20

The Brain Behind Nonliteral Language: Insights From Brain Imaging

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Nonliteral expressions constitute a challenge for comprehension as they go beyond the literal meaning of the words and require the ability to process more than the literal meaning of an utterance in order to grasp the speaker's intention in a given context. Several definitions exist for nonliteral ("figurative") language, however there is some consensus that metaphors, idioms, proverbs, and ironic expressions are among the most important types. This chapter will review the current functional brain imaging evidence on their comprehension.

A clearer picture of the functional neuroanatomy behind nonliteral language comprehension may be of interest for several reasons. First, nonliteral expressions constitute a challenging semantic phenomenon per se as they represent an integral part of our everyday language and thinking processes (Lakoff & Johnson, 1980) and are remarkably frequent in everyday speech (Gibbs, 1994, 2000; Markert & Hahn, 1997; Whalen, Pexman, & Alastair, 2009). Comprehension of figurative expressions optionally involves other processes like mapping of semantic domains (e.g., metaphor; Rapp, Leube, Erb, Grodd, & Kircher, 2004), integration of world knowledge (e.g., metonymy; Rapp, Erb, Grodd, Bartels, & Markert, in press), and theory of mind (TOM) processes (e.g., irony; Happe, 1996; Rapp et al., 2010). Beyond scientific, research on the functional neuroanatomy of nonliteral language is as well of clinical interest. For instance, much interest in the neuroanatomy of nonliteral language comes from psychiatry research. Patients with neurodevelopmental psychiatric disorders such as schizophrenia or autism show deficits in the comprehension of nonliteral expressions whereas other language skills are relatively preserved (Kircher, Leube, Erb, Grodd, & Rapp, 2007; Martin & McDonald, 2004; Rapp, 2009;

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Thoma & Daum, 2006). So far, more than 100 studies have investigated nonliteral language comprehension in schizophrenia (Rapp & Schmierer, 2010), and an increasing number of studies apply nonliteral language paradigms in patients with autism (Gold & Faust, 2010; Martin & McDonald, 2004) and Alzheimer's dementia (see Rapp & Wild, submitted).

Beyond psychiatric conditions, much interest on nonliteral language came from researchers interested in language impairment resulting from brain lesions in the left or right cerebral hemisphere. Although there is no question that the left hemisphere is the superior language processor, a growing body of research has demonstrated significant linguistic abilities in the "nonverbal" right hemisphere (Jung-Beeman, 2005; Lindell, 2006). Traditionally, especially the processing of nonliteral and figurative expressions is attributed to a greater or lesser extent to the right cerebral hemisphere (Bookheimer, 2002; Bottini et al., 1994; Burgess & Chiarello, 1996). For metaphors, this is sometimes named the "right hemisphere theory" of metaphor processing. One strong version of this theory predicts that metaphors are predominantly processed by the right hemisphere. Two other neurolinguistic theories strongly influenced research on the neuroanatomy of nonliteral language as well. Beeman's coarse semantic coding theory (Beeman et al., 1994; Beeman, 1998; Jung-Beeman, 2005; Mirous & Beeman, Volume 1, Chapter 16) proposes that the left hemisphere specializes in processing only fine (close) semantic relationships while the right hemisphere is adept at both fine (close) and coarse (distant) semantic relationships. According to this theory, mapping of distant semantic fields during metaphor comprehension would result in right hemisphere brain activity. Giora (Giora, 1997; Giora, Zaidel, Soroker, Batori, & Kasher, 2000) introduced the "graded salience hypothesis." According to this theory, only novel, nonsalient nonliteral stimuli are processed in the right hemisphere, whereas salient, "fossilized" expressions are processed in the left cerebral hemisphere.

