Lower- and higher-level models of right hemisphere language. A selective survey

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Summary

The models advanced to explain right hemisphere (RH) language function can be divided into two main types. According to the older (lower-level) models, RH language reflects the ontogenesis of conceptual and semantic-lexical development; the more recent models, on the other hand, suggest that the RH plays an important role in the use of higher-level language functions, such as metaphors, to convey complex, abstract concepts.

The hypothesis that the RH may be preferentially involved in processing the semantic-lexical components of language was advanced by Zaidel in split-brain patients and his model was confirmed by neuropsychological investigations, proving that right brain-damaged patients show selective semantic-lexical disorders.

The possible links between lower and higher levels of RH language are discussed, as is the hypothesis that the RH may have privileged access to the figurative aspects of novel metaphorical expressions, whereas conventionalization of metaphorical meaning could be a bilaterally-mediated process involving abstract semantic-lexical codes.

KEY WORDS: semantic representations, metaphorical language, right hemisphere language, verbal conceptual knowledge, pictorial conceptual knowledge.

Introduction

Right hemisphere (RH) language function is a controversial topic in contemporary neuroscience research, and the models advanced to explain it can be divided, basically, into two main types. The older (lower-level) models maintained that RH language reflects the onto-

genesis of conceptual and semantic-lexical development and that it mainly concerns concrete words. On the other hand, more recent models maintain that the RH plays an important role in the use of higher-level language functions, such as metaphors, to convey complex, abstract concepts. The aim of this paper is to illustrate (after a short discussion of the hypothesis that the RH may be involved in high-level metaphorical language) the principles underlying the representation, in the RH, of lower-level conceptual and semantic-lexical knowledge. The author's position, which stresses the selective involvement of the RH in gross-grained semantic-lexical processing, is in line with a general model (Gainotti, 2011, 2012), which assumes that conceptual knowledge may be represented in a different format in the right and left anterior temporal lobes (ATLs). This assumption is in partial contrast with standard version of the 'semantic hub' hypothesis (Patterson et al., 2007; Lambon Ralph and Patterson, 2008), which suggests that conceptual knowledge is represented in a unitary manner in the right and left ATL and has an 'amodal' format, because 'the range of concepts over which a component of knowledge should be generalized... requires (amodal) representations that abstract away from surface similarities' (Lambon-Ralph and Patterson, 2008, p. 65).

There are two main reasons for the author's choice to focus primarily on the lower-level (rather than the higher-level) models of RH language in this survey. First, both the data obtained in unilateral brain-damaged patients and the results of neuroimaging experiments relevant to the RH metaphorical language hypothesis are rather controversial; second, these higher-level metaphorical abilities of the RH could be a by-product of the different format that conceptual representations could have at the level of the RH and the left hemisphere (LH) and, in particular, at the level of the anterior portions of the right and left ATL.

The right hemisphere metaphorical language hypothesis

Clinical studies on relationships between the right hemisphere and metaphorical language

The hypothesis that the RH may be involved in high-level metaphorical language was advanced by Winner

and Gardner (1977) on the basis of observations in right brain-damaged (RBD) patients: these patients were found to be impaired in their understanding of words or phrases when interpretation beyond their literal meaning was required; however, the same authors noted that RBD patients gave a satisfactory explanation of familiar metaphorical expressions 85% of the time. Further clinical investigations (e.g. Brownell et al., 1984, 1990; Kempler et al., 1999; Champagne et al., 2004; Rinaldi et al., 2004) confirmed the presence of a defect of metaphorical language in RBD patients, and other authors (e.g. Tompkins, 1990; Tompkins et al., 1992; Giora et al., 2000; Gagnon et al., 2003; Klepousniotou and Baum, 2005; Papagno et al., 2006) found metaphorical language to be equally impaired after RH or LH injury, thus failing to support the hypothesis of a specific contribution of the RH to the processing of metaphorical meaning of words. Essential data about these clinical investigations (subjects, methodology and results) are reported in table I.

