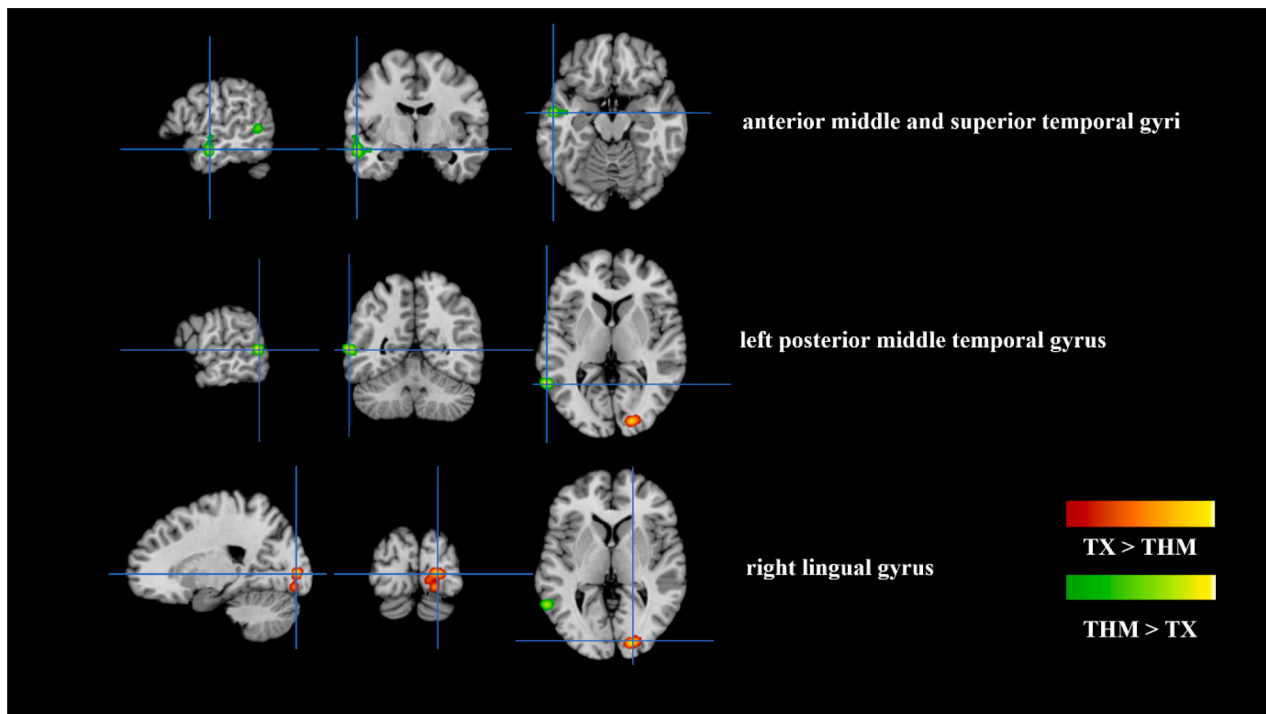
## 2.2. Results

The THM > TX contrast revealed two clusters, both in the left hemisphere (Fig. 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.

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<sup>3</sup> was applied to the results. For the THM > TX contrast, another 2 clusters in left pMTG and left SMG were found (Fig. 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.

## 2.3. 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



**Fig. 1.** Activation likelihood maps for taxonomic versus thematic relation (orange) and thematic versus taxonomic relation (green). Images are thresholded at cluster-corrected  $p < 0.05$ . (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

**Table 2**

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

Cluster	Anatomical region	Volume(mm <sup>3</sup> )	BA	x	y	z	ALE Value
<b>THM &gt; TX</b>							
1	Left Temporal Lobe	1856					
	Middle Temporal Gyrus		21	-56	-8	-18	0.016253173
	Sub-Gyral		21	-44	-8	-18	0.008369234
2	Middle Temporal Gyrus	1680	21	-58	-10	-6	0.007896487
	Left Temporal Lobe						
	Middle Temporal Gyrus		21	-62	-54	4	0.018458404
	Sub-Gyral		37	-52	-50	-4	0.009418378
	<b>TX &gt; THM</b>						
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

