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Review

The function of the anterior temporal lobe: A review of the empirical evidence

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ABSTRACT

Recent work on the anterior temporal lobe (ATL) has led to substantively different theoretical branches, of its putative functions, that have in some part developed independently of one another. The ATL has dense connectivity with a number of sensory modalities. This has resulted in empirical evidence that supports different functionality dependent upon the variables under investigation. The main bodies of evidence have implicated the ATL as a domain-general semantic hub, whilst other evidence points to a domain-specific role in social or 'person-related' processing. A third body of evidence suggests that the ATLS underlie processing of unique entities. Primarily, research of the ATL has been based on lesion studies and from clinical populations such as semantic dementia or temporal lobe epilepsy patients. Although important, this neuropsychological evidence has a number of confounds, therefore techniques such as functional neuroimaging on healthy participants and the relatively novel use of non-invasive brain stimulation may be more useful to isolate specific variables that can discriminate between these different theories concerning 'normal' function. This review focuses on these latter types of studies and considers the empirical evidence for each perspective. The overall literature is integrated in an attempt to formulate a unifying theory and the functional sub-regions within the ATL are explored. It is concluded that a holistic integration of the theories is feasible in that the ATLS could process domain-general semantic knowledge but with a bias towards social information or stimuli that is personally relevant. Thus, it may be the importance of social/emotional information that gives it priority of processing in the ATL not an inherent property of the structure itself.

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Abbreviations: ATL, Anterior temporal lobe; BA, Brodmann's Area; DTI, Diffusion tensor imaging; fMRI, Functional Magnetic Resonance Imaging; FTD, Frontotemporal dementia; IFG, Inferior frontal gyrus; ITG, Inferior temporal gyrus; LATL, Left anterior temporal lobe; MTG, Medial temporal gyrus; PET, Positron emission tomography; PFC, Prefrontal cortex; RATL, Right anterior temporal lobe; rTMS, Repetitive Transcranial Magnetic Stimulation; SD, Semantic dementia; STG, Superior temporal gyrus; STS, Superior temporal sulcus; tDCS, Transcranial Direct Current Stimulation; TLE, Temporal lobe epilepsy; TMS, Transcranial Magnetic Stimulation; ToM, Theory of Mind

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1. Introduction

Since the late 19th century, and the observation of seminal cases such as the two classic forms of aphasia described by Broca and Wernicke, there has been a long standing belief of a structure–function relationship in the brain. However, modern technology has established that this relationship is an oversimplification, and it is now widely accepted amongst neuroscientists that the attribution of specific function to discrete areas of the brain is bound to be flawed. The interconnectedness of the brain both physically and functionally is beyond dispute. However, it is also commonly accepted that one way neuroscience can advance is to accrete knowledge about the function of specific brain areas by manipulating or observing them, whilst to a greater or lesser degree disregarding their connectedness to the rest of the neural system. This methodological approach obviously necessitates a circumspect conclusion and foreknowledge that one's findings will be greatly revised if not replaced as the discipline advances. Inherent to this methodology, is the need for a periodical review of the current research within manageable clusters of subdisciplines of the field. This paper is an attempt to meet this objective by reviewing the literature on the anterior temporal lobes.

2. The anterior temporal lobe

The anterior temporal lobe (ATL) is the most anterior tip of the temporal lobe, and is located rostral to the perirhinal cortex (Insausti et al., 1998; Nakamura and Kubota, 1996). However, there are no precisely demarcated boundaries that indicate the end of the ATLs that are universally agreed upon. For example, in some studies, the temporal pole (Brodmann's Area [BA] 38) is considered analogous to the ATL, whilst others consider the temporal pole and the anterior aspects of superior,

middle and inferior temporal gyri (BA 22, 21, 20), which extend more laterally across the temporal lobe, as the ATL (see Fig. 1). Usually the boundaries of the ATLs have been defined functionally resulting at best in imprecision and at worst in an infinite regress between function and location, and the terms ATL, BA 38 and temporal pole are often used interchangeably.

The function of the ATL and the temporal pole has been perplexing and inconsistently described throughout the literature (Dupont, 2002; Olson et al., 2007; Simmons and Martin, 2009). This may be due to its diverse structure and connections with a number of regions including the prefrontal cortex (PFC), amygdala, and the three temporal gyri, connecting it to most of the sensory modalities. The temporal gyri include the inferior temporal gyrus (ITG) which receives input from the ventral visual processing stream (Jones and Powell, 1970). This visual stream is associated with object recognition and

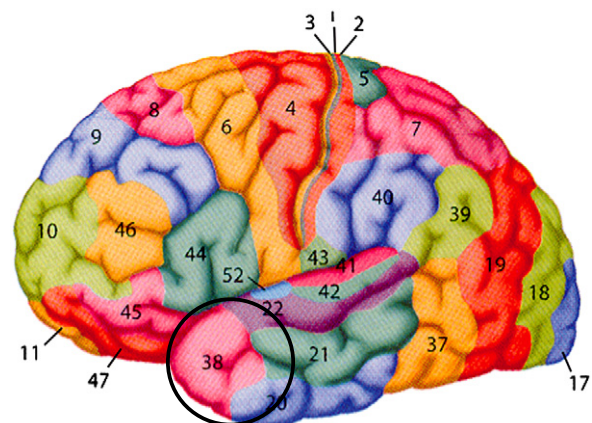


Fig. 1 – BA 38 (plus the anterior parts of BA 20, 21 and 22) is part of the ATL.

analyses of form and colour representation and includes the fusiform gyrus (Gross, 2008). Secondly, the middle temporal gyrus (MTG) which is thought to receive input from the somatosensory, visual, olfactory and auditory processing streams (Gloor, 1997; Jones and Powell, 1970). Thirdly, the superior temporal gyrus (STG) is important in auditory processing and also contains Wenicke's area which is important in speech and comprehension (Patesta and Gartner, 2006). The ATL is also connected with the superior temporal sulcus (STS) which is important in language processing and social attention (Redcay, 2008).

Consequently, the temporal pole has been associated with a number of functions including auditory and visual processing/discrimination (Humphries et al., 2001; Pinto Hamuy et al., 1957), learning and memory (Schiltz et al., 1973), social cognition (Olson et al., 2007), social and sexual behaviour (Miller et al., 1995), language processing (Hermann and Wyler, 1988), face recognition (Kazui et al., 1995), and olfactory and gustatory perception (Schellinger et al., 1983). Functions of the more general ATL, include semantic memory and knowledge (Rogers et al., 2004), language processing (Binder et al., 2010), social conceptual knowledge (Zahn et al., 2007), processing unique stimuli (Grabowski et al., 2001) and face recognition (Gainotti, 2007). Although there may be a number of putative functions of the ATL, many of these studies have come from animal, dementia or brain-damaged patients, temporal lobe epilepsy patients and lobectomy cases. Therefore it is difficult to elucidate the 'pure' anatomico-clinical correlations regarding ATL function (Dupont, 2002).

2.1. Historical background

The original data about the ATL stemmed from animal research, particularly from lesional studies carried out on monkeys. For example in 1938, Kluver and Bucy reported that bilateral lesions of the temporal lobe in monkeys led to abnormal sexual and social behaviour (hypersexuality, placidity, and hyperorality) as well as visual agnosia or 'psychic blindness' — the inability to recognise the meaning or significance of an event or object (Klüver and Bucy, 1938). This was supported by later animal research which found that specific ablation of the temporal pole resulted in deficits in visual discrimination, and oral syndrome, whereas there was a little change if the posterior sections of the temporal lobe were removed (Pinto Hamuy et al., 1957).

The prefrontal lobe has typically been thought to be implicated in social behaviour, however early research showed that damage to the ATL excluding the amygdala also leads to changes in social behaviour that are quite distinct from frontal lesions. Franzen and Myers (1973) specifically examined changes in social behaviour in monkeys after their bilateral prefrontal or anterior temporal cortices were removed. Monkeys with prefrontal ablations became passive, avoidant of their infants, had decreased aggression, and flattened affect. In comparison, the monkeys with anterior temporal cortical removals became more withdrawn and forcefully rejecting of their infants, showed more variations in aggression, increased smelling of objects, and inappropriate responses to social behaviours of other monkeys (vocal and facial signals). They showed little social interest in their peers and were often

rejected by their social groups. However, both frontal and temporal lesion groups of monkeys showed a generalised reduction in activities to maintain social bonds such as grooming, and near-body contact, as well as social communication. This study implicated both the ATL and PFC in the control and regulation of social behaviour, however it also suggests that the two areas may contribute differently to social processing. In addition, Horel et al. (1987) showed that cold suppression of the ventral and anterior inferior-temporal cortex also led to deficits in face discrimination of other monkeys, which is necessary when interpreting and navigating social contexts. This can account for why monkeys with ATL removals showed inappropriate social responses to the behaviour of other monkeys including their own infants.

This early research suggested a strong visual memory and social role of the ATLs and set an agenda for future research. Although, the animal research has been significant in demonstrating that the temporal lobe has functions in memory and learning, social behaviour, visual discrimination and face recognition, the majority of the studies were not confined to the ATL, and often neighbouring structures such as the amygdala, hippocampus, and temporal gyri were also affected. Therefore, until later techniques such as functional imaging, and comparisons with anatomical and clinical data in humans became available, a little precision was achievable in the conclusions that were made about the function of the ATL.

2.2. Neuropsychological data

The interest in the ATL in semantic memory came about from the identification of a population of patients with a specific type of dementia that markedly affected semantic knowledge and memory. These patients consistently exhibited significant atrophy in the bilateral temporal poles (Hodges et al., 1992; Mummery et al., 2000) therefore the disorder was classed as a subtype of frontotemporal dementia (FTD). These patients are characterised by a distinct and progressive loss of semantic memory including vocabulary (anomia) and word meaning, difficulties generating semantic categories, impoverished knowledge about a wide range of living things and objects, story comprehension and scripts, poor face and object recognition, and visual agnosia (inability to match semantically related pictures/objects) (Channon and Crawford, 2000; Funnell, 2001; Gainotti, 2007; Hodges et al., 1992, 1999; Mummery et al., 2000).

The deficits appeared to be very selective to semantic memory and were across a number of modalities including verbal and non-verbal memory. Thus Snowden et al. (1989) coined this disorder 'semantic dementia' (SD) due to the fact that all these symptoms seemed to indicate a specific deterioration of semantic memory and knowledge. Patients had relatively preserved autobiographical and episodic memory, non-verbal memory, executive function and perceptual and visuo-spatial skills (Hodges et al., 1992). Thus SD was said to provide a neurological model of semantic impairment that differed from other dementias or conditions where semantic deficits are also observed. For instance in Alzheimers disease, where both semantic and episodic memory are affected; herpes simplex virus encephalitis, where patients also show cognitive and executive function deficits; and stroke, where word

finding difficulties are often aided with cues, (e.g. 'it begins with b') (Patterson et al., 2007). In comparison, anomia in SD is not aided by cueing suggesting that it is not the word production or retrieval that is affected, but the underlying meaning of the word (Jefferies et al., 2008).