With regard to these data, it must be noted that Zaidel et al. (2002) and Oliveri et al. (2004) objected that methodological inconsistencies could have accounted for some of the positive results. For instance, in some of these studies (e.g. Champagne et al., 2004 and Rinaldi et al., 2004) only RBD patients and normal controls were tested, and many of them failed to consider the task difficulty effect in the statistical analysis. The observation that RBD patients are often able to explain verbally what a metaphor means (Winner and Gardner, 1977) made it possible to predict an interaction between groups (RBD vs LBD patients) and task (pictorial vs verbal metaphor comprehension). This prediction was partially confirmed by Zaidel et al. (2002): in their study the difference between LBD patients and RBD patients on pictorial metaphors was not significant, whereas the RBD patients performed significantly better on verbal metaphors. Finally, Tompkins (1990) and Tompkins et al. (1992) showed that in RBD patients metaphor comprehension defects were most evident in tasks that require controlled strategic processing or visual-spatial analysis and suggested that these patients can access the metaphorical meaning of words, but are impaired in their strategic use, due to limited attentional resources and impaired executive functions.

The contribution of functional neuroimaging investigations to the right hemisphere metaphorical language hypothesis

In the wake of the neuropsychological studies in brain-damaged patients, the hypothesis of a relationship between RH and metaphorical language gained support from a functional neuroimaging study conducted by Bottini et al. (1994), who reported RH activation on a task of metaphorical language. It should, however, be mentioned that this positron emission tomography (PET) study was performed in just six subjects and this limited number of subjects could explain why its

results differ from those subsequently reported in the literature. Indeed, many subsequent neuroimaging studies reported either bilateral or unilateral left activation during metaphor comprehension tasks. Recent meta-analyses (Bohrn et al., 2012; Rapp et al., 2012) have confirmed that no selective relationship exists between the RH and metaphorical language. The meta-analysis by Bohrn et al. (2012) combined data obtained in 22 functional magnetic resonance imaging (fMRI) studies and one PET investigation in order to identify differences in neural correlates of non-literal and literal language processing and to investigate the role of the RH in metaphorical language processing. No general RH advantage for metaphor processing was found. On the contrary, significant clusters of activation for metaphor conditions were mostly lateralized to the LH. Rapp et al. (2012) used coordinate-based activation-likelihood estimations to merge available fMRI data on non-literal language. Twenty-eight studies with direct comparisons of non-literal and literal conditions were included in the main meta-analysis. These studies indicated that a predominantly left lateralized network is activated during tasks involving non-literal language.

The selective involvement of the right hemisphere in processing the semantic-lexical components of language

Zaidel's pioneering investigations

The greatest impetus for the hypothesis that the RH may be preferentially involved in processing the semantic-lexical components of language was provided by Zaidel (1976) and the results he obtained in split-brain patients. In his investigations patients were requested to respond with their left hand to written words flashed to the left visual field, selecting one item out of a series of objects that best matched a word flashed to the RH. Zaidel showed that the isolated RH is able to comprehend reasonably well many single words (even if only a coarse-grained lexical knowledge was demonstrated, because the objects among which the RH had to choose belonged to different conceptual categories). In contrast with these relatively spared lexical abilities, Zaidel showed that the RH has much less developed phonological and syntactic capacities, being unable to match objects on the basis of the phonological properties of their names (e.g. "key" and "bee"), and poorly developed syntactic abilities with respect to its lexical comprehension capacity.

Neuropsychological investigations evaluating the selective presence of semantic-lexical disorders in right brain-damaged patients

The results of several neuropsychological investigations have shown that when RBD patients are submitted to word-picture matching tasks and their results are compared with those of healthy subjects, they

show a deficit of language comprehension that selectively affects the semantic-lexical level. The first clear evidence in this direction was provided by a study by Lesser (1974), in which three word-picture matching tasks, selectively assessing phonological, lexical and syntactic discrimination, were administered to RBD and left brain-damaged (LBD) patients. Semantic-lexical errors were found both in LBD aphasic patients and (to a lesser extent) in RBD patients, whereas no pathological scores were observed in RBD patients on tests of phonological and syntactic comprehension.