Brain Lesion Studies on Metaphor

The last decade brought an enormous increase in our knowledge of the functional neuroanatomy of language. One reason is the widespread use of functional brain imaging techniques, i.e., functional magnetic resonance imaging. However, the first direct evidence on the functional neuroanatomy of nonliteral language came from patients with brain lesions (Benton, 1968; Van Lancker, 1990; Winner & Gardner, 1977) and several new brain lesion studies during the last decade improved our understanding. At least 16 studies investigated the comprehension of metaphoric expressions (Table 20.1), supplemented by additional studies on proverb (Benton, 1968; Brundage & Brookshire, 1995; Paul, Van Lancker Sidtis, Schieffer, Dietrich, & Brown, 2003; Ulatowska et al., 1995, 2001) and idiom comprehension (e.g., Cacciari et al., 2006; Kempler, Van Lancker, Marchman, & Bates, 1999; Papagno & Caporali 2007; Papagno, Curti, Rizzo, & Crippa, 2006; Papagno, Tabossi, Colombo, & Zampetti, 2004; Tompkins, Boada, & McGarry, 1992; Van Lancker, 2006; see also

Table 20.1 Brain lesion studies on metaphor comprehension.

Authors	*Year*	*Stimuli (word vs. Sentence level)*	*Probands*	*Number of RHD probands*	*Number of metaphoric stimuli*	*Task*
Winner & Gardner	1977	phrasal	RH LH AD HC	22	18	sentence-to-picture matching
Brownell et al.	1984	word	LH RH HC	10	4	word matching
Brownell et al.	1990	word	RH LH HC	15	16	word matching
Tompkins	1990	word	RH LH HC	25	18	word/nonword decision
Hillekamp et al.	1996	word	RH LH HC	18	30	word-to-picture matching
Mackenzie et al.	1997	phrasal	RH HC	17	?[1]	sentence-to-picture matching
Giora et al.	2000	phrasal	RH LH HC	27	4	verbal explanation
Zaidel et al.	2002	phrasal (aber kurz)	RH LH HC	27	2 mal 4	sentence-to-picture matching
Gagnon et al.	2003	word	RH LH HC	10	20	word matching
Rinaldi et al.	2004	phrasal	RH HC	50	20	sentence-to-picture matching, multiple choice
Champagne et al.	2004	phrasal	RH HC	10	2 mal 10	verbal explanation plus MC
Klepousniotou & Baum	2005	word	RH LH HC	8	18?	word/nonword decision
Klepousniotou & Baum	2005	phrasal	RH LH HC	8	18?	lexical decision
Brownell et al.	2007	phrasal	RH	3	3	verbal explanation
Champagne et al.	2007	phrasal	RH SCZ HC	15	?	?

? = not reported; HC = healthy control subjects; LH = left hemisphere damaged; RH = right hemisphere damaged; AD = Alzeimer's disease.

[1]Metaphor subtest of the right hemisphere language battery (Bryan, 1989).

Cacciari & Papagno, Volume 1, Chapter 18 and Van Lancker Sidtis, Volume 1, Chapter 17).

In a seminal study of the field, Winner and Gardner (1977) investigated the comprehension of conventional metaphoric expressions (like "A heavy heart can really make a difference") in probands with damage to either the left or the right cerebral hemisphere. The results showed an effect of both task and lesion lateralization on performance: patients with right hemisphere lesions had preserved ability to understand phrasal metaphors (Winner & Gardner, 1977), a finding that was later replicated with other studies (Giora et al., 2000; Rinaldi, Marangolo, & Baldassarri, 2004; Zaidel, Kasher, Soroker, & Batori, 2002). This preserved ability of right hemisphere lesioned patients to understand metaphors correctly suggests that the left hemisphere has the ability to process conventional phrasal metaphors correctly. However, in a different task of the same study, Winner and Gardner tested the ability to match the same metaphors with an appropriate picture. In this task, patients with right hemisphere lesioned probands were impaired, which could suggest an impairment to work with a metaphoric meaning, but could alternatively be confounded by impaired skills in picture matching (Zaidel et al., 2002). The methodological quality of lesion studies on metaphor is on average high (Table 20.1), however altogether lesion studies are heterogeneous in their results and cannot provide a definite picture on what modulates right hemisphere involvement in metaphor comprehension. For example, Rinaldi et al. (2004) replicate Winner's and Gardner′s finding of right-hemisphere-damaged impairment in matching metaphors with an appropriate picture. However, the same group of patients was less impaired in matching metaphors with an appropriate verbal description. As well, language impairment in right hemisphere lesions may partially recover (Brownell et al., 2007; Lundgren, Brownell, Cayer-Meade, & Roy, 2006; Lundgren, Brownell, Roy, & Cayer-Meade, 2006) and some studies have considerable intervals between lesion onset and time of assessment.

