Review

The neuropsychology of narrative: story comprehension, story production and their interrelation

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Abstract

Stories are used extensively for human communication; both the comprehension and production of oral and written narratives constitute a fundamental part of our experience. While study of this topic has largely been the domain of cognitive psychology, neuroscience has also made progress in uncovering the processes underlying these abilities. In an attempt to synthesize work from both literatures, this review: (1) summarizes the current neuroimaging and patient research pertaining to narrative comprehension and production, (2) attempts to integrate this information with the processes described by the discourse models of cognitive psychology, and (3) uses this information to examine the possible interrelation between comprehension and production. Story comprehension appears to entail a network of frontal, temporal and cingulate areas that support working-memory and theory-of-mind processes. The specific functions associated with these areas are congruent with the processes proposed by cognitive models of comprehension. Moreover, these same areas appear necessary for story production, and the causal-temporal ordering of selected information may partially account for this common ground. A basic description of comprehension and production based solely on neuropsychological evidence is presented to complement current cognitive models, and a number of avenues for future research are suggested.
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1. Introduction

Human experience, both interpersonal and intrapersonal, is highly influenced by the act of comprehending stories, producing stories, and executing the subprocesses that enable such understanding and productions. As narrative consumers we appear insatiable, finding the personal stories of others absolutely compelling (e.g. anecdotes or gossip) and spending a great deal of time engaged with novels, plays, films and television shows (i.e. crafted or "public" narratives). This affinity for narrative emerges at a very young age, when we develop deep and long-lasting emotional attachments to the storybooks and movies that surround us at childhood (Alexander, Miller, & Hengst, 2001). Importantly, our interactions with fictional narratives should not be viewed as frivolous; stories have the power to change our beliefs about the real world. Researchers have repeatedly found that reader attitudes shift to become more congruent with the ideas expressed in a narrative after exposure to fiction (Green & Brock, 2000; Prentice, Gerrig, & Bailis,

1997; Strange & Leung, 1999; Wheeler, Green, & Brock, 1999).

As human communicators we are prolific story producers, predominately utilizing a distinctly story-like structure to communicate with others (Miller, 1995; Schank & Abelson, 1995). This structured narration of experience is also not to be taken lightly, as it appears necessary for maximal health. Researchers have found that the more coherent and organized an account that one creates for a past trauma, the greater the likelihood of salutary gains as a result of such narration (Pennebaker & Graybeal, 2001; Pennebaker & Seagal, 1999; Smyth, 1998). Along similar lines, many clinicians have posited that creating a coherent story of a traumatic event and incorporating it into one's self-representation is fundamental for the successful treatment of post-traumatic stress disorder (Brewin, Dalgleish, & Joseph, 1996; Herman, 1992; van der Kolk & Fisler, 1995). The benefits of narration may also generalize beyond the realm of personal trauma; some evidence exists that similar advantages accrue when the content of personal narrations are future-oriented and distinctly non-traumatic (King, 2001). Storytelling is thus not only a native element of our social interactions, from a health standpoint

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there is evidence to suggest it may also be a necessary one.

Aside from the direct expression and consumption of stories, there is evidence to suggest that we may use processes akin to narrative construction in the formation of our individual history. Humans select and order personal memories, building a coherent and organized representation of the self (i.e. a 'self-narrative'; Gergen & Gergen, 1988; Habermas & Bluck, 2000). These same processes may also be employed when we make reasoned judgements. In a judiciary context, researchers have found that jurors arrive at courtroom verdicts based upon the creation and coherence-testing of multiple different stories constructed to account for the presented evidence (Pennington & Hastie, 1986, 1992).

In psychology, the study of narrative processes has primarily fallen within the domain of cognitive psychology, although the broad appeal of this topic is reflected in the large number of researchers labouring in a variety of other disciplines. Despite the distributed nature of research in this area, however, the synthesis of ideas from different domains is disappointingly rare. The current review hopes to address one specific absence of integration, that between narrative neuroscience and the discourse models of cognitive psychology. This particular omission is especially striking given that cognitive processing is necessarily bounded by the limits of neural architecture. The current writing attempts to draw cognitive theory and neuropsychology closer together, in the hopes that their marriage will be of mutual benefit to both areas. Admittedly, there are some formidable hurdles to such an attempt. First, the body of brain research specifically devoted to narrative is relatively young and by no means extensive. There exists, nevertheless, enough research within the neuropsychology of narrative to construct an interesting, preliminary portrait of this fundamental human process. In conjunction, work that has touched on narrative somewhat tangentially can serve a useful and illustrative, although not definitive, function. The second major hurdle is not so much an obstacle as a caution. Current knowledge of the brain and its functions does not yet approach the specificity at which most cognitive models are described. This separation inevitably raises difficult questions regarding the role of theory in neuroscientific empiricism (Jennings & Aamadot, 2000). Should cognitive models be limited to what is known about the brain? Conversely, should endeavours in brain research be constrained by the predictions of current theories? One conservative approach may be to question all models that contradict our understanding of brain processes, while provisionally retaining any model for which a coherent neural account can be made so that its predictions may be further tested. Firmly discarding or accepting individual models on the basis of brain research is thus likely to be quite difficult. It may be, however, as Gernsbacher and Kashak (2003) conclude in their review, that "making fundamental progress in understanding how the brain processes language will require the exploration of neural processing in a way that does not rely as heavily on the theoretical baggage of cognitive psychology" (p. 110).