Lesser's (1974) data were confirmed by the results of neuropsychological investigations conducted by Gainotti et al. (1979, 1981), Chiarello and Church (1986) and Cappa et al. (1990). Gainotti et al. (1979) submitted RBD patients and normal controls (NCs) to a word-picture matching task, in which errors were classed as semantic, phonemic or unrelated. Only the number of semantic-lexical errors obtained by RBD patients was higher than that obtained by NCs. Similar results were obtained by Gainotti et al. (1981) in a study in which RBD patients and NCs were given an

Table I - Clinical investigations on the hypothesis of right hemisphere involvement in figurative-metaphorical language.

Authors	Patients	Methods	Results
Brownell et al., 1984	RBD vs LBD pts	Word triads related by literal (denotative) or metaphorical (connotative) links	RBD pts were more sensitive to the literal than to the metaphorical facets of meaning, whereas the opposite pattern was shown by LBD pts.
Brownell et al., 1990	RBD vs LBD pts	Patients had to sort polysemous target words on the basis of their less frequent meaning.	LBD pts showed a greater tendency to choose metaphorical alternative meanings.
Tompkins, 1990	RBD vs LBD and NCs	Ambiguous adjectives conveying metaphorical or literal meanings were used as targets in auditory lexical decision tasks.	RBD pts performed similarly to LBD pts and NCs, indicating that they retained some knowledge of metaphorical meanings.
Tompkins et al., 1992	RBD vs LBD pts and NCs	Comprehension of non-literal metaphorical sentences was assessed.	Brain-damaged subjects performed similarly to NCs on this task.
Kempler et al., 1999	RBD vs LBD pts and children	Comprehension of literal and non-literal sentence-picture matching tasks was studied.	RBD pts performed worse than LBD pts on non-literal, but better on novel, literal sentences.
Giora et al., 2000	RBD vs LBD pts and NCs	Sarcasm comprehension and metaphor comprehension tests were used.	In metaphor comprehension, a significant disadvantage of LBD pts vs both RBD pts and NCs was found.
Gagnon et al., 2003	RBD vs LBD pts and NCs	In word-triad and word-dyad tasks pts had to associate metaphorical and non-metaphorical words with a target word.	Both RBD and LBD groups presented a semantic deficit for the processing of metaphorical meaning.
Champagne et al., 2004	RBD pts vs NCs	Participants were tested on metaphorical and executive function abilities.	Approximately 50% of the RBD pts showed metaphorical language impairment.
Rinaldi et al., 2004	RBD pts vs NCs	Metaphor comprehension was studied with a visuo-verbal and a verbal test.	RBD patients performed more poorly in the visuo-verbal than in the verbal condition.
Klepousniotou and Baum, 2005	RBD vs LBD pts and NCs	Homonymous, metonymous and metaphorical words were used as primes in an auditory semantic priming paradigm.	No significant group effects were found, indicating that RBD pts can access the multiple meanings of ambiguous words.
Papagno et al., 2006	RBD vs LBD pts	Idiom comprehension was assessed with sentence-to-picture matching tasks.	LBD patients were significantly more impaired than RBD pts on both literal sentence and idiom comprehension.

Abbreviations: RBD= right brain-damaged; LBD= left brain-damaged; pts= patients; NCs= normal controls

aural and a written test of semantic-lexical discrimination and a phoneme discrimination task. RH consistently impaired semantic-lexical comprehension in both modalities but spared phoneme discrimination. In Chiarello and Church's (1986) study, patients with unilateral LH or RH lesions were asked to make similarity judgements on visually presented words on the basis of rhyme, meaning or visual similarity. Patients with RH injury were impaired only in lexical judgements based on meaning, whereas LBD patients were significantly impaired, compared with controls, in all types of lexical judgements. Finally, Cappa et al. (1990) compared the language and verbal memory test performances of RBD patients with those of NCs and of non-aphasic LBD patients. While phonological and syntactic performance was unimpaired, a subgroup of RBD patients with CT scan evidence of subcortical lesions was mildly impaired in naming tasks.