Neuropsychological data has also described patients with behavioural variant FTD (affecting predominantly the right ATL and frontal lobe) who show gross changes in social behaviour (Edwards-Lee et al., 1997). Previous research on FTD has emphasised frontal lobe involvement as the cause for behavioural and clinical symptoms. However, social behavioural changes, such as lack of empathy, social awkwardness, disinhibition and eccentric behaviour, are often seen independent of any frontal lobe damage (Edwards-Lee et al., 1997; Liu et al., 2004; Rankin et al., 2006; Thompson et al., 2003). Edwards-Lee et al. (1997) compared two populations of FTD patients; patients with frontal variant FTD (frontal atrophy with sparing of temporal lobes), and patients with temporal variant FTD (anterior temporal damage with sparing of frontal regions). They also compared those with predominant left versus right hemisphere atrophy. They noted that whilst patients with frontal lesions showed more passive, apathetic behaviour, patients with temporal lobe damage display more eccentric social behaviour, such as bizarre alterations in dress, poor personal hygiene, sociopathic behaviours such as violence and theft, impulsiveness, irritability and social ineptness. These behavioural changes were mainly seen in patients with right temporal damage. Many of the left temporal patients managed to function well in their daily activities. Many were living alone, working, cooking and cleaning; and were described as pleasant and socially appropriate (Edwards-Lee et al., 1997). The authors suggested a possible role for hemispheric dominance for a lateralised social function in the temporal lobes.

This right hemispheric dominance for social behaviour, empathy and emotions has been supported by a number of studies (Perry et al., 2001; Rankin et al., 2006; Thompson et al., 2003). For example, this finding was complemented in a later study using a larger sample ($n=47$) of left and right temporal variant FTD, where major right temporal atrophy was more associated with social awkwardness, loss of empathy and insight, disinhibition, bizarre affect and difficulties with recognising persons (Thompson et al., 2003). Further, these patients showed more stereotyped and repetitive behaviours. In comparison the left temporal group showed more cognitive problems such as anomia, semantic deficits and reduced comprehension. The authors proposed that the behavioural changes observed in the right temporal variant FTD patients may have previously led to misdiagnosis as frontal variant FTD or other psychiatric illnesses. The neuropsychological findings however, corresponded with earlier animal data in that damage to the ATLs leads to abnormal social behaviour. They also suggest a distinct behavioural and cognitive profiles between patients with left versus right ATL atrophy — with the right subserving emotional and social behaviour and the left more involved in general semantic cognition.

Another source of evidence about the role of the ATL comes from temporal lobe epilepsy (TLE) patients who have received resection of the ATL to reduce intractable seizures (Kawamura et al., 1982). Behavioural and psychiatric changes

from temporal lobe epilepsy (TLE) affecting the ATLs have been documented over the past few decades (Geschwind, 2009; Jensen and Larsen, 1979). One study reported that approximately 50% of patients with a spike focus in the ATL show psychiatric symptoms compared with less than 11% of patients whose seizure foci were in other brain regions (Gibbs, 1997). Patients with TLE often show paranoia, depression, or hysteria after a seizure, and have an increased prevalence of aggression, antisocial behaviour (Nielsen and Kristensen, 1981) and cluster C personality disorders (Lopez-Rodriguez et al., 1999). Many of these behavioural changes appear to be analogous to those reported with behavioural temporal-variant FTD.

TLE patients have also shown changes in memory and social behaviour (Bell and Giovagnoli, 2008; Hill et al., 1957; Shaw et al., 2007); however they do not show the same semantic deficit pattern as patients with SD (Drane et al., 2008; Hermann et al., 1994). A patient who underwent right ATL lobectomy described by Ellis et al. (1989) showed relatively preserved generalised semantic memory for living and non-living things but appeared to have a specific marked impairment in identifying famous faces and names. Although her autobiographical memory was good, she showed an explicit loss of memory for people, such as remembering where she had met people and what they did, remembering their voices, faces and what they looked like. The authors interpreted this as a loss of memory for persons, and hypothesized the ATL (in particular the right ATL) which may be a store for our knowledge about people. However, her impairment also extended to famous animals, products and buildings which led the authors to call the memory system a storage unit for information about singular objects.

In a comparable investigation, Kapur et al. (1994) documented a case of a 45 year old patient with damage to the anterior and inferior temporal lobes that spared the hippocampus and amygdala. The patient initially complained of memory difficulties and showed changes in personality becoming more childish and emotional. He showed mild to moderate impairments on paired associative learning and story recall, mild retrograde amnesia, but similarly had severe impairment in memory for famous faces and past events. Deficits in famous face naming and recognition have been commonly found in patients with temporal lobe removal following TLE (Drane et al., 2009; Glosser et al., 2003). This also corresponds with the earlier animal research showing deficits in visual discrimination. However, TLE surgery cases should also be regarded with care, as lobectomies are not always restricted to the ATL, sample sizes are often small (or single case studies), and long-term intractable epilepsy may lead to functional reorganisation of the brain (Olson et al., 2007).

The neuropsychological evidence suggests that memory is always affected in damage to any part of the ATL, however, the precise nature of that memory impairment is variable. In almost all cases, other impairments also occur. These can be largely clumped as 'social' deficits in the case of behavioural variant FTD (typically with RATL damage) and TLE, and domain-general cognitive deficits for semantic dementia (typically with bilateral atrophy or predominant LATL damage). However, the general confound with using clinical patients as evidence for function is that damage is never localised to

one area. For example, although SD patients generally show atrophy in the temporal poles, studies have also reported grey matter loss in the fusiform gyrus, inferior, middle and superior temporal gyri, hippocampus, amygdala, thalamus and orbitofrontal areas (Desgranges et al., 2007; Mummery et al., 2000). Distinguishing laterality differences is further complicated as although FTD patients show predominant atrophy in one hemisphere which they nearly always have bilateral atrophy.

In comparison, functional neuroimaging techniques offer a distinct advantage over neuropsychological data due to the specificity with which they enable associations between function and location. Therefore functional neuroimaging techniques such as functional magnetic resonance imaging (fMRI) and positron emission tomography (PET) on healthy participants and the relatively novel use of non-invasive brain stimulation may be more useful to study brain function in the 'normal' brain. Transcranial magnetic stimulation (TMS) is a non-invasive brain stimulation technique that allows temporary suppression of a localised area of the brain, enabling the probing of the relationship between function and location (Hilgetag et al., 2001). Current studies have further developed the body of evidence initially established by the neuropsychological data and dominant views/theories have started to emerge. The current review will outline these accounts and the empirical evidence supporting each of them.

3. Dominant views regarding the ATL

Although there is now a widespread agreement that the ATLs are involved in memory, there is no conclusive agreement on the exact role which they play in semantic memory. At present there are several bodies of evidence/observation about the function of the ATL (Simmons and Martin, 2009). In one domain, which is largely based on the SD literature, the ATLs are seen as a semantic processing unit. A representative example from this cluster of theories is that it is a 'hub' for linking together conceptual information from different modalities in the brain to form amodal, domain-general semantic representations or concepts (Lambon Ralph and Patterson, 2008; Patterson et al., 2007; Rogers et al., 2004). Secondly, there is evidence that the ATL is a store for representations of social or 'people-related' knowledge including moral, theory of mind, and emotional cognition (Olson et al., 2007; Zahn et al., 2007). However, the argument is further complicated as damage to the ATLs can lead to deficits in domain-specific stimuli such as famous and familiar faces and landmarks, which led to a third account that the ATLs are a repository for knowledge for 'unique entities'.

These three bodies of evidence are described in turn below. Due to the confounds of using neuropsychological data, the review will focus on the functional neuroimaging evidence as well as studies that uses non-invasive brain stimulation techniques such as transcranial magnetic stimulation (TMS) and transcranial direct current stimulation (tDCS). In contrast to the neuroimaging literature non-invasive brain stimulation techniques interfere with the activity of defined areas in the human cortex, thus enabling the observation of the behavioural impact of an increase or decrease in the cortical

excitability of the stimulated brain region (Pascual-Leone et al., 2000). This has the benefit of being able to make causal inferences about brain regions with function/behaviour. By confining the review to these types of studies it will be easier to compare and contrast the techniques. In doing so, we hope to elucidate that if one account is more robustly supported by the evidence or alternatively whether the function of the ATLs should be explained under one all-encompassing theory with delineated areas for particular functions.

3.1. Semantic hub theory

Semantic memory can be defined as memory for meanings, including knowledge about meaning of words, concepts, sentences, objects, events, people, and facts (Tulving, 1972). Due to this broad definition, often the terms 'semantic memory' and 'conceptual knowledge' are used interchangeably within the domain of cognitive science (Rogers, 2008). Rogers et al. (2004) proposed the semantic 'hub' theory and developed a computational parallel-processing model which theorised that the brain must contain a central semantic hub for bringing together information from different modalities to form the coherent whole or 'concept'. They suggested that the ATLs could act as this semantic 'hub' for linking together conceptual information from different modalities in the brain to form amodal, domain-general semantic representations as this area is known to receive convergent input and send output to sensory and motor systems (Rogers et al., 2004). More specifically, the temporal pole has connections with the PFC, and all three temporal gyri which receive input from the ventral visual processing stream, the somatosensory, visual and auditory processing streams; and areas in speech perception (Rogers et al., 2004). Thus the semantic representation of a particular object or thing (e.g. canary) will have different perceptual units (e.g. is yellow, has wings), as well as functional properties (e.g. can fly, can sing) and encyclopaedic properties (e.g. descended from birds in the Canary Islands), and this information must be tied together to form the whole concept (McClelland and Rogers, 2003; Rogers et al., 2006). Since the ATLs are the predominantly affected region in SD, this area was proposed to be the most likely candidate for this 'hub'. Further, Rogers et al. argued that increasing damage to this area should lead to a gradual decline in semantic memory, across various verbal and non-verbal domains. This is a characteristic of SD where concepts appear to "gradually dissolve" rather than disappearing abruptly (Lambon Ralph and Patterson, 2008; Patterson and Hodges, 2000) so that higher order concepts and subordinate categories appear to be affected before lower order concepts and superordinate categories. This theory is akin to Damasio et al. (2004) 'convergence zone' model of semantic memory which proposed that certain regions in the brain act as a converging zone to bind sensory and motor output. They also believed that the temporal lobe played a critical role in semantic memory.