Functional Magnetic Resonance Research

An alternative approach to investigating the functional neuroanatomy of nonliteral language is research with functional magnetic resonance imaging (fMRI). Compared to brain lesion studies, a *disadvantage* of fMRI is that a lack of activation indicates far less evidence that a brain region is *not* involved in a task (for further considerations related to interpretation of fMRI data, see Van Lancker Sidtis, Volume 1, Chapter 17). However, an advantage of this technique is that healthy individuals with selected properties can be investigated.

So far, at least 29 fMRI studies have been published on nonliteral language in healthy subjects (Table 20.2). The available research covers a variety of different tasks and nonliteral language types: 5 studies used idioms as stimuli, 7 ironic/sarcastic expressions, 18 investigated metaphors, and one metonymy. At least three additional studies were published as an abstract (Mason, Prat, & Just, 2008;

Table 20.2 fMRI studies on nonliteral language comprehension.

	Autoren	*Year*	*NL Language type*	*Language*	*Number of subjects*	*Novel stimuli*	*Salient*	*Evidence for RH involvement*	*Included in metanalysis below*
1	Rapp et al.	2004	metaphor	German	15	x		no	x
2	Mashal et al.	2005	metaphor	Hebrew	15	x	x	yes	
3	Uchiyama et al.	2006	irony	Japanese	20			no	x
4	Eviatar & Just	2006	irony metaphor	English	16		x	yes / no	
5	Wang et al.	2006	irony	English	(18) (+18)			yes	
6	Wang et al.	2006	irony	English	12 (+12)			yes	x
7	Lee & Dapretto	2006	metaphor	English	12		x	no	x
8	Stringaris et al.	2006	metaphor	English	12		x	yes	
9	Aziz-Zadeh et al.	2006	metaphor	English	12		?	–	
10	Wakusawa et al.	2007	irony, metaphor	Japanese	38		x	yes	x
11	Ahrens et al.	2007	metaphor	Chinese	8	x	x	yes	x
12	Stringaris et al.	2007	metaphor	English	11		x	no	x
13	Mashal et al.	2007	metaphor	Hebrew	15	x	x	yes	x
14	Rapp et al.	2007	metaphor	German	17	x		no	
15	Zempleni et al.	2007	idiom	Dutch	15		x	yes	x

16	Shibata et al.	2007	metaphor	Japanese	13	x		no	x
17	Mashal et al.	2008	idiom	Hebrew	14		x	yes	x
18	Lauro et al.	2008	idiom	Italian	22		x	yes	x
19	Boulenger et al.	2008	idiom	English	18		x	yes	x
20	Chen et al.	2008	metaphor	English	14		x	no	x
21	Mashal et al.	2009	metaphor	Hebrew	15	x		yes	x
22	Hillert & Buracas	2009	idiom	English	10		x	yes	x
23	Yang et al.	2009	metaphor	English	18	x	x	yes	x
24	Schmidt & Seger	2009	metaphor	English	10	x	x	yes	x
25	Rapp et al.	2010	irony	German	15			yes	x
26	Yang et al.	2010	metaphor	English	18	x		yes	x
27	Mashal & Faust	2010	metaphor	Hebrew	10		x	–	
28	Rapp et al.	2010	metonymy	German	14		x	yes	x
29	Shibata et al.	2010	irony	Japanese	13			yes	x

Mejía-Constaín, Arsenault, Monchi, Senhadji, & Joanette, 2008) or book-chapter (Yu, Kim, Kim, & Nam, 2009).