Possible relations between right hemisphere language and format of conceptual representations in the right and left ATL

The characterization of RH language just outlined is consistent with a view that the present author recently expressed about the different format that conceptual representation could have within the left compared with the right ATL (Gainotti, 2011, 2012, 2015). Starting from an impressive set of data gathered in semantic dementia (SD), Patterson et al. (2007) proposed that the neural network for semantic memory is based on a single convergence zone or 'hub' bilaterally located in the ATL that supports the interactive activation of conceptual representations in all modalities and for all semantic categories. However, the format of the conceptual representation 'stored' in the 'semantic hub' was not univocal. On the one hand, Patterson et al. (2007) referred to Damasio's (1989) construct of 'convergence zones' (which is an 'embodied' construct, based on the idea that concept retrieval results from a dynamic process of recollection of modality-specific fragments of memories, stored near the sensory portals and motor output sites of the system). On the other hand, the same authors argued that the 'semantic hub' should contain amodal representations, to allow generalizations that abstract away from surface similarities and this acceptance has usually been taken as the standard version of the 'semantic hub' hypothesis.

Modality-specific aspects of conceptual impairment and asymmetries observed at the level of the ATLs in the earliest stages of semantic dementia

Thorough reading of the literature on SD — the 'semantic hub' hypothesis was constructed on the basis of this disease — suggested, however, that the semantic impairment is 'multi-modal' only in the moderate to advanced stages of the disease, when atrophy affects the ATL bilaterally. On the contrary, in its early stages, when important asymmetries can be

observed at the level of the ATLs, the semantic impairment can mainly affect specific modalities. In these cases, it tends to concern semantic-lexical knowledge when the left temporal lobe is more atrophic (Hodges et al., 1992; Lambon Ralph et al., 2001; Snowden et al., 2004; Butler et al., 2009; Mion et al., 2010), and pictorial representations when the atrophy prevails on the right side (Knott et al., 1997; Snowden et al., 2004; Butler et al., 2009; Mion et al., 2010). This observation suggests different degrees of involvement of the right versus the left ATL in the representation of the pictorial/sensory and verbally-mediated aspects of conceptual knowledge.

Relations between prevalent activation of the right and left ATL and material used in conceptual activation studies in normal subjects

Results consistent with those observed in the early stages of SD have been obtained in functional neuroimaging studies conducted in normal subjects (NSs) during verbal and non-verbal conceptual tasks. For instance, Humphries et al. (2001) and Thierry et al. (2003) scanned NSs while they listened to environmental sounds or to words or sentences matched as closely as possible in meaning. Verbal stimuli enhanced activation in the left superior temporal gyrus, while environmental sounds enhanced activation in the right superior temporal gyrus. Similar results were obtained by Thierry and Price (2006) and by Hocking and Price (2009), who compared conceptual processing of verbal and non-verbal stimuli in both visual and auditory modalities. Verbal matching increased activation in a region of the left superior temporal sulcus associated with phonological processing, whereas pictorial non-verbal stimuli increased activation in the right fusiform region. Both results obtained in the early stages of SD and those obtained with functional neuroimaging studies during administration of verbal and non-verbal conceptual tasks suggest, therefore, that concepts subsumed by the left ATL are verbally coded, whereas those subsumed by the right ATL are mainly stored in a perceptual/pictorial format.

Imbalance observed between the weight of verbally-coded information in the left ATL and the weight of non-verbal information in the right ATL

Gainotti (2014) observed that in SD cases with asymmetric atrophy, the loss of semantic-lexical knowledge when the atrophy mainly affected the left ATL was more striking than the loss of non-verbal representations when it was the right ATL that was more atrophic. An analogous imbalance was observed in functional neuroimaging experiments, where the LH activation by verbal stimuli was more extensive and severe than the activation observed in the RH in response to non-verbal stimuli. This clinical impression was recently confirmed by an activation likelihood estimation meta-analysis of 97 functional neuroimaging studies, conducted by Rice et al. (2015) to evaluate the role of the