The broad definition of 'semantic' processing is problematic for the semantic theory about the ATL because it is difficult, if not paradoxical, to give positive attributes to any processing that is not conceptual to some degree. In practice therefore, theories that suggest that the ATL supports more specific modes of processing such as social or unique entities are

differentiated on a predominance of this target processing whilst accepting that this specific processing is also ‘semantic’. Semantic theorists, inversely, have had to demonstrate that the ATLs process semantics at a broader level and behave as an amodal system. There is a logical problem for this theory in that there appears to be an infinite regress; it would appear that any information sent to the semantic hub would already be semantic and compound in nature otherwise they would have to be fundamental particles of meaning. For example, ‘is yellow’ or ‘can fly’ are semantic concepts in themselves. In this case, why would ‘canary’ be processed in the ATL, but not ‘can fly’? If it is granted that compound semantic units are received by the ATL then where were these simple units ‘put together’ and why should such areas not be considered separate semantic hubs? Nevertheless, the evidence for semantic processing from SD patients is strong as semantic deficits following focal damage to the ATL challenges the assumption that semantic memory is based on a widely distributed system of semantic representations.

Apart from the neuropsychological evidence the semantic ‘hub’ theory suggests that functional neuroimaging should show significant activations of the ATLs in healthy subjects during semantic tasks for all different modalities (e.g. words, pictures, faces, objects, sounds, smells). This has been confirmed in some cases described in the following section. Although studies using social and unique stimuli/measures could still, in many instances, also fall under general semantic processing, for the purpose of this review but these will be only included under the social account. The studies included under evidence for semantic cognition focused on ‘semantic memory’, ‘conceptual knowledge’, ‘language processing’ and ‘comprehension’.

3.1.1. Empirical evidence for the ATLs in semantic cognition

There is adequate but not substantial evidence showing ATL activation in healthy people during semantic tasks in functional neuroimaging studies. Other common areas of activation include the fusiform gyrus, MTG, STG, PFC and inferior frontal gyrus (IFG). The majority of the positive studies have utilised PET techniques, and have used lexical tasks involving naming, reading sentences, categorising, or semantic decisions.

PET studies have shown significant LATL activation in lexical decision tasks (Mummery et al., 1999); semantic categorisation tasks using pictures and words (e.g. is — ‘taxi’, ‘boat’, ‘bicycle’ followed by ‘AEROPLANE’ or ‘SPOON?’) (Bright et al., 2004); naming objects learnt early in life (Ellis et al., 2006); and making semantic decisions about words, (e.g. ‘does this word relate to religion?’) (Noppeney and Price, 2002a, 2002b; Price et al., 1997). Bilateral activations have been found when categorising specific level concepts (e.g. robin) over more general concepts (e.g. bird/animal) (Rogers et al., 2006); in tasks using living stimuli relative to man-made items (Devlin et al., 2002); and making semantic encyclopaedic knowledge decisions about objects (i.e. does this item exist in the modern world?) (Kellenbach et al., 2005). There is some evidence for significant RATL activation over left in semantic tasks however this has only been found when comparing abstract words to concrete ones (Kiehl et al., 1999; Perani et al., 1999).

As mentioned, there have been more studies using PET as compared to fMRI showing positive results for ATL activation in semantic processing. In comparison, the majority of functional magnetic resonance imaging (fMRI) studies have failed to report consistent activation in the ATLs during semantic tasks (Visser et al., 2010b). Activations were more commonly seen in the prefrontal and temporo-parietal areas. A recent meta-analysis by Visser et al. (2010b) attributed this lack of fMRI evidence to technical issues including imaging modality. fMRI may have more inherent distortions as compared to PET, as the ability of fMRI to detect activation is not constant across the brain (Devlin et al., 2000). The ATL is located near air–bone interfaces that cause inhomogeneities in the magnetic field which can lead to image distortion and signal loss. Other technical issues reported were field of view (FOV) problems as the ATL is one of the most inferior parts of the brain and therefore excluded from image acquisition in studies using a restricted FOV (Visser et al., 2010b). The choice of semantic task may also affect imaging results. For example, Rogers et al. (2006) found that the ATL is more active for specific level concepts rather than basic concepts. Finally use of a control tasks may influence the effect, as ATL activation may be concealed when a ‘rest’ or baseline level is used. It can be argued that even daydreaming requires some use of conceptual processing (Visser et al., 2010a, 2010b).

Visser et al. (2010a) attempted to address these technical issues by using a novel distortion-corrected fMRI. Their results showed that the bilateral inferior ATL including the fusiform gyrus and inferior temporal gyrus was active in healthy participants when they completed semantic categorisation tasks similar to the word task used by Bright et al. (2004). RATL activation was somewhat weaker than the left perhaps reflecting the language processing of the particular task. Another study using distortion-corrected fMRI and a semantic judgement task where participants had to judge the most related word to a target also found activation in inferior LATL regions including the fusiform gyrus, anterior ITG and anterior MTG (Binney et al., 2010). These studies suggested that there may be a functional division within the ATL where more inferior aspects are involved in semantic memory. They also account for why many fMRI studies fail to show ATL activations, as the inferior parts of the temporal lobe are more susceptible to distortions.

There are some other fMRI studies that have also supported the role of the ATL in semantic cognition; however, more of these studies have focused on sentence comprehension. For example, significant LATL activation was found when listening to sentences (Friederici et al., 2000; Humphries et al., 2005, 2006). Further, reading sentences was found to activate the LATL more than reading word lists (Stowe et al., 1999) which could account for why many fMRI studies using more simple lexical tasks do not report ATL activation. Some researchers challenged the semantic theory of the ATL reporting that it was more important for the syntactic structure of sentences rather than the semantic content (Brennan et al., 2010; Friederici et al., 2000; Humphries et al., 2006). Syntax processing involves analysing relationships between words based on information such as lexical category and word order.

However, SD patients do not show deficits in the syntactical structure of sentences, and usually have well articulated and syntactically correct sentences but anomie speech (Hodges and Patterson, 1996)

There are a small number of fMRI studies reporting ATL activation for more simple semantic tasks. For instance Diaz and McCarthy (2009) found the LATL to be active for ‘content’ words that contain semantic information, compared to ‘function’ words which do not (e.g. ‘above’, ‘onto’). Significant ATL activation has also been found when making ‘conceptual combinations’ — the process by which complex concepts are constructed from simpler ones. For example forming the compound concept ‘young man’ from ‘young’ and ‘man’, or ‘boy’ from ‘male’ and ‘child’ (Baron and Osherson, 2011; Baron et al., 2010). Baron and colleagues used face stimuli for these compound and simple concepts, and found the LATL to be activated for this overlap onto conceptual combinations to be more significant than any other neural region.

Functional imaging studies investigating semantic cognition, have shown a mix of bilateral, left and right activation of ATLs, however a larger proportion have shown more significant LATL activation for semantic tasks (see Table 1). This corresponds to the neuropsychological evidence that suggests those with predominant LATL atrophy show more semantic deficits particularly in word finding and comprehension

(Thompson et al., 2003). Although, the semantic hub theory proposes that the ATL is involved in amodal semantic processing, the majority of imaging studies have used lexical or sentence tasks. This may also reflect the left hemispheric bias as these types of tasks have a heavy language processing component.

The semantic hub theory also contends that the ATL processes information from all modalities. However, some studies have found significant activation of the ATL for certain stimuli and modalities over others. In Visser et al. (2010a, 2010b) meta-analysis, they found that there was a significant effect for the likelihood of ATL activation for auditory over visual modalities, and auditory sentences compared to pictures, written sentences and written words. Auditory sentences have been contended to elicit the ATL more than other stimuli as sentences contain more combinations of meaning (Hickok and Poeppel, 2004). The imaging studies reporting ATL activation in semantic processing also appear to be higher for tasks requiring more specific recognition or classifications of stimuli such as higher level concepts (Rogers et al., 2006) and abstract words (Kiehl et al., 1999; Perani et al., 1999). It has been suggested that this may be because a specificity gradient exists within the temporal lobe with specificity increasing along the posterior to anterior axis (Martin and Chao, 2001). Alternatively, Patterson et al. (2007) suggest that the ATL regions encode similarity relations among different concepts

Table 1 – List of ATL or TP activations, stimuli for semantic tasks from functional imaging studies.

Authors	Bilateral	Left	Right	Stimuli	Function of ATL
Devlin et al. (2002)	✓			Words depicting living things	Living things/non domain-general semantic
Humphries et al. (2001)	✓			Listened to sentences describing an event	Sentences/semantic
Kellenbach et al. (2005)	✓			Associative-encyclopaedic knowledge about objects	Domain-general semantic
Kiehl et al. (1999)	✓		✓	Bilateral — abstract and concrete words Right — abstract words	Domain-general semantic
Rogers et al. (2006)	✓			Identifying specific level concepts	Domain-general semantic
Visser et al. (2010a, 2010b)	✓			Inferior ATL for semantic categorisation of words	Domain-general semantic
Baron and Osherson (2011)		✓		Faces denoting conceptual combinations	Social or semantic
Baron et al. (2010)		✓		Faces denoting conceptual combinations	Social or semantic
Brennan et al. (2010)		✓		Syntactic structure of sentences	Syntax
Bright et al. (2004)		✓		Semantic categorisation task for words and pictures	Domain-general semantic
De Zubicaray et al. (2010)		✓		Pyramids and Palm trees, naming task, sentence-picture matching, category fluency	Domain-general semantic
Diaz and McCarthy (2009)		✓		Inferior LATL for content words with semantic information	Domain-general semantic
Ellis et al. (2006)		✓		Naming objects learnt early in life	Non domain-general semantic
Friederici et al. (2000)		✓		Syntactic structure of sentences	Syntax
Humphries et al. (2005)		✓		Listened to sentences	Sentences/Semantic
Humphries et al. (2006)		✓		Listened to normal sentences; semantically incongruent sentences;	Syntax
Mummery et al. (1999)		✓		Semantic priming	Domain-general semantic
Noppeney and Price (2002a, 2002b)		✓		Making semantic decisions about auditory or visually presented words	Domain-general semantic
Price et al. (1997)		✓		Made semantic decisions about words	Domain-general semantic
Stowe et al. (1999)		✓		Visual sentences	Domain-general semantic
Ferstl et al. (2007)			✓	Sentence comprehension	Sentences
Perani et al. (1999)			✓	Abstract words	Non domain-general semantic

Table 2 – List of all non-invasive brain stimulation studies on the ATL.