The first fMRI study on *metaphor* comprehension was published by Rapp et al. (2004). In their study, the comprehension of short, novel, syntactically simple metaphors (like "the lover′s words are harp sounds") relative to literal control stimuli (like "the lover′s words are lies") matched for tense and word frequency were investigated. Both hemispheres were involved in the contrasts for metaphoric and literal stimuli against baseline, but – contrary to the study hypothesis – no right hemisphere activation was detected in the direct comparison.

Metaphoric relative to matched literal stimuli activated a left frontotemporal network with maxima in the anterior-inferior part of the left inferior frontal gyrus (IFG; BA 45/47), anterior temporal (BA 20) and posterior middle/inferior temporal (BA 37) gyri. This result was divergent from a previous, often cited, positron emission tomography (PET) study by Bottini et al. (1994), in which right hemisphere activation was found for phrasal metaphoric expressions.

More evidence for a role of the left IFG in metaphor comprehension came from subsequent fMRI studies. For instance, Eviatar and Just (2006) used a ROI-analysis (region-of-interest analysis) in 16 subjects whilst reading brief three-sentence stories that concluded with either a literal, metaphoric, or ironic sentence. Metaphoric utterances resulted in significantly higher levels of activation in the left IFG and in bilateral inferior temporal cortex than the literal and ironic utterances.

Some evidence for right hemisphere theory of metaphor comes from fMRI research by Stringaris and colleagues (Stringaris, Medford, Giampetro, Brammer, & David, 2007). In their fMRI study, subjects read short English sentences with either metaphoric ("Some surgeons are butchers"), literal ("Some surgeons are fathers"), or nonmeaningful sentences ("Some surgeons are shelves"). Metaphoric relative to literal stimuli showed activation differences in both cerebral hemispheres: on the one hand, results further strengthened Rapp et al.'s finding (2004) of an important role for BA 47 in metaphor comprehension, on the other hand, right hemisphere contribution was found in the right middle temporal gyrus. In another study (Stringaris et al., 2006), 12 healthy subjects read metaphoric or literal stimuli, followed by a single word, which could be semantically related or not to the preceding sentence context. Judging unrelated words as contextually irrelevant was associated with increased fMRI signal in the right ventrolateral prefrontal cortex (BA 47) in the metaphoric, but not the literal, condition.

Using Chinese stimuli, Ahrens et al. (2007) found a small difference between conventional metaphors and literal sentences in the right inferior temporal gyrus, but the differences between anomalous metaphors and literal sentences were quite large and involved bilateral activation. However, a limitation of this study is the significantly reduced understandability of the novel metaphors and the relatively small number of study subjects (n = 8) which makes the results presumably more susceptible for interindividual differences. In another study, Aziz-Zadeh, Wilson, Rizzolatti, and Iacoboni (2006) investigated comprehension of metaphorical phrases describing actions. A severe limitation of this study is that only 5 metaphorical stimuli were used.

So far 5 studies directly compared novel and salient metaphoric expressions (Ahrens et al., 2007; Mashal, Faust, Hendler, & Jung-Beeman, 2005, 2007; Schmidt & Seger, 2009; Yang, Edens, Simpson, & Krawcyk, 2009). In all studies, novel metaphoric expressions induced stronger blood oxygen level dependent (BOLD) response than salient stimuli. However, in the latter 4 studies (with whole brain analysis) only 43% of the reported maxima for direct comparison data locate to the right cerebral hemisphere.

Three fMRI-studies investigated the comprehension of metaphoric word pairs (Lee & Dapretto, 2006; Mashal et al., 2005, 2007; see also Faust, Volume 1, Chapter 21). The distinction between word and sentence level could be of importance since metaphoric words might have different lateralization patterns (Faust & Weisper, 2000; Rapp, Leube, Erb, Grodd, & Kircher, 2007). However, the word-level fMRI studies are themselves heterogeneous in terms of hemispheric lateralization. Lee and Dapretto (2006) found no fMRI activation in the right cerebral hemisphere. In contrast, Mashal and colleagues (2005, 2007) found evidence for a significant RH contribution on word level. Mashal and colleagues (2007) investigated novel metaphors ("pearl tears") in comparison to conventional metaphors ("bright student). Novel metaphoric expressions activated more the right superior temporal sulcus and RH IFG as well as BA 46 of the left hemisphere. Recently, one study (Mashal & Faust, 2010) investigated text level (stanzas). Unexpectedly, this study did not find any activation maxima for metaphoric > literal stimuli.