right and left ATL in verbal and non-verbal conceptual knowledge. These authors showed that both hemispheres are usually activated, irrespective of the input modality, but that the left ATL is significantly more activated after verbal input and the right ATL non-significantly more activated after non-verbal input. These findings suggest that the difference between the (verbal) semantic representations subsumed by the left ATL and the (sensory-based) conceptual representations subsumed by the right ATL is quantitative, rather than qualitative. To be qualitative, as it has been proposed to be, for example, by Paivio's (1971) 'dual code' theory, visual and verbal information would have to be processed differently and along distinct channels in the human brain, creating independent representations, which would be separately processed (and independently disrupted by pathologies affecting each hemisphere). On the other hand, a greater prevalence of verbally-coded knowledge in the semantic representations of the language-dominant LH, and a less striking prevalence of sensory-motor information in the conceptual representations of the RH, could be predicted by the 'sensory-motor account of conceptual knowledge' (e.g., Saffran and Schwartz, 1994; Gainotti et al., 1995; Chao et al., 1999; Gainotti, 2000, 2006; Martin, 2007), which can be considered a development of Warrington and Shallice's (1984) 'differential weighting hypothesis'.

The 'sensory-motor account of conceptual knowledge' and its extension to inter-hemispheric differences

According to the 'sensory-motor account of conceptual knowledge', each conceptual representation derives from the convergence of different sensory, motor and verbal sources of knowledge, but the weight of these contributions is different for different conceptual categories. Thus, visual and other perceptual features could play a major role in representations of animals and other living things, whereas manipulation, somatosensory inputs and functional features could play a leading role in the representations of tools and other artifacts (Gainotti, 2006; Gainotti et al., 2009; Hoffman and Lambon Ralph, 2013). This hypothesis thus offers an explanation of (for instance) why the anterior parts of the temporal lobes (where the ventral stream of visual processing converges with auditory, olfactory and gustatory inputs) play a critical role in the representation of biological entities, whereas the left frontoparietal sensory-motor cortices (where the dorsal stream of visual processing converges with body-related and action-oriented structures) play a major role in the representation of artifacts. The extension of this model from categorical to inter-hemispheric differences, in conjunction with the Hebbian correlation learning theory (Hebb, 1949), could also provide an explanation as to why concepts are mainly represented in a verbal format in the left ATL, whereas in the right ATL they are mainly represented in a non-verbal format.

The Hebbian correlation learning theory and right hemisphere language

According to the Hebbian correlation learning theory (Hebb, 1949), words which frequently co-occur with typical actions or with the corresponding visual and auditory stimuli may be an integral part of cell assemblies coupling neurons located in motor, visual, auditory and language areas. Furthermore, as cell assemblies involving all components of these networks are present (although with different weights) in both hemispheres, the RH representations corresponding to these cell assemblies should also include specific verbal components. Recently, Binney and Lambon Ralph (2015), using a combination of fMRI and ATL stimulation to measure intrinsic and induced activation changes across the semantic cognition network, stimulated through a written word synonym judgement task, confirmed the involvement of the right ATL in the processing of verbal semantic stimuli. Their results support the notion that the RH possesses and utilizes the functional architecture needed to perform language operations, even though the neuronal assemblies corresponding to different concepts are represented with more verbal than non-verbal features in the left ATL and with more non-verbal than verbal features in the right ATL. They also suggest that the verbal components of the right ATL are limited to semantic-lexical representations of concrete entities, a pattern which corresponds to the features of RH language as described by Zaidel (1976). The position of this author, who defined RH lexical knowledge as coarse grained, is not inconsistent with the 'coarse-semantic-coding' (CSC) theory of Jung-Beeman (2005), which maintains that during word processing the LH carries out fine semantic coding and activates a strong and focused semantic field, whereas the RH carries out coarse semantic coding and activates a weak and large semantic field. This difference is probably due to the strength of the intra-linguistic connections existing in the LH, in contrast with the prevalence of connections linking concrete lexical items with extra-linguistic features in the RH cell assemblies.

Concluding remarks: possible links between lower and higher levels of right hemisphere language