	Bilateral	Left	Right	Stimuli	Function of ATL
Ross et al. (2010)			✓	Name recall	Person specific/social-emotional
Gallate et al. (2011)	✓			Racial IAT	Person specific/social-emotional
Wong et al. (2012)	✓			Gender IAT	Person specific/social-emotional
Wong and Gallate (2011)			✓	Social and animal concepts	Domain general semantic
Pobric et al. (2007)			✓	Naming task from Snodgrass and Vanderwart set; semantic synonym judgement task	Domain general semantic
Pobric et al. (2009)			✓	Synonym judgement task	Domain general semantic
Pobric et al. (2010)	✓			Pyramids and Palmtrees test — word and picture versions.	Domain general semantic
Lambon Ralph et al. (2009)	✓			Synonym judgement task	Domain general semantic
Ishibashi et al. (2011)			✓	Function matching of tools	Domain general semantic
Holland and Lambon Ralph, 2011			✓	Generating past tense of irregular verbs	Domain general semantic
Snyder et al. (2006)			✓	Estimate number of discrete elements on screen	Conceptual knowledge
Gallate et al. (2009)			✓	Roediger and McDermott's (DRM) paradigm task	Conceptual knowledge
Boggio et al. (2009)			✓	Roediger and McDermott's (DRM) paradigm task	Conceptual knowledge
Chi et al. (2010)			✓	Visual memory paradigm	Conceptual knowledge
Chi and Snyder (2011)			✓	Matchstick arithmetic insight/problem-solving task	Conceptual knowledge

so that semantically related items (e.g. different types of fruit) are coded with similar patterns in the ATL. Therefore when presented with a specific instance of a semantic category (e.g. banana), the ATL is recruited to distinguish the conceptual similarities and differences within all modalities to exactly name it. However, to name the same item 'fruit' does not require a specific representation of banana, only something that is 'fruit-like'. This interpretation can also account for why patients with ATL atrophy are more impaired with retrieval of specific instances or higher level concepts than more general ones.

Only in the last 5–6 years have researchers begun to explore the ATLs using non-invasive brain stimulation studies. The evidence for the role of the ATL in semantic cognition is supported by repetitive transcranial magnetic stimulation (rTMS) studies which have shown that inhibiting either the left or right ATL in normal participants leads to increased RTs in naming pictures and semantic judgement tasks. A series of studies by Pobric et al. (2007, 2009, 2010) and Lambon Ralph et al. (2009) showed that inhibiting either left or right ATL leads to a similar pattern of performance in semantic tasks to that of semantic dementia, including a slowing of naming pictures, and semantic synonym or picture judgement tasks. The impairments in performance were also higher for more abstract concepts with low imageability, as well as higher order concepts (e.g. robin) compared to more basic ones (e.g. bird). All types of concepts (living and non-living) were affected, therefore the authors concluded that the ATL processed category or domain-general semantic information. The rTMS findings were recently confirmed by a study that found the site of stimulation corresponding more to the lateral anterior MTG, which also correlates with the site of atrophy in SD and neuroimaging activations in healthy participants (Binney et al., 2010).

This group of researchers have also found that inhibiting the ATL leads to longer responses for 'function' judgements about tools (e.g. scissors and guillotines have the same function) (Ishibashi et al., 2011). This was compared to a left

inferior parietal lobe rTMS condition which led to longer responses for 'manipulation' judgements about tools (e.g. scissors and staplers are manipulated in the same way). Inhibition of the LATL has also been shown to slow reaction times for generating past tenses of irregular verbs (Holland and Lambon Ralph, 2011) indicating that the LATL is crucial for semantic aspects of language. The authors concluded that semantic cognition is supported by a three-part semantic network comprising of the left PFC, the temperoparietal junction and ATLs. Further, the rTMS studies were able to show a causal influence of the ATLs on semantic cognition.

Snyder et al., 2006 used rTMS to inhibit the LATL in an attempt to show improvements in tasks. The authors showed that participants improved on a numerosity task after inhibition of the LATL where they had to estimate the number of discrete items post-stimulation. This was attributed to inhibiting 'conceptual' thinking leading to a more literal processing style enabling participants to see the items as discrete and disconnected, and interfering with the 'normal' tendency to group elements into meaningful patterns. This enhancement of 'literal' processing was also shown in following studies which found inhibition of the LATL reduced false memories in a Roediger & McDermott paradigm (DRM; Roediger and McDermott, 1995) where typically people make false recall errors due to semantic associations between the target words (Gallate et al., 2009). Correspondingly, there is some research on semantic dementia patients that has found they have reduced false recognition of semantically associated words due to reduction in 'gist' memory (Simons et al., 2005). Boggio et al. (2009) also used the DRM paradigm but used transcranial direct current stimulation (tDCS) to the ATL instead of rTMS. tDCS is another form of non-invasive brain stimulation that uses constant low electrical current through an anodal and cathodal electrode. This current flow can either increase or decrease neuronal excitability as the current flows from the anodal to the cathodal electrode forming a circuit (Fregni and Pascual-Leone, 2007). Boggio et al. (2009) found that anodal (excitatory) stimulation of the LATL together with cathodal (inhibitory) stimulation of the RATL (L+R-) as

Table 3 – List of ATL or TP activations, stimuli for social and unique entity tasks from functional imaging studies.

Authors	Bilateral	Left	Right	Stimuli	Function of ATL
Aalto et al. (2002)	✓			Emotional movies	Social-emotional
Assaf et al. (2009)	✓			Playing online games with human vs. computer	ToM
Burnett and Blakemore (2009)	✓			Reading social scenarios of embarrassment/guilt	Social-emotional
Den Ouden et al. (2005)	✓			Answering questions about intentions (ToM)	ToM
Dougherty et al. (1999)	✓			Anger induction from person events	Social-emotional
Eugene et al. (2003)	✓			Sad movies	Social-emotional
Grezes et al. (2007)	✓			Videos of a fearful body reaction	Social-emotional
Heekeren et al., 2003	✓			Making moral decisions about sentences	Moral/social-emotional
Heekeren et al. (2005)	✓			Making moral decisions about sentences	Moral/social-emotional
Hooker et al. (2008)	✓			Predicting emotion from characters with false beliefs in social scenes (ToM)	ToM
Kampe et al.	✓			Perceiving intention to communicate (ToM)	ToM
Levesque et al. (2003)	✓			Sad movies	Social-emotional
Ma et al.	✓			Inferring people's traits from descriptions (ToM)	ToM
Moriguchi et al. (2006)	✓			Hieder and Simmel task (ToM)	ToM
Pichon et al. (2008)	✓			Watching videos of dynamic angry body reactions	Social-emotional
Pichon et al. (2009)	✓		✓	Watching videos of fearful body reactions	Social-emotional
Reiman et al. (1997)	✓			Watching happy, sad and disgusting movies	Social-emotional
Ross and Olson (2009)	✓	✓		Bilateral — Hieder and Simmel task (ToM)	Social-emotional/ToM
				Left — semantic judgements about social concepts	
Sergent et al. (1992)	✓			Famous and familiar faces	Unique entities
Shin et al. (2000)	✓			Guilt induction from personal events	Social-emotional
Spreng and Mar (2012)	✓			Remembering events from personal past and mentalizing	ToM
Spunt et al. (2011)	✓			Inferring mental state of actor (ToM)	ToM
Sugiura et al. (2001)	✓			Famous and familiar faces	Unique entities
Sugiura et al. (2006)	✓			Famous and familiar names	Unique entities
Tsukiura et al. (2003)	✓	✓		Bilateral — immediate recognition of face-name associations	Person-specific knowledge/ social-emotional
				Left — delayed recognition of face-name associations	
Tsukiura et al. (2008)	✓		✓	Bilateral — retrieving job titles from names and faces	Person-specific knowledge/ social-emotional
				Right — retrieving job titles from faces	Social-emotional
Vollm et al. (2006)	✓			Reading ToM and empathy comic strips	ToM
Zahn et al. (2007)	✓		✓	Bilateral — semantic judgements about social concepts	Social-emotional
				Right — superior RATL correlated with descriptiveness	
Brunet et al. (2000)		✓		Attribute intentions picture comic strips (ToM)	ToM
Calarge et al. (2003)		✓		Attributing mental states to imagined others (ToM)	ToM
Crosson et al. (1999)		✓		Generating words with emotional connotations	Social-emotional
Ferstl et al. (2007)		✓		Reading emotional stories	Social-emotional
Gorno-Tempini and Price (2001)		✓	✓	Left — famous faces and building recognition	ToM
				Right — famous faces	
Grabowski et al. (2001)		✓	✓	Left — famous faces and building recognition	ToM
				Right — famous faces	
Iwase et al. (2002)		✓		Amusing movies	Social-emotional
Kimbrell et al. (1999)		✓		Anxiety and anger induction from personal events	Social-emotional
Moll et al. (2002)		✓		Reading moral and unpleasant nonmoral sentences	Moral/social-emotional
Pelletier et al. (2003)		✓		Happy and sadness induction from personal events	Social-emotional
Ruby and Decety (2003, 2004)		✓		Taking third person perspective (ToM)	ToM
Schaich Borg et al. (2006)		✓		Reading moral sentences	Moral/social-emotional
Sugiura et al. (2005)		✓		Personally familiar faces	Unique entities
Tsukiura et al. (2006)		✓	✓	Left — retrieving names from faces	Person-specific knowledge/ social-emotional
				Right — retrieving faces from names	social-emotional
Tsukiura et al. (2011)		✓		Encoding names with faces	Person-specific knowledge/ social-emotional
Blair et al. (1999)			✓	Sad faces	Social-emotional
Dolan et al. (2000)			✓	Memory retrieval for emotional pictures	Social-emotional
Erk et al. (2005)			✓	Encoding words after inducing negative mood from personal events	Social-emotional
Finger et al. (2006)			✓	Reading moral statements	Moral/social-emotional
Green et al. (2010)			✓	Reading statements regarding guilty actions	Moral/social-emotional
Leveroni et al. (2000)			✓	Famous faces	Unique entities
Liotti et al. (2000)			✓	Anxiety induction from personal events	Social-emotional
Mataix-Cols et al. (2008)			✓	Disgusting pictures	Social-emotional
Moll et al. (2001)			✓	Making moral judgements from sentences	Moral/social-emotional
Ohira et al. (2006)			✓	Attending to emotional pictures	Social-emotional

Table 3 (continued)

Authors	Bilateral	Left	Right	Stimuli	Function of ATL
Ranote et al. (2004)			✓	Viewing videos of own infant	Social-emotional
Spiers and Maguire (2006)			✓	Spontaneous mentalising whilst playing virtual game (ToM)	ToM
Straube et al. (2010)			✓	Watching videos of actors facing the participants and information contained person related content (ToM)	ToM
Wakusawa et al. (2007)			✓	Watched series of pictures between 2 actors with ironic messages (ToM)	ToM
Zahn et al., 2009			✓	Superior RATL for descriptiveness of moral-social concepts	Moral/social-emotional

well as just left excitatory stimulation (L+) alone, also led to a reduction of false memories. Chi et al (Chi and Snyder, 2011; Chi et al., 2010) found that cathodal stimulation of the LATL together with anodal stimulation of the RATL (L–R+) led to improvements in a visual memory task where participants had to correctly remember a series of shapes, and on an ‘insight’ problem solving task. Table 2 lists all the non-invasive brain stimulation studies that investigate the ATL, and which function of the ATL they support.