Five studies from 5 different countries so far have investigated the comprehension of *idioms* (Boulenger, Hauk, & Pulvermüller, 2009; Hillert & Buracas, 2009; Lauro, Tettamanti, Cappa, & Papagno, 2008; Mashal, Faust, Hendler, & Jung-Beeman, 2008; Zempleni, Haverkort, Renken, & Stowe, 2007). Studies used four different languages (Table 20.2). Zempleni and colleagues investigated comprehension of familiar idioms in sentence context in 17 healthy subjects (Zempleni, 2006; Zempleni et al., 2007). Two types of idioms were used as stimuli: literally plausible, ambiguous idioms and literally implausible, unambiguous idioms. The idiomatic versus literal sentence contrast elicited activation in the bilateral inferior frontal gyri and in the bilateral middle temporal gyri. The right temporal lobe was particularly involved in the processing of ambiguous idioms. Whereas Zempleni et al. applied a word-relatedness task in Dutch language, in another study by Lauro et al. (2008) subjects had to decide whether Italian idioms matched in meaning with a picture. Idioms specifically activated the left frontal and temporal cortex. Activations were also seen in the right superior and middle temporal gyri, in the temporal pole, and in the right IFG. Mashal et al. (2008) investigated processing of idioms in a block design with Hebrew stimuli. Again, both hemispheres were involved in direct comparison contrasts. Two studies used English-language stimuli: Hillert and Buracas (2009) found a role of Broca's area during comprehension of idioms, a finding that was also found in a study by Boulenger and colleagues (2009). The study by Mashal and colleagues (2008) provided evidence for the graded salience hypothesis using

Hebrew idioms: whereas processing salient meanings (the idiomatic meaning of idioms and the literal interpretations of a literal sentence) involved left hemisphere regions, the processing of nonsalient meanings (the literal interpretation of idioms) was associated with increased activity in right brain regions (Mashal et al., 2008).

So far, only one study investigated the comprehension of *metonymies* using fMRI (Rapp et al., in press). In this study, short phrasal metonymies activated a predominantly left frontotemporal network with maxima in the left and right IFG and the left middle temporal gyrus relative to matched literal control stimuli.

In contrast to other types of nonliteral language, research on *ironic expressions* is less dominated by the question of hemispheric lateralization. Irony comprehension draws clinical interest mostly because it essentially involves perspective-taking and second-order theory of mind processes (Blasko & Kazmerski, 2006; Colston & Gibbs, 2002; Happé, 1996; Sprong, Schothorst, Vos, Hox, & van Engeland, 2007). Lesions studies on irony comprehension sometimes do not disentangle the role of the cerebral hemispheres. Consistently, they point towards an important role of the medial prefrontal cortex in irony comprehension (see Rapp et al., 2010, for overview on lesion studies). A role of the medial prefrontal regions is as well supported by the six fMRI studies that so far used ironic stimuli (Rapp et al., 2010; Shibata, Toyomura, Itoh, & Abe, 2010; Uchiyama et. al, 2006; Wakusawa et al., 2007; Wang, Lee, Sigman, & Dapretto, 2006a, 2006b).

An ALE Meta-Analysis

An additional approach to illustrate the current evidence of nonliteral language anatomy is the application of a coordinate-based meta-analysis technique, the so-called activation likelihood estimation (ALE) method (Eickhoff et al., 2009; Turkeltaub, Eden, Jones, & Zeffiro, 2002). This research tool identifies consistent regions of activation across a collection of fMRI studies. The calculation is based on the reported activation maxima in the study publications and their number of study subjects. Coordinates are then modeled with a Gaussian function to accommodate the spatial uncertainty associated with a reported coordinate and are analyzed for where they converge (Laird et al., 2009).