If this interpretation of RH language is correct and the RH cell assemblies corresponding to conceptual representations are made up much more by sensory-based than by lexical features, then some links between lower and higher levels of RH language could be hypothesized. Many forms of metaphorical language are, indeed, based on evocation of the pictorial features typical of the concrete concepts on which the metaphorical expressions are based. If these sensory-motor features are mainly present in the cell assemblies subsuming the RH conceptual representations, it seems logical to expect that this characteristic may give the RH an advantage in the com-

prehension of metaphorical language. Some support for this hypothesis has been provided by data obtained by Ansaldo et al. (2002), studying, with a lateralized lexical decision task, the contribution of the RH to recovery from aphasia, and by results obtained by several authors applying the graded salience hypothesis (GSH) proposed by Giora (1997) and by Giora et al. (2000). In agreement with the hypothesis that RH semantic representations may be based mainly on the concrete perceptual features of objects, Ansaldo et al. (2002) showed that the RH is faster with high-imageability words than with low-imageability words. The GSH is based on the notion that the salience of a metaphor may change from its early (novel) stage to the stage in which it is conventionalized and lexicalized. The notion that the RH plays a prominent role when a figurative expression is still 'novel', and that there is a subsequent shift to a bilateral representation in the 'conventionalized and lexicalized' stage, has been confirmed: i) by results obtained by Desai et al. (2011) and by Cardillo et al. (2012), studying the 'neural career' of sensory-motor metaphors; ii) by data obtained by Mashal and Faust (2009) using the divided visual field technique to test the possibility that the conventionalization of novel metaphors may be accompanied by a shift from RH to LH processing, and iii) by results of the previously mentioned meta-analysis of neuroimaging studies on non-literal language (Bohrn et al., 2012). The results of all these investigations consistently suggest that the RH plays a greater role in processing novel, low-salience figurative meanings, but that conventionalization of metaphorical meaning is a bilaterally-mediated process, which involves abstract semantic-lexical codes. Both the CSC theory and the GSH therefore suggest that literal language is primarily processed in the LH, whereas the RH has privileged access to the figurative aspects of novel metaphorical expressions. The hypothesis of a relationship between lower and higher levels of RH language is also supported by results obtained by Schmidt-Snoek et al. (2015), who recently showed, in an event-related potential study, that words used metaphorically show signs of "embodiment", confirming the neural links between metaphors and sensory-motor aspects of experience. No conflict exists, therefore, between the older, lower-level models of RH language, based on selective, coarse-grained, semantic lexical knowledge, and the more recent models which maintain that the RH plays an important role in the use of higher-level language functions, such as metaphors, to convey complex, abstract concepts. On the contrary, the lower-level, embodied semantic abilities of the RH could constitute an important prerequisite for the development of its higher-level metaphorical skills.

References

Ansaldo AI, Arguin M, Roch Lecours A (2002). The contribution of the right cerebral hemisphere to the recovery from aphasia: a single longitudinal case study. *Brain Lang* 82:206-222.

Binney RJ, Lambon Ralph MA (2015). Using a combination of fMRI and anterior temporal lobe rTMS to measure intrinsic and induced activation changes across the semantic cognition network. *Neuropsychologia* 76:170-181.

Bohrn IC, Altmann U, Jacobs AM (2012). Looking at the brains behind figurative language—a quantitative meta-analysis of neuroimaging studies on metaphor, idiom, and irony processing. *Neuropsychologia* 50:2669-2683.

Bottini G, Corcoran R, Sterzi R, et al (1994). The role of the right hemisphere in the interpretation of figurative aspects of language. A positron emission tomography activation study. *Brain* 117:1241-1253.

Brownell HH, Simpson TL, Bihrie AM, et al (1990). Appreciation of metaphoric alternative word meanings by left and right brain-damaged patients. *Neuropsychologia* 28:375-383.

Brownell HH, Potter HH, Michelow D, et al (1984). Sensitivity to lexical denotation and connotation in brain-damaged patients: a double dissociation? *Brain Lang* 22:253-265.

Butler CR, Brambati SM, Miller BL, et al (2009). The neural correlates of verbal and nonverbal semantic processing deficits in neurodegenerative disease. *Cogn Behav Neurol* 22:73-80.

Cappa SF, Papagno C, Vallar G (1990). Language and verbal memory after right hemispheric stroke: a clinical-CT scan study. *Neuropsychologia* 28:503-509.

Cardillo ER, Watson CE, Schmidt GL, et al (2012). From novel to familiar: tuning the brain for metaphors. *Neuroimage* 59:3212-3221.

Champagne M, Desautels MC, Joannette Y (2004). Lack of inhibition could contribute to non-literal language impairments in right-hemisphere-damaged individuals. *Brain Lang* 91:172-174.