In summary there is considerable empirical support and widespread agreement for a role of the ATL in semantic cognition. However, imaging evidence particularly using fMRI has been inconsistent, which is likely to be due to technical limitations (Visser et al., 2010a, 2010b). Further, the empirical evidence has not yet shown that the ATL is *amodal* or domain-general, processing semantic information from all different modalities. Some studies have found that the ATL is more active for certain types of information such as living things (Devlin et al., 2002) and abstract words (Kiehl et al., 1999; Perani et al., 1999) which challenges the theory that the ATL is a semantic hub for domain general or all types of semantic knowledge. The distinct behavioural patterns of left versus right temporal FTD and lesion patients led other researchers to consider that there may be domain-specific functions of the ATLs, particularly in relation to social-emotional cognition.

3.2. Social cognition

A second body of evidence about the function of the ATL implicates a putative role in social-emotional cognition (Olson et al., 2007; Zahn et al., 2007) or more specifically in representing knowledge relating to people (Giovanello et al., 2003; Gorno-Tempini et al., 2001; Leveroni et al., 2000). Profound social alterations appear to occur after lesions to the temporal lobes, frontal cortex and/or the amygdala, thus it is widely agreed upon that these areas are connected in a network often referred to as the ‘social brain’ (Brothers, 1990; C.D. Frith, 2007). The amygdala and frontal regions have been the most explored neuroanatomical regions in social and emotional processing, however less attention has been paid to the temporal cortex (Olson et al., 2007). The ATLs have dense connections with a number of ‘social’ regions including limbic structures such as the amygdala and hippocampus, the PFC, and fusiform gyrus (Kubicki et al., 2002; Simmons et al., 2010; Squire and Zola-Morgan, 1991; Wilson et al., 1990). Research using diffusion tensor imaging (DTI) has been able to map

white matter trajectories connecting multiple regions in the brain (Le Bihan et al., 2001). Using DTI, white matter tracts have been found between the ATL and the frontal lobe via the uncinate fasciculate (Kubicki et al., 2002); and also the occipital lobe, which when disrupted are thought to lead to visually specific semantic/emotional memory deficits such as prosopagnosia (Catani et al., 2003). Indeed, there are many studies reporting that ATL damage leads to prosopagnosia (Evans et al., 1995; Gainotti et al., 2003; Josephs et al., 2008; Kazui et al., 1995).

Gibbs (1997) investigated TLE patients with ATL spike focus and proposed that the ATLs are crucial to the pathophysiology of psychiatric disorders and may be a higher level integration centre. They theorise that bizarre and psychopathic behaviour could result from a manifestation of judgement defects because the brain would not be able to integrate information coming from different sensory modalities. This is similar to the convergence or hub theory for semantic cognition. However, not all patients with ATL damage show social changes (Edwards-Lee et al., 1997) therefore this area of research requires further investigation.

3.2.1. Empirical evidence for the ATLs in social cognition

In contrast to semantic tasks, PET and fMRI studies have shown consistent ATL and temporal pole activation in tasks with social or socially relevant content such as theory of mind tasks (Gallagher and Frith, 2003), viewing familiar and famous faces (Brambati et al., 2010), and making moral judgements (Zahn et al., 2009; see Olson et al., 2007 for review). ATL activation occurs along with other socio-emotional related regions including the PFC, temporoparietal junction, amygdala and hippocampus.

Bilateral ATL activation was reported when watching emotional films (Eugene et al., 2003; Levesque et al., 2003; Reiman, 1997); recalling guilty experiences (Shin et al., 2000); and inducing anger from personal narrative scripts (Dougherty et al., 1999). Significantly stronger RATL activation has been found for viewing sad faces (Blair et al., 1999); inducing anxiety (but not sadness) from personal events (Liotti et al., 2000); during memory retrieval for emotional pictures (Dolan et al., 2000); attending to emotional pictures (Ohira et al., 2006) and when mothers watched videos of their own infants compared to unknown babies (Ranote et al., 2004). There are also a number of studies reporting stronger LATL activation including when watching funny films (Iwase et al., 2002); reading stories about with emotional content (Burnett and

Blakemore, 2009; Ferstl et al., 2007); inducing anxiety, anger (Kimbrell et al., 1999), sadness and happiness (Pelletier et al., 2003); and generating words with emotional connotations (Crosson et al., 1999).

No consistent evidence has emerged for any laterality or valency effects from the imaging studies of emotional processing (see Table 3). Some studies have found ATL activation to be activate independent of whether stimuli were pleasant or unpleasant (Lane et al., 1999; Maratos et al., 2001; Reiman et al., 1997) suggesting that this region is involved in some aspect of externally generated emotion independent of the particular emotion experienced or elicited (Reiman, 1997). However, this result has not always been found with some studies showing significant ATL activations for specific emotions over others.

The behavioural evidence from TLE and FTD patients showing increased violence, aggression and psychiatric symptoms relates to imaging studies showing that the ATLs are involved in moral cognition. de Oliveira-Souza et al. (2008) and Harenski et al. (2010) examined the neurobiology of psychopathy, which is characterised by a 'moral insensitivity'. For example, psychopaths show emotional callousness, lack of remorse, and antisocial behaviour. Using MRI scans and voxel-based morphometry, de Oliveira-Souza et al. reported that compared to normal matched controls, psychiatric patients scoring high on the psychopathy checklist (PCL) but living in the community, had reduced grey matter in the left ATL, bilateral frontal polar, orbitofrontal, superior temporal sulcus (STS) and insula. This was supported by Harenski et al.'s (2010) fMRI study which showed that incarcerated inmates who score high on the PCL showed reduced activity in the bilateral anterior temporal cortex and PFC when watching videos with unpleasant moral scenes compared to nonpsychopathic inmates.

Evidence from normal participants includes a series of fMRI studies by Moll et al. (2001, 2002). Participants had to make true/false judgements about statements containing moral content (e.g. every human being has the right to live) or factual content (e.g. stones are made of water). Moral statements produced increased activity in the RATL, left orbitofrontal cortex, bilateral frontal pole and STS. However, later when they compared moral vs. non-moral unpleasant statements (e.g. he licked the dirty toilet), then significant ATL activation was no longer observed. The authors then suggested that this was in agreement with the general semantic role of the ATL, or that it is involved in more general emotional processing. However, other evidence in normal populations have also found greater right temporal pole activity when reading moral transgression vignettes (e.g. theft or assault) compared to social transgressions (e.g. pratfalls or loss of bodily control) that evoked embarrassment or shame (Finger et al., 2006); and bilateral temporal pole activation when making ethical moral decisions, but not when participants had to judge if the same statements were semantically correct (Heekeren et al., 2003). These studies counter the view for a general semantic processing account, and suggest that the temporal pole may be specific in making complex decisions with moral content. Further they indicate that moral cognition may be distinct from general emotional

processing. These moral cognition studies often used tasks which required participants to judge actions of others and attribute intentions. This is a known aspect of theory of mind.

Moral cognition may be closely related to theory of mind (ToM) and accordingly a number of ToM studies have reported ATL and temporal pole activation, again with a mixture of left, right and bilateral involvement. ATL activation has been found when imagining or inferring another's mental state (Calarge et al., 2003; Spunt et al., 2011); taking a third person perspective (Ruby and Decety, 2003); the Heider and Simmel task (shapes moving like humans versus randomly) (Castelli et al., 2000); and the mind in the eyes test (Platek et al., 2004). Spreng and Mar (2012) found overlapping activation in the bilateral temporal pole when remembering events from personal past and inferring thoughts and feelings of other people. They interpreted this overlap as showing that autobiographical memories and mentalising depend on a single process, perhaps semantic memory. Both cognitive processes require conceptual knowledge related to actions, relationships and the self. Alternatively, these areas may be essential for transfer of information from experience to the formation of social conceptual information which in turn guides social behaviour. Unfortunately, a limitation seen in many imaging studies implicating the ATL in social cognition is that it is difficult to dissociate whether activation of the ATL is due to semantic or social processing.

Interestingly, due to the involvement of the ATLs in ToM and moral cognition, it may also have a role in social stereotypes. Stereotypes require person-related knowledge and associations about groups of people and their generalised attributes (Quadflieg et al., 2009). An fMRI study investigating sexist attitudes (Cikara et al., 2010) found that bilateral activation of the temporal pole, medial PFC and posterior cingulate was negatively correlated with higher scores of hostile sexism on an implicit association test in male participants. The authors suggested that since these areas are known to be involved in mental state attribution or theory of mind as well as knowledge about people, they may also be necessary when seeing another entity as a human being. Prejudice such as sexualisation may disrupt normal social processes in recognising another being as an agent with intentions, emotions, beliefs and desires of their own, a kind of 'dehumanisation' (Cikara et al., 2010). This is supported by neuropsychological evidence where patients with lesions to the ATL (predominantly right) showed increased implicit gender stereotypes on an implicit association test (Gozzi et al., 2009).

Zahn et al. (2007) originally showed with fMRI that the ATL was involved in social conceptual knowledge. The authors developed a semantic task where participants had to make judgements about the meaning relatedness of two words. The words either described social behaviour (e.g. honour-brave; tactless-impolite) or animal or biological function (e.g. nutritious-useful). They also examined whether brain activation would change with increasing descriptiveness and meaning relatedness between word pairs. The authors found that social concepts activated the bilateral superior ATL, temporo-parietal junction, orbitofrontal and frontal areas. However right superior ATL activation was strongly correlated with descriptiveness of

social behaviour compared with the other regions. The ATL was activated independent of emotional valence and indicated that the area was involved more with social conceptual detail. In a second study using patients with frontotemporal lobar degeneration (FTLD) and corticobasal syndrome, Zahn et al. (2009) measured neuronal glucose uptake whilst patients performed a similar social versus animal semantic judgement task to the one described previously. Both patients performed equally poorly on the animal function concepts however FTLD patients performed worse on social concepts. Further FTLD patients with superior ATL degeneration were significantly more impaired on social concepts and showed more inappropriate social behaviours such as disinhibition and emotional withdrawal. However, FTLD patients also had hypometabolism in the dorsolateral, medial frontal and orbitofrontal lobes therefore the contribution of damage to other areas to the social deficit could not be ruled out.