We (Rapp, Mutschler et al., submitted) recently applied this methodology to the available fMRI studies on nonliteral language. Not all studies reported in Table 20.2 could be included, since inclusion of studies reporting data only from "region of interest" analysis could bias the analysis towards these regions. Twenty-one studies were included (Table 20.2). In these studies, approx. 250 activation maxima for direct comparison of nonliteral > literal stimuli are reported, about 30% of them correspond to the right cerebral hemisphere. An important cautionary remark is, however, that the number of reported maxima in fMRI research strongly interdepends with the chosen significance level (the lower the significance level, the larger the number of reported maxima; see also Wilke & Lidzba, 2007, for lateralization effects). Results could therefore be biased in the direction of the chosen significance levels.

Results of the meta-analysis of all studies comparing nonliteral and literal stimuli directly are shown in Figure 20.1a. Overall, nonliteral stimuli induce stronger activation in bilateral, yet more left-lateralized frontotemporal network. The strongest cluster is located in the left IFG (BA 45/9/44). Sixteen out of the 21 studies contribute to this cluster. The right hemisphere homologue of this brain region represents the second strongest cluster (right IFG/BA 47).

The ALE meta-analysis thus strengthens evidence for *a* role of the right hemisphere in nonliteral language comprehension. However, there is no right hemisphere *dominance* as only two out of 14 significant clusters are located in the right cerebral hemisphere. Such a dominance would be predicted by a strong version of the right hemisphere theory. Other clusters locate in the middle temporal gyrus bilaterally and in the left hemisphere paracingulate gyrus and the left thalamus.

A similar, but not identical pattern of activation was seen when only the 10 studies on *metaphor* were included into another ALE analysis. Again, bilateral, left > right clusters were detected in the IFG. Other clusters were activated inter alia in the left middle frontal gyrus (BA 9), and bilaterally in the parahippocampal gyrus and middle temporal gyrus.

A subanalysis only for salient metaphoric stimuli (with the activation reported for salient stimuli in Ahrens et al., 2007; Chen, Widick, & Chatterjee, 2008; Lee & Dapretto, 2006; Mashal et al., 2007; Schmidt, Kranjex, Cardillo, & Chatterjee, 2009; Stringaris et al., 2007) showed only left hemisphere clusters (Figure 20.1a). In contrast, a subanalysis only for nonsalient stimuli (from Ahrens et al., 2007; Mashal et al., 2007; Mashal, Faust, Hendler, & Jung-Beeman, 2009; Rapp et al., 2004; Schmidt & Seger, 2009; Shibata, Abe, Terao, & Miyamoto, 2007, Yang et al., 2009) showed clusters of activation in both hemispheres (Figure 20.1a). Of note, however, still more clusters were located in the left cerebral hemisphere, so that the right cerebral hemisphere seems to be involved, but not dominant.

The 5 studies on *idiom* comprehension (Boulenger et al., 2009; Hillert & Buracas, 2009; Lauro et al., 2007; Mashal et al., 2008; Zempleni et al. 2007) were included into another ALE meta-analysis (Figure 20.1b). A cautionary remark is that 5 studies is presumably a low number for an ALE analysis. All studies reported activation maxima in both hemispheres (18 out of 48 reported maxima are in the right hemisphere). The ALE analysis showed four significant clusters (Rapp, Mutschler, et al., submitted). The strongest cluster was once more in the left IFG. Only one cluster in the medial frontal lobe showed small elongation into the right cerebral hemisphere. Altogether, the network for idioms is similar to the one for salient metaphors (Figure 20.1b).