Chao LL, Haxby JV, Martin A (1999). Attribute-based neural substrates in temporal cortex for perceiving and knowing about objects. *Nat Neurosci* 2:913-919.

Chiarello C, Church KL (1986). Lexical judgments after right- or left-hemisphere injury. *Neuropsychologia* 24:623-30.

Damasio AR (1989). Time-locked multiregional retroactivation: a systems-level proposal for the neural substrates of recall and recognition. *Cognition* 33:25-62.

Desai RH, Binder JR, Conant LL, et al (2011). The neural career of sensory-motor metaphors. *J Cogn Neurosci* 23:2376-2386.

Gagnon L, Goulet P, Giroux F, et al (2003). Processing of metaphoric and non-metaphoric alternative meanings of words after right- and left-hemispheric lesion. *Brain Lang* 87:217-226.

Gainotti G (2015). Is the difference between right and left ATLs due to the distinction between general and social cognition or between verbal and non-verbal representations? *Neurosci Biobehav Rev* 51:296-312.

Gainotti G (2014). Why are the right and left hemisphere conceptual representations different? *Behav Neurol* 2014:603134.

Gainotti G (2012). The format of conceptual representations disrupted in semantic dementia: a position paper. *Cortex* 48:521-529.

Gainotti G (2011). The organization and dissolution of semantic-conceptual knowledge: is the 'amodal hub' the only plausible model? *Brain Cogn* 75:299-309.

Gainotti G, Ciaraffa F, Silveri MC, et al (2009). Mental representation of normal subjects about the sources of knowledge in different semantic categories and unique entities. *Neuropsychology* 23:803-812.

Gainotti G (2006). Anatomical, functional and cognitive determinants of semantic memory disorders. *Neurosci Biobehav Rev* 30:577-594.