Ross and Olson (2009) attempted to replicate Zahn et al.'s (2007) imaging study using the social-animal concept task and also included a ToM task that is dependent on visual motion (the Heider and Simmel animation task), rather than language. They used both tasks to examine whether there would be overlapping ATL activation in the two tasks for lexical and visual tasks with social stimuli. In contrast to Zahn et al. (2007), Ross and Olson found that the lexical task produced stronger activation in the left ATL for social words. The Heider and Simmel task also showed activation in the bilateral ATL and STS but this was stronger in the right hemisphere. There was however, clear overlap of activation between the two tasks in the LATL. Therefore although there appeared to be ATL involvement in social processing, laterality effects were unclear.

In a series of studies, Tsukiura and colleagues investigated the role of the ATLs in person-specific knowledge, or the associations between faces, names and other person-related semantics. Using fMRI they showed that the bilateral superior ATL contributes to the retrieval of newly learned people's names from faces (Tsukiura et al., 2003). They reported that since the ATL has strong connections with the amygdala, the LATL may play a role in processing of emotional information from faces. Later Tsukiura et al. (2006) also found the ATLs to be active when encoding person-related semantics (such as job titles) with names and faces. Further functional sub-regions within the ATL were found where the dorsal (or superior) LATL showed greater activity for encoding of names with person-related semantics compared to just names or job titles alone, whereas the bilateral ventral (or inferior) ATL was more active for encoding faces with person-related semantics (Tsukiura et al., 2009). Table 3 below lists and summarises the studies supporting the function of the ATL in a number of social areas.

In contrast to these studies, there is also research demonstrating that the ATL is more active for *famous* or *familiar* names and faces compared to unfamiliar ones (Leveroni et al., 2000; Nakamura et al., 2000; Pourtois et al., 2005; Sergent et al., 1992; Sugiura et al., 2001, 2006). This is discussed in the following section on 'unique entities'.

A review of the temporal pole in socio-emotional processing (Olson et al., 2007) noted that a consistent problem with the neuroimaging literature is that although ATL activations

are often listed, authors tend to focus on activations in the frontal lobe and amygdala. This de-emphasis of the ATL consequently obscures the reader's ability to distinguish its function and more research focusing on the area and interpreting its activation is needed. This de-emphasis might account for why very few researchers have used non-invasive brain stimulation techniques to investigate the ATLs in social processing (see Table 2).

Ross et al. (2010) used tDCS to investigate name recall for famous people and landmarks. They found that anodal (excitatory) stimulation to the RATL but not LATL, led to improvements in naming famous people. No significant changes were found in naming famous landmarks. They concluded that the ATLs are critically involved in proper name recall and that the RATL may process person-specific semantic information. Further, a study investigating the ATL in stereotypes found that low frequency rTMS to the LATL and RATL decreased scores on a racial IAT (Gallate et al., 2011). This reduction was later replicated on a gender stereotype IAT (Wong et al., 2012), and further no changes were found on a control IAT which used living and non-living categories, indicating the ATLs may be more important for social information. Wong and Gallate (2011) utilised inhibitory rTMS in conjunction with the social versus animal concept task developed by Zahn et al. (2009), and found that reaction time decreased significantly for participants undergoing LATL stimulation. However, this decrease in reaction time was for both social and non-social concepts suggesting that the LATL was involved in all types of concepts. It was theorised that the change in the LATL group only may have been due to the strong language or lexical demands of the task. Further it suggested that low frequency inhibition facilitated performance in a semantic task possibly via dynamic inhibition or interhemispheric competition (Wong and Gallate, 2011). It is clear that more research is needed using non-invasive brain stimulation to identify if a distinct social function is to be attributed to the ATL. Nevertheless a social role of the ATL is strongly supported by the empirical evidence from neuropsychological and neuroimaging data. The literature suggests that a variety of socially related tasks using stimuli from verbal and non-verbal modalities are able to reliably activate the ATL.

In summary, there is strong evidence that the ATL is involved in social cognition. The ATL has been implicated in a number of roles within social cognition including emotion processing, moral cognition, person-specific knowledge, knowledge about social behaviour, stereotypes, and ToM. However the extent to which this can be dissociated from the general semantic hub theory is contentious. As stated previously social knowledge is by nature, also semantic, therefore more research is needed that directly compares the processing of social versus non-social knowledge in the ATL. This would assist in determining whether the ATL has a stronger signal for social information.

3.3. Unique entities

A third account of the role of the ATLs is that they are a store for 'unique entities'. ATL activity has also been associated with viewing famous or familiar faces, buildings and

landmarks compared to non-famous ones (Gainotti, 2007; Gorno-Tempini and Price, 2001; Grabowski et al., 2001). Patients with TLE lend support to the 'unique entities' theory about the ATL as deficits in famous face, animal and building naming and recognition are common (Drane et al., 2009; Glosser et al., 2003). The theory is perhaps an extension of what Ellis et al. (1989) originally termed a deficit of 'singular objects'. Unique entities may be items that are personally relevant, such as people or things that we are familiar with or have been seen in the past. There is some neuroimaging evidence showing support for the role of the ATL in unique entities described below. Again, these although these studies could also fall under a 'semantic' category, the studies supporting unique entities reviewed here only include those that show the ATL processes famous and/or familiar stimuli.

3.3.1. Empirical evidence for unique entities

There are a small number of neuroimaging studies reporting significant ATL activation specifically for famous or familiar stimuli (see Table 3). Gorno-Tempini and Price (2001) and Grabowski et al. (2001) found significant LATL activation when deciding if pairs of famous faces and buildings were the same/different compared to non-famous ones, and a small RATL effect for famous faces but not buildings. Sugiura et al. (2001, 2005) found significant LATL activation for recognising famous and personally familiar faces compared to the participants own face. Their studies suggest that the ATL may be necessary for face identity and recognition of others and is a distinct mechanism from self-recognition. Sugiura et al. (2005) proposed that this difference in activation may be due to the ATL representing names of people which is not necessary for the self. Leveroni et al. (2000) compared imaging results for recognition of famous faces, newly learned or scrambled face images. They found significant RATL activation for famous faces compared with a scrambled image, and bilateral activation in the general temporal lobe [BA 21, 39, 37] for famous faces versus newly learned faced.

A systematic review of famous person recognition disorders suggested that the LATL is more active when retrieving verbal information about people such as names, whilst the RATL may be greater for nonverbal information such as faces (Gainotti, 2007). However, there have also been a number of studies showing bilateral activation of the ATL for both verbal and non-verbal stimuli. For example, Sugiura et al. (2006) later compared famous versus familiar names, rather than faces, and found bilateral ATL activation for both types of names compared to unfamiliar names. The reason for significant activation for famous or familiar entities rather than unfamiliar ones might suggest a role of personal memory or experience in the ATL (Dolan et al., 2000). Alternatively, the ATL may be involved in identity or semantic repetition priming effect as famous/familiar things have been repeatedly presented compared to non-familiar things (Sugiura et al., 2001).

Simmons and Martin (2009) stated that there are reasons to be cautious about extending the famous face findings to a third theory rather than just attributing the result to the social/person knowledge theory. Several studies have shown that the ATL is more specific for faces or people compared to other famous objects such as buildings (Kriegeskorte et al., 2007; Ross et al., 2010; Simmons et al., 2010). Moreover, ATL

activation can occur without any reference to a unique or famous individual for example when inferring mental states or others, or even when watching shapes move with intention (Ross and Olson, 2009). Therefore, the unique entities theory could fit among the wider functions of social or semantic cognition in the ATL. However, the finding that some patients with ATL damage show specific deficits for famous/familiar compared to unfamiliar entities, whilst others show a more general semantic deficit suggests at least the logical possibility that there may be a specific sub-region of the ATL involved in unique entity processing. However, no studies looked at distinguishing sub-regions within the ATL that activated for unique stimuli.

4. Comparison of theories

In a brief review, Simmons and Martin's (2009) compared these accounts of the function of the ATL. They suggested that they have largely, been developed in parallel, and need to be united under a single theory. Further, there has been very little effort in the literature to directly test these accounts against each other. However, Zahn et al. (2007) argue that the 'social' function of the ATLs does fit into the wider semantic cognition theory as social knowledge also relies on semantic knowledge. The research clearly points to a role of the ATLs in social cognition, but its specific role is it not well understood and is difficult to discretely separate from more domain-general semantic processing. At present only three studies have directly attempted to compare social versus non-social semantic processing (Ross et al., 2010; Wong and Gallate, 2011; Wong et al., in press). All utilised non-invasive brain stimulation and administered tasks that contained social and non-social semantic information. Two studies found that the stimulation produced changes in social tasks only (Ross et al., 2010; Wong et al., in press), and one did not (Wong and Gallate, 2011). More empirical evidence is needed to establish whether social processing can be dissociated from general semantic processing. Future studies could directly compare specific categories to test whether the ATL processes in a category-specific or domain-general manner. To investigate if the ATL processes modality specific stimuli, future studies could also compare information across different sensory modalities such as face (visual), name (verbal) and voice (auditory) stimuli.

It could be that functional sub-regions exist within the ATL that preferentially code for social, non-social and unique stimuli. There is evidence suggesting that there may be hemispheric lateralisation between the ATLs were the LATL is responsible for domain-general semantic knowledge, whilst the right ATL may preferentially process the social nature of concepts (Simmons and Martin, 2009). Distinct profiles of left versus right temporal variant FTD support this notion as patients with predominant left damage tend to show more semantic deficits, whilst those with right atrophy show more abnormal changes in social behaviour (Edwards-Lee et al., 1997; Thompson et al., 2003).

Further, there is evidence that topographical sub-regions within the ATL may be responsible for specific functions. For example, based on evidence from functional imaging, Zahn

et al. (2007) propose that the superior region of the RATL may be more responsible for social conceptual detail, while recent evidence suggests that the inferior ATL regions are crucial for general semantic cognition (Binney et al., 2010; Visser et al., 2010a, 2010b). Other functional sub-regions within the ATL have been found by Tsukiura et al. (2009) who found that the left superior [dorsal] ATL showed greater activation for when encoding names and person-related semantic information, whilst the bilateral inferior [ventral] ATL showed more activity when encoding faces and person-related semantic information. These potential functional sub-regions are explored in the following section.