Five studies were included into an ALE meta-analysis *of irony/sarcasm* (Rapp et al., 2010; Shibata et al., 2010; Uchiyama et al., 2006; Wakusawa et al., 2007; Wang et al., 2006b). Although this is a small number of studies for an ALE analysis, three clusters came out significant. The largest cluster was in the right superior/middle temporal gyrus (BA 22/21/41). The studies by Uchiyama et al., Wang et al., and

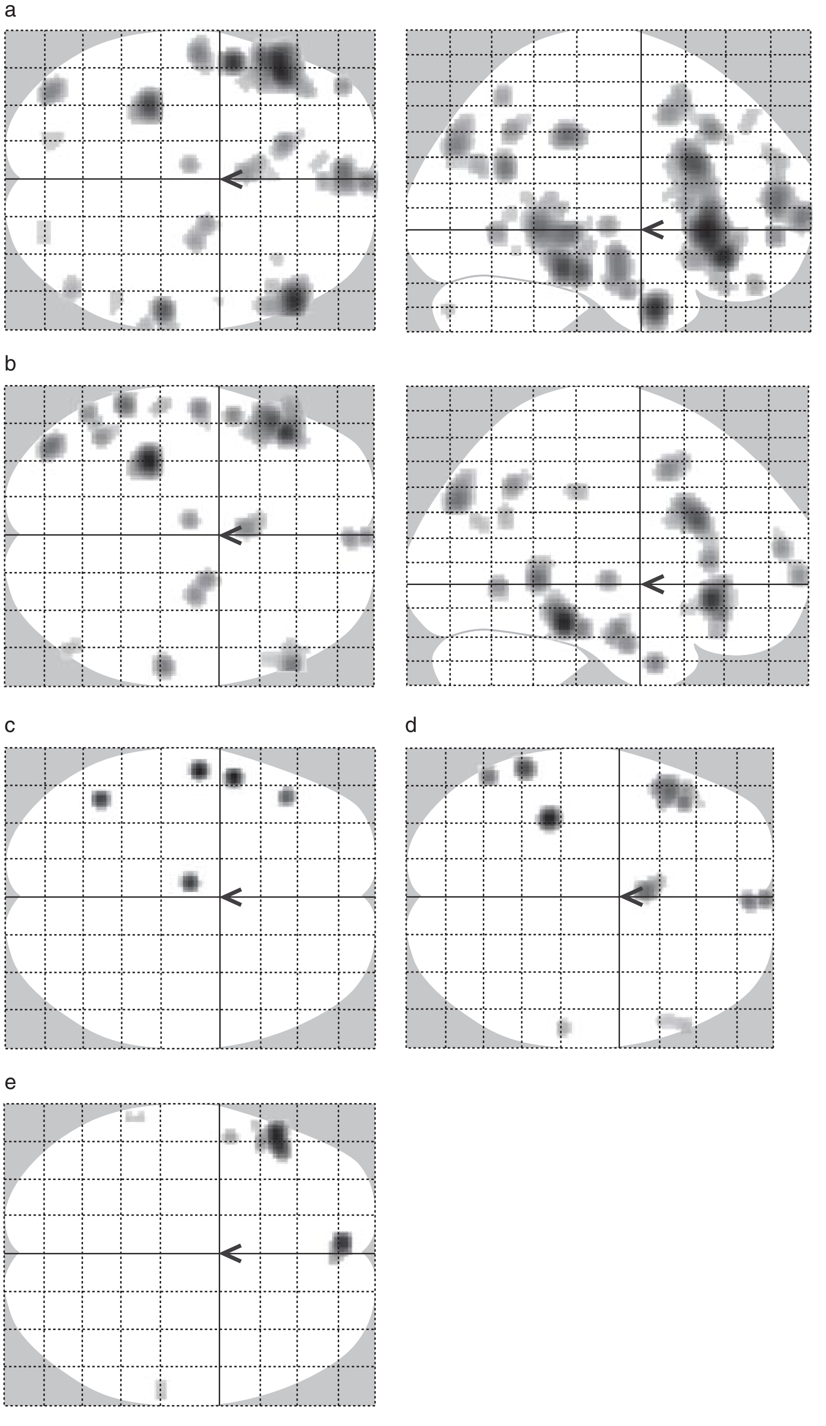

Figure 20.1 ALE meta-analysis of studies on nonliteral language (from Rapp, Mutschler, et al., submitted). Significance level $p < 0.001$, extent 5 vx in all analysis. (a) ALE meta-analysis of 21 fMRI studies on nonliteral language (marked with X in Table 20.2). (b) ALE meta-analysis of studies reporting contrasts for salient metaphoric > literal stimuli. Data included from studies no. 1, 7, 11, 12, 13, 16, 20, 21, 23, 24 in Table 20.2. (c) ALE meta-analysis of studies reporting contrasts for salient metaphoric > literal stimuli. Data included from studies no. 7, 11, 12, 13, 20, 24 in Table 20.2. (d) ALE meta-analysis of studies reporting contrasts for novel metaphoric > literal stimuli. Data included from studies no. 1, 11, 13, 16, 21, 23, 24 in Table 20.2. (e) ALE meta-analysis of studies reporting contrasts for idioms > literal stimuli. Data included from studies no. 15, 17, 18, 19, 22 in Table 20.2.

Shibata et al. contribute to this cluster. This finding is congruent with the fMRI studies by Eviatar and Just (2006) who found BOLD response induced by ironic stimuli in this region using a ROI-approach and the study by Wang et al. (2006a) indicating a role of the right temporal lobe for irony comprehension in children. Recently, Rapp et al. (2010) reported a correlation between right temporal lobe BOLD response during irony comprehension and psychometric schizotypy. Schizotypy is a personality trait that likewise is associated with hemispheric lateralization differences (Somers, Sommer, Boks, & Kahn, 2009) and has genetic and clinical similarities with schizophrenia (Raine, 2006). Findings from the brain lesion studies are compatible with the fMRI studies in respect to the right middle superior temporal gyrus in irony appreciation (Giora et al., 2000; Zaidel et al., 2002). Another cluster of activation was present in the medial frontal gyrus. Like in most brain lesion studies, this cluster was located in the right medial prefrontal lobe. In contrast, most fMRI studies on irony reported more left medial frontal contribution (see Rapp et al., 2010). Medial frontal brain activation could likewise be a correlate of second-order theory of mind processing, a mental operation that is essentially involved in irony comprehension (Blasko & Kazmerski, 2006; Colston & Gibbs 2002; Happé, 1996; Sprong et al. 2007). The two latest-published studies (Rapp et al., 2010; Shibata et al., 2010) contributed to a third cluster located in the right premotor cortex.