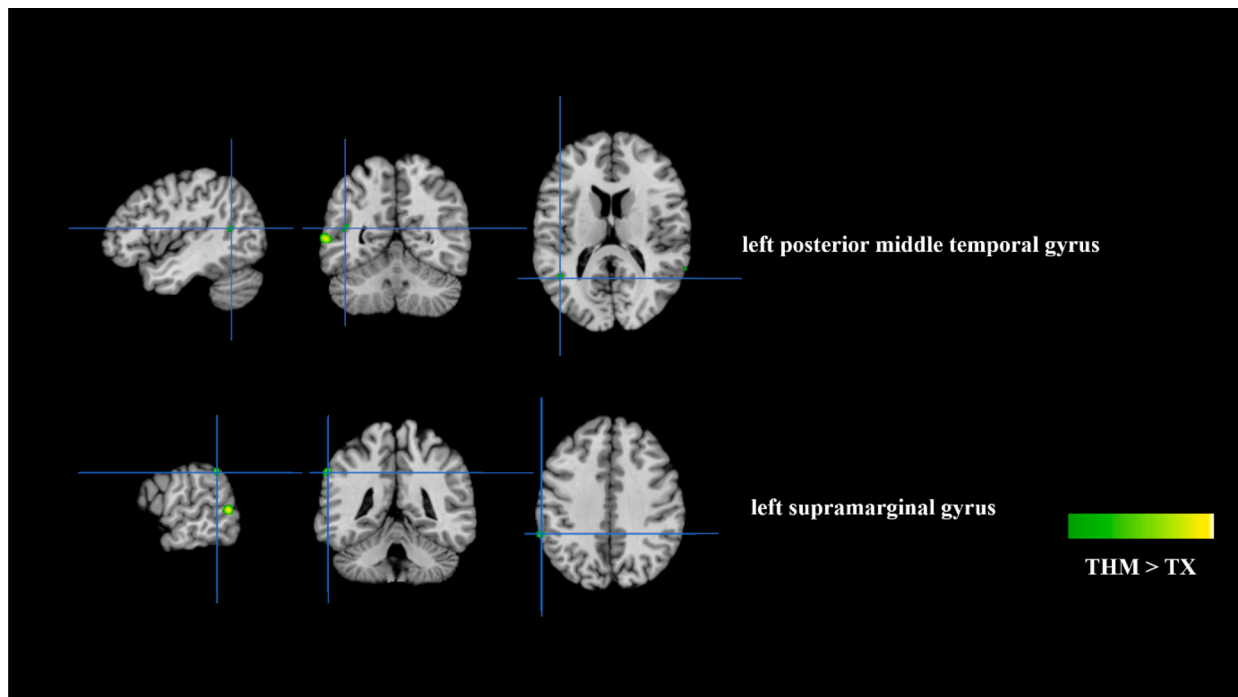
Note: BA, Brodmann Area.

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 posterior middle temporal gyrus (pMTG, see Fig. 1, corrected results) and supramarginal gyrus (SMG, Fig. 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 (Struiksmas 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 is consistent with the feature reliance hypothesis, since thematic relations appear to preferentially activate regions involved in processing action and location information.

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, 2008), 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



**Fig. 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. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

used pictures to elicit taxonomic and thematic processing (Abel et al., 2009; De Zubicaray et al., 2014; 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.

### 3. 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.

#### 3.1. Method

##### 3.1.1. 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.

##### 3.1.2. Design and materials

Participants made semantic judgements to trials arranged in pairs (see Fig. 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).