5. Functional sub-regions in the ATL

5.1. Laterality differences

Neuropsychological evidence has shown that patients undergoing right anterior temporal lobectomy display more psychiatric symptoms compared to left anterior temporal lobectomy patients (Glosser et al., 2000), and FTD patients with right temporal damage show more social behavioural changes and deficits in famous and familiar face processing (Edwards-Lee et al., 1997; Zahn et al., 2009). As well as not being able to recognise faces of famous/familiar people, many of the patients were also unable to identify people from their names or voices indicating a cross-modal person-based deficit. Although the majority of imaging tasks using face stimuli reported bilateral activation, there seemed to be a bias towards stronger activation in the RATL (Blair et al., 1999; Gorno-Tempini et al., 2001; Grabowski et al., 2001; Leveroni et al., 2000; Tsukiura et al., 2006). It has been proposed that the RATL may be more responsible for visual information and accordingly a number of studies reported stronger RATL activation for face and picture stimuli with emotional content (Dolan et al., 2000; Mataix-Cols et al., 2008; Ohira et al., 2006). However, as there was still a mixture of bilateral, right and left ATL activations, an explicit laterality effect for social or visual stimuli is not able to be concluded from the literature.

In comparison FTD patients with predominant LATL atrophy have shown more semantic deficits. Although the evidence is still inconsistent for a left versus right effect, more neuroimaging studies using semantic and sentence tasks reported stronger activation of the LATL (see Table 1). A number of studies have suggested that the LATL may be more necessary for the lexical information such as people's names, or linked to level of specificity of word retrieval rather than the conceptual class of the stimulus (Tranel, 1991). The LATL has been shown to be more actively engaged in tasks that include a strong verbal component, which is likely to be due to its closer proximity and more extensive connections to the left lateralized dominant language centres. This is supported by imaging studies showing significant LATL activation for retrieval of names (Tsukiura et al., 2006, 2011), reading sentences (Ferstl et al., 2007; Moll et al., 2002; Schaich Borg et al., 2006; Stowe et al., 1999) and naming/word tasks (Diaz and McCarthy, 2009; Ellis et al., 2006; Noppeney and Price, 2002b) over a range of different contexts. Bright et al. (2004) suggested that the LATL is necessary for word retrieval and processing

detailed aspects of object attributes. In other words, when fine-grained discrimination among similar objects is required, the ATL is engaged, but not when discriminating among semantically meaningless stimuli. In line with this, the LATL has been shown to be more active for abstract and content words, which require more detailed semantic information compared to function words (Diaz and McCarthy, 2009), and conceptual combinations of words which are more complex and need more discrimination than single words (Baron and Osherson, 2011). However, Visser et al. (2010a) later used the same semantic task as Bright et al. and found bilateral ATL activation using distortion corrected fMRI, particularly in the inferior ATL.

Some researchers have proposed that the LATL may play a significant role in representation of living and non-living concepts (Antonucci et al., 2008; Cappa et al., 1998; Strauss et al., 2000; Thompson et al., 2003), whereas the RATL is thought to be involved in person-specific knowledge (Ellis et al., 1989; Evans et al., 1995; Gainotti et al., 2003). However, person-related information has also been found in both the left and right ATL but for different modalities. Damage to the LATL has been associated with deficits in retrieving people's names, whereas the RATL damage is more related to difficulties recognising persons from visual information such as their faces (Gainotti, 2007; Gainotti et al., 2010). However, Gainotti et al. (2010) explain that this does not mean we know different things about a particular person when we see their face compared to when we hear their name. Our knowledge may be represented asymmetrically on the two sides of the brain but they are continuously integrated through callosal connections. Patients with lesions in the right versus left ATL will produce differing patterns as they disrupt two different potential paths to person-specific information.

Differences in these pathways between the left and right ATL may potentially be less detected by imaging or non-invasive brain stimulation techniques. Specific processing of 'person-related' information may be masked by the general semantic demands of a task, leading to activation of the bilateral ATL. In the case of brain stimulation studies, rTMS to one hemisphere may cause interhemispheric compensation where the uninhibited hemisphere compensates for the usual function of the inhibited area. Therefore although the current review is not able to make any definitive conclusions about hemispheric laterality from the neuroimaging and brain stimulation data, it does not rule out the hypothesis that the ATL may be lateralised in function.

It is apparent that there are still no clear-cut laterality differences and further research is needed to make this distinction. Non-invasive brain stimulation studies have generally found similar effects for LATL and RATL stimulation in semantic tasks (e.g. Lambon Ralph et al., 2009, 2010), however few studies that have attempted to separate social vs. non-social functions have found differing left versus right effects (Ross et al., 2010; Wong and Gallate, 2011).

5.2. Topographical differences

There is some evidence for topographical sub-regions within the ATL that may be responsible for specific functions or processing from different sensory modalities. The distinction

between superior and inferior parts of the ATL appears to show a trend where the superior ATL may process lexical items and the inferior aspects processes non-lexical visual information. This corresponds to the connectivity of the ATL where the inferior or ventral regions are connected to the ventral visual processing stream where the fusiform gyrus is located (McCarthy et al., 1997), whilst the middle and superior temporal gyrus have more connections with auditory and speech processing areas. Examples from the imaging evidence include Zahn et al.'s (2007) finding that the superior region of the RATL is more active for words with higher social conceptual detail. Tsukiura et al. (2009) found that the left dorsal (superior) ATL showed greater activation when encoding names and person-related semantic information, whilst the bilateral ventral ATL showed more activity when encoding faces and person-related semantic information.

Studies using auditory sentences have also tended to find more superior ATL activation (e.g. Friederici et al., 2000; Humphries et al., 2001, 2005, 2006), Visser et al. (2010b) meta-analysis found the majority of imaging studies reporting ATL effects used auditory sentences rather than other stimuli such as pictures, written sentences and words. Anatomically the superior ATL is closely located to the two important language centres, Broca's and Wernicke's areas. The STG has been shown to have dense connectivity with these two areas and therefore it is not surprising that the superior ATL is more active for tasks requiring more complex language such as sentence comprehension and syntactic information. It has been proposed that auditory sentence comprehension may activate the ATL as it is specialised for computation of combinatorial meaning, or that comprehension of sentences requires more fine-grained semantic distinctions (Hickok and Poeppel, 2004). Alternatively, it could be due to the fact that auditory information is processed in superior aspects of the ATL which are less susceptible to image distortion and signal loss than the inferior ATL (Visser et al., 2010a, 2010b).

However, recent evidence using distortion corrected fMRI report that the inferior anterior temporal lobe region is crucial for semantic cognition from all modalities, including lexical, picture, auditory words and environmental sound stimuli (Binney et al., 2010; Visser et al., 2010a). This contradicts the argument that the superior region is more specific for lexical stimuli. However, it is possible that there is a semantic gradient down the ATL where the superior region processes more abstract concepts that require detailed semantic distinctions whilst the inferior regions process more basic level concepts. This accounts for why words with higher conceptual detail activated the superior ATL (Zahn et al., 2007) and why sentences which require higher levels of semantic distinction than words alone have also been shown to activate superior regions of the ATL. In contrast, tasks that activated the inferior regions of the ATL have more often been semantic tasks relating to single words or pictures (e.g. Visser and Lambon Ralph, 2011; Visser et al., 2010a, 2010b).

There is also evidence that the medial section of the temporal lobe or the MTG supports domain-general semantic processing. Zahn et al. (2007) found that the MTG was active for all types of concepts, perhaps accounting for why no difference was found between social and animal concepts in Wong and

Gallate's (2011) rTMS study. Further, Simmons et al. (2010) found significant activation of the left MTG across a number of semantic domains including facts about people, hammers and buildings. This area may be of particular interest in future studies for domain-general conceptual processing, and may possibly be a more specific site for the domain-general semantic deficits seen in SD, rather than the more anterior aspects of the temporal lobe. Accordingly, many semantic neuroimaging studies have reported significant activation in the left or bilateral MTG (e.g. Diaz and McCarthy, 2009; Kellenbach et al., 2005; Kiehl et al., 1999). Using a combination of the data from rTMS, semantic dementia and distortion corrected fMRI, this contention has been supported (Binney et al., 2010). The anterior MTG was the site of most overlap for semantic processing when combining all data.

Few studies have investigated the topographical subdivision of the ATL and how damage to superior or inferior regions may be specifically related to different neuropsychological and behavioural characteristics. It seems likely that patients with deficits in recognising people or objects may have more damage to inferior regions of the ATL, whereas those with superior ATL damage may have more difficulties with auditory stimuli and word-finding. Additionally Simmons et al. (2010) suggested that the topographical pattern in the ATL could reflect an animate versus inanimate gradient. They proposed that the superior ATL may be more responsive to human-animate attributes which can account for why Zahn et al. (2007) found significant activation in the superior aspects of the ATL for social concepts. Therefore it is possible that patients with superior ATL damage may show more difficulties with complex person and emotional knowledge such as theory of mind and moral cognition, resulting in aberrant social behaviour. However, usually atrophy in semantic dementia covers large regions of the ATL therefore it is not clear which deficit each sub-region contributes too. A recent fMRI study found that the bilateral ventral ATL responded to semantic decision tasks presented auditorily or visually, whereas the superior LATL responded only to auditory stimuli (Visser and Lambon Ralph, 2011). Unfortunately for rTMS and tDCS studies, the techniques are not yet focal enough to target specific superior and inferior regions of the ATL. Further research is necessary to elucidate the topographical regions of the ATL. However, below is a diagram combining the evidence from all the literature of the potential sub-divisions of the ATL (Fig. 2).

6. Can general semantic processing account for all of the empirical evidence?

The dominant views about the ATL are that they process 1) domain-general or nonspecific semantic memory; 2) social information; and 3) 'unique' stimuli such as famous/familiar people or landmarks. Although there is separate evidence for each of these accounts, very few studies have explicitly attempted to test them against each other (Simmons and Martin, 2009). In light of this review, there is not irrefutable support for any one account; however, significant activations or changes after brain stimulation could all fall under a general semantic processing account.

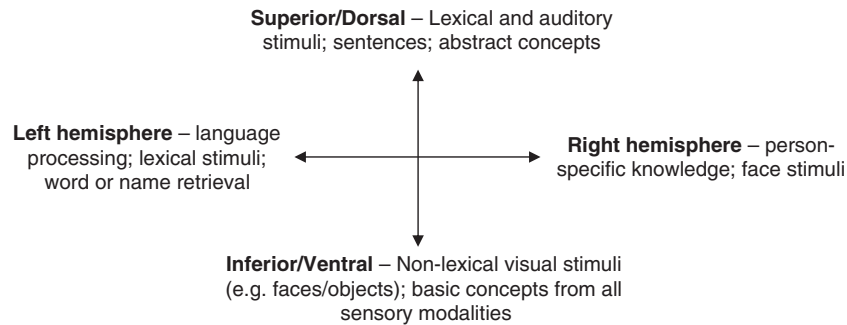


Fig. 2 – Schematic diagram of the potential sub-regions of the ATL.