- Gainotti G (2000). What the locus of brain lesion tells us about the nature of the cognitive defect underlying category-specific disorders: a review. *Cortex* 36:539-559.
- Gainotti G, Silveri MC, Daniele A, et al (1995). Neuroanatomical correlates of category-specific semantic disorders: a critical survey. *Memory* 3:247-264.
- Gainotti G, Caltagirone C, Miceli G, et al (1981). Selective semantic-lexical impairment of language comprehension in right-brain-damaged patients. *Brain Lang* 13:201-211.
- Gainotti G, Caltagirone C, Miceli G (1979). Semantic disorders of auditory language comprehension in right brain-damaged patients. *J Psycholinguist Res* 8:13-20.
- Giora R, Zaidel E, Soroker N, et al (2000). Differential effects of right- and left-hemisphere damage on understanding sarcasm and metaphor. *Metaphor and Symbol* 15:63-83.
- Giora R (1997). Understanding figurative and literal language: the graded salience hypothesis. *Cognitive Linguistics* 8:183-206.
- Hebb DO (1949). *The Organization of Behaviour: A Neurophysiological Theory*. Hoboken, NJ, Wiley.
- Hocking J, Price CJ (2009). Dissociating verbal and nonverbal audiovisual object processing. *Brain Lang* 108:89-96.
- Hodges JR, Patterson K, Oxbury S, et al (1992). Semantic dementia: progressive fluent aphasia with temporal lobe atrophy. *Brain* 115:1783-1806.
- Hoffman P, Lambon Ralph MA (2013). Shapes, scents and sounds: quantifying the full multi-sensory basis of conceptual knowledge. *Neuropsychologia* 51:14-25.
- Humphries C, Willard K, Buchsbaum B et al (2001). Role of anterior temporal cortex in auditory sentence comprehension: an fMRI study. *Neuroreport* 12:1749-1752.
- Jung-Beeman M (2005). Bilateral brain processes for comprehending natural language. *Trends Cogn Sci* 9:512-518.
- Kempler D, Van Lancker D, Marchman V, et al (1999). Idiom comprehension in children and adults with unilateral brain damage. *Dev Neuropsychol* 15:327.
- Klepousniotou E, Baum SR (2005). Unilateral brain damage effects on processing homonymous and polysemous words. *Brain Lang* 93:308-326.
- Knott R, Patterson K, Hodges JR (1997). Lexical and semantic binding effects in short-term memory: evidence from semantic dementia. *Cogn Neuropsychol* 14:1165-1216.
- Lambon Ralph MA, Patterson K (2008). Generalization and differentiation in semantic memory: insights from semantic dementia. *Ann N Y Acad Sci* 1124:61-76.
- Lambon Ralph MA, McClelland JL, Patterson K, et al (2001). No right to speak? The relationship between object naming and semantic impairment: neuropsychological evidence and a computational model. *J Cogn Neurosci* 13:341-356.
- Lesser R (1974). Verbal comprehension in aphasia: an English version of three Italian tests. *Cortex* 10:247-263.
- Martin A (2007). The representation of object concepts in the brain. *Ann Rev Psychol* 58:25-45.
- Mashal N, Faust M (2009). Conventionalisation of novel metaphors: a shift in hemispheric asymmetry. *Laterality* 14:573-589.
- Mion M, Patterson K, Acosta-Cabronero J, et al (2010). What the left and right anterior fusiform gyri tell us about semantic memory. *Brain* 133:3256-3268.
- Oliveri M, Romero L, Papagno C (2004). Left but not right temporal involvement in opaque idiom comprehension: a repetitive transcranial magnetic stimulation study. *J Cogn Neurosci* 16:848-855.
- Paivio A (1971). *Imagery and verbal processes*. New York, Holt, Rinehart and Winston.
- Papagno C, Curt R, Rizzo S et al (2006). Is the right hemisphere involved in idiom comprehension? A neuropsychological study. *Neuropsychology* 20:598-606.
- Patterson K, Nestor PJ, Rogers TT (2007). Where do you know what you know? The representation of semantic knowledge in the human brain. *Nat Rev Neurosci* 8:976-987.
- Rapp AM, Mutschler DE, Erb M (2012). Where in the brain is nonliteral language? A coordinate-based meta-analysis of functional magnetic resonance imaging studies. *Neuroimage* 63:600-610.
- Rice GE, Lambon Ralph MA, Hoffman P (2015). The roles of left versus right anterior temporal lobes in conceptual knowledge: an ALE meta-analysis of 97 functional neuroimaging studies. *Cerebral Cortex* 25:4374-4391.
- Rinaldi MC, Marangolo P, Baldassarri F (2004). Metaphor comprehension in right brain-damaged patients with visuo-verbal and verbal material: a dissociation (re)considered. *Cortex* 40:479-490.
- Saffran EM, Schwartz MF (1994). Of cabbages and things: semantic memory from a neuropsychological perspective - a tutorial review. *Attention and Performance* 25:507-536.
- Schmidt-Snoek GL, Drew AR, Barile EC, et al (2015). Auditory and motion metaphors have different scalp distributions: an ERP study. *Front Hum Neurosci* 9:126.
- Snowden JS, Thompson JC, Neary D (2004). Knowledge of famous faces and names in semantic dementia. *Brain* 127:860-872.
- Thierry G, Price CJ (2006). Dissociating verbal and nonverbal conceptual processing in the human brain. *J Cogn Neurosci* 18:1018-1028.
- Thierry G, Giraud AL, Price C (2003). Hemispheric dissociation in access to the human semantic system. *Neuron* 38:499-506.
- Tompkins CA, Boada R, McGarry K (1992). The access and processing of familiar idioms by brain-damaged and normally aging adults. *J Speech Hear Res* 35:626-637.
- Tompkins CA (1990). Knowledge and strategies for processing lexical metaphor after right or left hemisphere brain damage. *J Speech Hear Res* 32:307-316.
- Warrington EK, Shallice T (1984). Category-specific semantic impairments. *Brain* 107:829-854.
- Winner E, Gardner H (1977). The comprehension of metaphor in brain-damaged patients. *Brain* 100:717-729.
- Zaidel E, Kasher A, Soroker N, et al (2002). Effects of right and left hemisphere damage on performance of the "Right Hemisphere Communication Battery". *Brain Lang* 80:510-535.
- Zaidel E (1976). Auditory vocabulary of the right hemisphere following brain bisection or hemidecortication. *Cortex* 12:191-211.