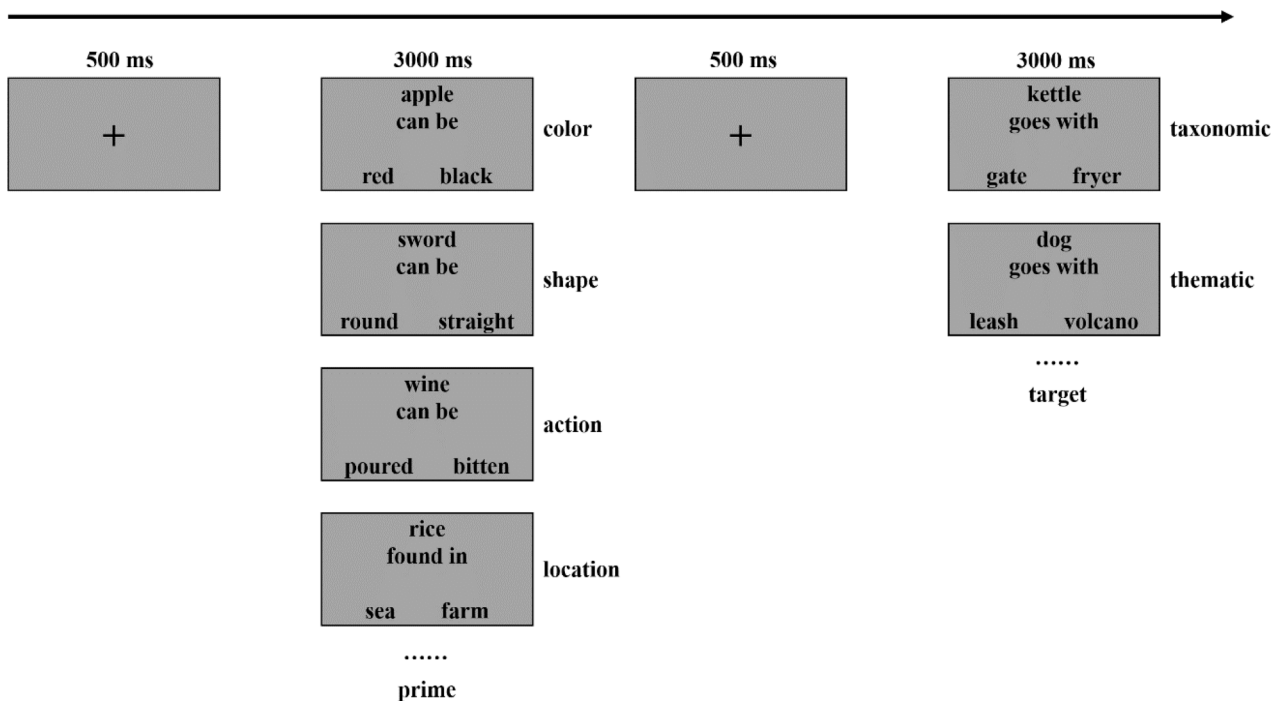


Fig. 3. Procedure of the semantic task.

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 ( $t(198) = -105.75, p < 0.001$ ).

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

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

	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)

judgement for half of the participants and a thematic judgement for the other half.

All materials and data can be accessed on OSF:  
[https://osf.io/mrvns/?view\\_only](https://osf.io/mrvns/?view_only)

### 3.1.3. 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 Fig. 3): (1) a fixation cross in the middle of screen for 500 ms; (2) prime judgement for a maximum of 3000 ms; (3) a fixation cross in the middle of screen for 500 ms; (4) target judgement for a maximum of 3000 ms. For both primes and targets, if participants made a wrong decision or did not choose any option within 3000 ms, then a feedback screen showing ‘wrong’ or ‘too slow’ would be displayed for 2000 ms. The whole experiment took 20–30 min, including one practice session and 4 blocks of the main experiment. Participants were allowed to rest between every 2 blocks.

### 3.1.4. 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 < 500 ms, 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 < 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.

### 3.2. 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.

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 Fig. 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 judgements.

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.

### 3.3. Discussion

By using a primed semantic decision task, this behavioural experiment investigated the priming effects of accessing different types of

**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	<0.001*
Prime Type (AL > CS)	-5.021	2.594	123.933	-1.935	0.0552
Target Type (THM > TX)	-64.830	3.251	640.518	-19.944	<0.001*
Prime Type * Target Type	-4.436	2.119	207.681	-2.093	0.0375*
Prime RT	67.629	2.075	30176.198	32.588	<0.001*
Target Cor Pos	-30.427	3.322	7055.922	-9.158	<0.001*

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 (Fig. 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 color and shape knowledge. We consider possible reasons for this in the General Discussion.

## 4. 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 regions 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.