Conclusion

So far, it is evident that right hemisphere contribution is present in most studies of nonliteral language. However, it is less clear which factors contribute to the extent of the right hemisphere′s involvement. Rather than "nonliterality" per se, other factors like salience (Giora, 2007) or figurativeness (Schmidt et al., 2010) could play an important role. The exact role of such influencing factors, however, is so far not yet clear. Overall, studies using salient stimuli reported less right hemisphere contribution than novel stimuli (Rapp, Mutschler, et al., submitted). However, some inconsistent findings are incompatible with a strong version of the graded salience hypothesis (e.g. Rapp et al. 2007). Many current findings point towards a central role of the left (and to a lesser extent the right) IFG in the comprehension of nonliteral language. In their initial study, Rapp et al. (2004) claimed that especially the anterior-inferior part, corresponding to BA 45/47, plays a key role in nonliteral language comprehension. However, newer research indicates that not only the anterior-inferior, but additional other parts of the IFG (including Broca's area) are active during nonliteral language comprehension. The IFG plays a key role in semantic language comprehension on a sentence level (Bookheimer, 2002). Research on literal language indicates that this brain region plays a central role in integrating semantic meanings into a sentence context (e.g., Arcuri, 2003; Zhu et al., 2009). During metaphor comprehension, activation of this region could be a correlate of bringing together distant semantic meanings. As well, this region plays an important role in integrating world knowledge into a sentence context (Pylkkänen, Oliveri, & Smart, 2009). For example, Hagoort and colleagues (Hagoort, Hald, Bastiaansen, & Petersson, 2004; Hagoort, 2005) found an effect of integrating world knowledge on the BOLD reponse in the left IFG, especially in BA 45 and 47. Beyond this, the IFG of both hemispheres may contribute to unification of discourse information with previously stored knowledge in long-term memory during comprehension of literal and nonliteral sentences (Hagoort, 2005; Menenti, Petersson, Scheeringa, & Hagoort, 2009).

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