Supporting the social account, some researchers have proposed that the ATL is crucial for knowledge about people. Person-specific impairments in recognition, identification and accessing information about people have been seen in patients with both predominant left and right ATL damage (Gainotti et al., 2010; Giovanello et al., 2003; Joubert et al., 2006). The ATL, particularly in the right hemisphere, has been suggested as a ‘person identity node’ which is a gateway to semantic information about people such as their occupation, nationality and other uniquely identifying information (Gainotti et al., 2010; Haslam et al., 2004; Tsukiura et al., 2009). Nevertheless, person knowledge can still fall under a general semantic processing account. None of the studies reporting the ATL to be involved in person-specific knowledge attempt to explain why the ATL may process information about people over other things. It could be that information about people has greater signal strength because it is important and necessary for survival. Recognising an individual person also requires the ability to make fine-grained distinctions, for example, dissociating their perceptual features and distinguishing characteristics such as their name and job. This may result in greater activation of the ATL. Until improved control tasks are developed to dissociate social vs. non-social knowledge, it is difficult to make any definitive conclusions.

The unique entities account proposes that the ATL should process famous or familiar people/objects over unfamiliar ones. However, significant changes in tasks were found with stimuli not related to famous or familiar things (e.g. the social/animal concepts task; ToM; semantic tasks; and unfamiliar people), and there is evidence that the ATL is more involved in recognising people rather than buildings (Ross et al., 2010; Simmons et al., 2010). This account appears to have the least support in the literature. Although there is evidence showing that processing famous or familiar faces/objects results in strong ATL activation this does not establish ‘unique entities’ as a distinct theory from a social or general semantic processing roles of the ATL.

Researchers have proposed that the ATLs may be a store for *personal* semantic and episodic memories (Dolan et al., 2000; U. Frith and Frith, 2003; Gallagher and Frith, 2003) which could account for why it is active for famous/familiar entities and other social-emotional processing tasks. Personal memories may be particularly useful for mentalising. For example, if an individual is deceiving someone, they also have to remember what was said to that person before, or draw

on past experiences to imagine themselves in the situation of another person. This is supported by ATL activations shown in studies where participants are required to remember emotional personal events, mentalising tasks, and for ‘unique entities’ which require personal memory for recognition. Further, the ATLs could be involved in accessing emotional or social contexts and in developing social scripts (C.D. Frith, 2007). Through experience we learn to appropriate behaviours in response to particular events, and also which feelings and dispositions are related to these events. They are a form of cognitive heuristic to organise information and can be useful to predict how a certain person may behave based on the typical ‘script’ or sequence of events. Therefore the ATL may act as a store for these general scripts through convergence of information. This implies that when a new social situation arises, we can apply these general ‘scripts’ to the novel event (C.D. Frith, 2007; U. Frith and Frith, 2003). Accordingly, semantic dementia patients lose knowledge about scripts (Funnell, 2001) and often can only recognise objects when they are in familiar contexts, but not when they are somewhere else. For example, Snowden et al. (1994) found that an SD patient could only identify a clothes peg when it was retrieved from her own peg bag but not when it was in a different location. Interestingly and clinically relevant, TP activation has been found during emotional script-driven imagery and therefore has been linked to posttraumatic stress disorder (PTSD) (Dougherty et al., 1999; Shin et al., 2000). PTSD patients have shown greater activation in the ATL and orbitofrontal cortex for remembering traumatic personal events, compared to normal controls (Shin et al., 2000).

These interpretations could fit under a wider ‘semantic’ function of the ATLs in that general semantic memory is necessary for any social function whether it be emotions, personal memories, recognising people or theory of mind. Although a social component may be necessary to activate this region, it may not be sufficient (Olson et al., 2007). Further if the ATL is more involved in personal memories then it needs to be determined whether there are distinct differences in activation between personal compared to non-personal memories. However, the ATLs can be activated from tasks that do not require personal memories or social context, for example basic synonym judgement tasks, and reading sentences without any personal or social relevance. Therefore this suggests that the ATLs could be processing domain-general semantic knowledge which also encompasses social-emotional information. However, it is very difficult to find a socially relevant task

that occurs in the absence of any semantic knowledge to try and dissociate these two functions. Several studies indicate that the social information is not necessary to activate the ATL to at least a measurable degree.

A possible integrative approach is that the ATLs could process domain-general semantic knowledge but with a bias towards social information. Future studies could manipulate the degree of 'social' information to see if this bias exists. An alternative perspective is that, although the ATL processes general semantic knowledge, it could show a greater intensity of signal for things that are important or meaningful to the individual. This is why it more consistently shows activation for personal memories, emotions, familiar and famous people/landmarks, theory of mind, and concepts that fall under the social domain.

The domain-general semantic account would be challenged if damage or inhibitory rTMS to the ATL consistently affected specific categories over others. Under the hub theory, the ATL should process *all* types of semantic information from every modality. This is supported by the semantic dementia literature where patients show semantic deficits across all categories and modalities. In contrast to this, category specific deficits have been documented in patients with ATL abnormalities, for example deficits in living things compared to non-living things (Antonucci et al., 2008), people over landmarks (Ross et al., 2010), and nouns over verbs (Damasio and Tranel, 1993). Lambon Ralph et al. (2007) reported that category specific deficits are more commonly seen in patients with herpes simplex virus encephalitis (HSVE) compared to SD. Although both disorders affect the bilateral ATL, they contended that the difference was that HSVE 'distorts' representations rather than 'degrades' or dims semantic representations (as found in SD). The distortion of signals would then lead to confusing items with similar representations, such as different animals. Their conclusions were based on computational models, so whether this actually occurs in humans is yet to be confirmed. Nevertheless, if any category-specific changes can be consistently and robustly found in the ATL, this would provide evidence against the domain-general semantic hub theory.

A question that arises from this body of research is whether the ATL works differently within the social neural network compared with the semantic network. The social network is commonly reported as the prefrontal cortex, amygdala and temporal cortex (Brothers, 1990; C.D. Frith, 2007). This is confirmed by imaging studies of social cognition included in this review which generally report activation of the PFC, orbitofrontal cortex, inferior frontal gyrus, superior temporal sulcus, temporoparietal junction (TPJ) and amygdala, as well as the ATL. The semantic cognition network has been reported to consist of the left PFC, TPJ and temporal poles (Jefferies and Lambon Ralph, 2006; Lambon Ralph et al., 2009). Clearly there is overlap between the two networks, and consequently overlap between social and semantic cognition. However, exactly how these networks are linked together to produce a semantic or social representation is debated. Olson et al. (2007) suggested that the function of the RATL may be to link higher-level sensory representations with emotional responses and social memory, and is thus necessary for emotional stability forming the basis for personal semantic

memory. In contrast, the LATL may function to link higher-level sensory representation with semantic information. Although this laterality division may be too crude, there is some evidence that episodic memory retrieval may be more lateralised to the right hemisphere (Fink et al., 1996), and consequently this would involve emotional, personal and autobiographical memory. However, there is also evidence that the division could be represented in a superior-inferior or an anterior–posterior gradient with semantic specificity increasing along one axis (Martin and Chao, 2001; Zahn et al., 2007).

Thus, it would be epistemologically advantageous if future research investigates and clearly reports whether activations are in specific sub-regions within the ATL. It is possible that the ATL works similarly within both the social and semantic functional network, as a 'convergence point' or 'hub' bringing information from separate modalities together. However, it is also possible that particular areas within the ATL (the more anterior or superior aspects) process more specific information, thereby including social–emotional information which requires higher semantic discrimination. Differing theoretical accounts may need to make more definitive boundaries of what constitutes the ATL. The semantic hub theory refers to the ATL as the area damaged in SD, which often includes the anterior aspects of the three temporal gyri. As mentioned, the MTG may be more involved in domain-general processing than the more anterior aspects of the temporal lobe and temporal pole. Thus, when discussing the ATL in this definition, more modalities are involved. The social and unique entity accounts often refer to the temporal pole as the ATL, which is a smaller area and therefore may have more limited functions. It is necessary that the boundaries of the ATL, as well as particular sub-regions within the ATL, are defined more precisely before any functional theory can be substantiated.

7. Conclusion

The main purpose of this review was to investigate the function of the ATL with a particular focus on the functional neuroimaging and non-invasive brain stimulation literature. A large number of studies were reviewed implicating the ATL in both the social and semantic domains. It is possible that there may be functional sub-divisions within the ATL that process different stimuli. These are compatible with the anatomy of the ATL and its connections to different sensory streams. However, no consistent laterality or topographical patterns were found, still leaving many questions unanswered. The evidence for ATL function in the social domain or unique entities could fit under the wider and more general theory of the ATL as an amodal semantic hub that binds together information from different sensory modalities. This seems more parsimonious with the data. However there are two inversely related overarching problems with this conclusion. Firstly when considering the ATL in relation to the entire brain, it is too general to assign such a holistically fundamental function to one particular region, (or even regions), when a considerable amount of the evidence points to more specific and clinically relevant functions such as social and emotion regulation. For the sake of clarification, this point can be *overstated* as such — there is only modest evidence and no reason

that the ATL has influence over such large and disparate domains. On the other hand, when considering the whole brain in relation to the ATL, it appears too specific to suggest that all 'semantic' processing occurs in one particular hub of the brain. Again, (notwithstanding some loss of subtlety to the original theory), there is much evidence to suggest that all brain areas perform intra-regionally amodal semantic integration.

Future studies could directly compare specific categories to test whether the ATL processes in a category-specific or domain-general manner. For example, to investigate if the ATL processes modality specific stimuli, future studies could vary social content in discrete, increasing incremental steps, or compare information across different sensory modalities such as famous or familiar faces, names and auditory stimuli. We conclude, and certainly not uniquely, that semantic knowledge is processed in a wide network of neural structures including the frontal lobe, TPJ and ATL. Based on the review of the evidence, it is possible that although the ATLs are required for general semantic processing, they have a greater intensity of signal for information that is personal, social or emotional. All of these types of information could alternatively be thought of as semantic 'items' or memories that are important to the individual. If this is the case, it might not be that the ATLs are specific for social knowledge, only that social knowledge is important to humans and essential for survival. Thus, it may be the importance of social/emotional information that gives it priority of processing in the ATL not an inherent property of the structure itself.

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