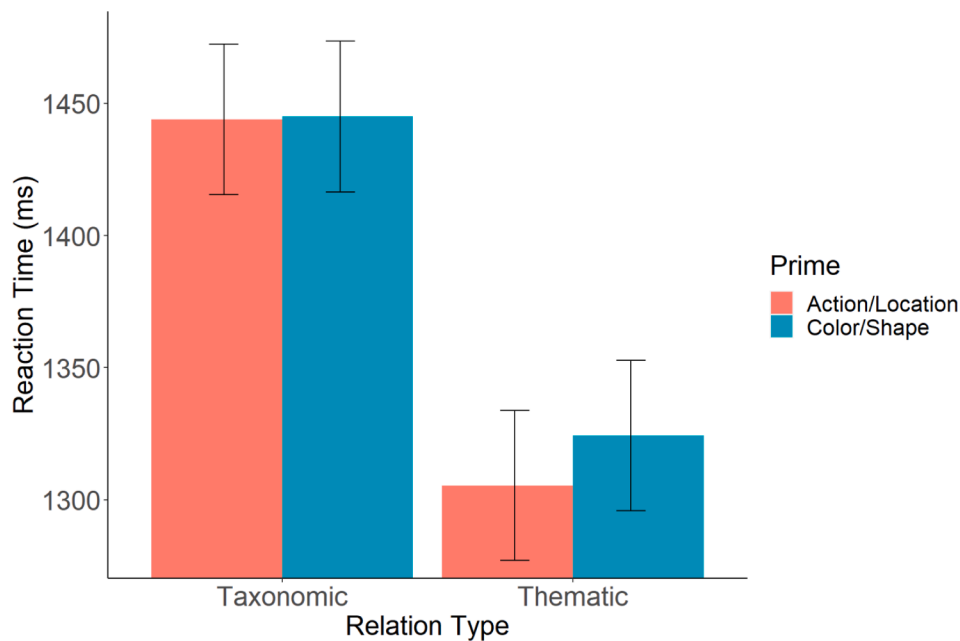
For the contrast of thematic over taxonomic relations, our meta-analysis showed significant activation likelihood in left pMTG. At a more lenient, uncorrected threshold, an additional cluster was found in left SMG. These effects are consistent with the proposal that action and location associations are particularly important in determining thematic relations. A range of sites in the posterior temporal lobe and inferior parietal lobe are implicated in representing motion- and action-relevant concepts and in spatial cognition. 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 part of inferior parietal lobe,



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

Target	Prime	Accuracy		Reaction Time (ms)		
		Prime	Target (primed correctly)	Prime	Target (primed correctly)	Combined target (color/shape; action/location)
Taxonomic	Color	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	Color	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	

Note: AL, action/location; CS, color/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.



**Fig. 4.** Model estimates for the effects of prime type on reaction time of taxonomic and thematic relations.

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

TargetType	Fixed effects	b	S.E.	df	t	p
Taxonomic	Intercept	1450.602	17.428	194.692	83.233	<0.001*
	Prime Type (AL > CS)	-0.087	3.652	80.870	-0.024	0.981
	Prime RT	71.295	3.033	14784.413	23.502	<0.001*
	Target Cor Pos	-1.641	6.723	1402.623	-0.244	0.807
Thematic	Intercept	1308.120	15.016	227.270	87.113	<0.001*
	Prime Type (AL > CS)	-10.549	3.116	81.821	-3.386	0.001*
	Prime RT	63.521	2.842	14338.929	22.351	<0.001*
	Target Cor Pos	-47.199	6.765	544.918	-6.976	<0.001*

Note: AL, action/location; CS, color/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.

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 et al., 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 executive 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

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

Fixed effects	b	S.E.	z	p
Intercept	3.019	0.077	39.110	<0.001*
Prime Type (AL > CS)	-0.045	0.025	-1.794	0.0729
Target Type (THM > TX)	0.359	0.034	10.463	<0.001*
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

Note: AL, action/location; CS, color/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.

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 (Fig. 4, Table 6). This could indicate 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.

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 Ralph et al., 2017; Rice 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.

## 5. 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.

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#### 6. Data accessibility statement

The raw data, experimental stimuli and code are publicly available (<https://osf.io/mrvns/>).

#### Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

#### Data availability

The raw data, experimental stimuli and code are publicly available (<https://osf.io/mrvns/>).

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