One question that may be answered by a review of neuropsychological findings, in the absence of testing any elaborate theory, is how narrative production and comprehension might be related. To the extent that these two processes share a common substrate, one would expect to observe similar activations during brain imaging and similar brain damage in patients with these functional deficits. Divergent associations with particular brain regions should indicate the degree to which these two abilities differ, and possibly the nature of this parting. In this review, two subprocesses are hypothesized to underlie both the production and comprehension of narratives: selection and causal-temporal ordering.

In sum, this article aims to: (1) review the current neuropsychological literature on narrative, (2) compare current cognitive theories of narrative comprehension and production to these findings, and (3) investigate the relation between narrative comprehension and production. To begin, a preliminary, working definition of narrative is proffered with a particular focus on distinguishing this genre from other forms of discourse. Cognitive theories of story comprehension are then reviewed and compared to the relevant brain-imaging and lesion research. An examination of story production follows, and the relation between production and comprehension is subsequently examined.[1]

2. Defining narrative

One fundamental characteristic of stories is the presence of a causal event-structure. Following a distinction by Graesser, Hauft-Smith, Cohen, and Pyles (1980), a narrative presentation can be thought of as the description of a series of actions and events that unfold over time, according to causal principles. These rules of causation demand that events occur in a constrained, logically coherent order. Episodes and actions that allow for other events must take temporal precedence given the conflation of logical (if x then y), causal (because x then y), and temporal priority (first x then y) found in narratives (Barthes, 1982; Dixon, 1996). Coherence is also derived from a lack of superfluous or tangential information, a fact that Aristotle was perhaps the first to identify in his *Poetics* (trans. 1987). As Roland Barthes (1982) also observed, "a narrative is never made up of anything other than functions: in differing degrees, everything in it signifies" (p. 261). The significance of a narrative element appears to be determined by the goals and intentions of story characters. The most basic elements of a story include a setting, and an agent who holds a certain goal (e.g. the purchase of a car) and whose progress towards that goal is impeded (e.g. the loss of a job) or facilitated (e.g. the gain

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[1] Imaging research on the recall of narratives (e.g. Paradiso et al., 1997) is not discussed in this review as it is often difficult to separate the relative contribution of comprehension from production and vice versa.

of an inheritance) by certain events (Oatley, 1992; Peterson, 1999). With crafted narratives it is often left, in part, to the audience to infer why the elements included in a narrative are significant. In a way, comprehending literary narratives entails the reverse of certain processes employed in real-world experience. With regard to the latter, attention is often directed as a function of current goals (Yantis, 1996); the former demands the inference of intentions and goals through interpretation of the objects and episodes selected by the author. If a well-crafted story contains mention of an event or character, it is assumed that this element is in some way relevant to the goals of the protagonist.

While narrative and expository texts both comprise connected sentences that have local and global coherence, narrative is unique in a number of ways. It is only in stories that one witnesses the creation of an imagined world which mirrors our own realm of experience (Bruner, 1986; Gerrig, 1993; Graesser, Mills, & Zwaan, 1997; Oatley, 1999). The world of stories is one of intentional, autonomous agents who hold unique goals, and who act and emote in ways congruent with these goals. Readers of narrative often comprehend the depicted events by assuming the perspective of a character (Black, Turner, & Bower, 1979; Özyürek & Trabasso, 1997; Rall & Harris, 2000), mentally representing his or her emotional states (Gernsbacher, Goldsmith, & Robertson, 1992). This mental simulation can result in the experience of affect on the part of the reader, in a manner congruent with a character's situation and equivalent to the emotional experiences encountered in the real-world (László & Cupchik, 1995; Oatley, 1992, 1994, 1999). Understanding narrative, then, requires the understanding of intentions, goals, emotions and other mental states held by characters (Frith & Frith, 1999); the ability to attribute mental states to autonomous agents is known as theory-of-mind (Carruthers & Smith, 1996). Language and theory-of-mind are closely linked developmentally (Astington & Jenkins, 1999; Garfield, Peterson, & Perry, 2001), and there is evidence that acquiring this capacity at around age 4 mediates children's capacity to understand narrative (Astington, 1990). Expository texts, in contrast, lack characters, elaborated depictions of events and environments, and rarely elicit the type of emotional reaction commonly resultant from good literature. At best, while reading an essay one may become excited by an interesting idea, or saddened at the quality of a student's writing. These reactions, however, are most unlike the simulation of experience that appears to drive the emotional response which often accompanies narrative comprehension.

One must be careful not to confuse the discrimination between narrative and expository texts with that between fiction and nonfiction. A narrative may be nonfiction, provided it still follows the tenets of a story presentation (Oatley, 1999). As Aristotle (trans. 1987) noted, there exists no reason why true events can not be the basis of a crafted narrative, and in fact, journalists have begun to use narrative tropes in their portrayal of actual events in order to capitalize upon the compelling nature of stories (Wolfe & Johnson, 1975). Similarly, narratives may be embedded within an expository text, in the form of illustrative anecdotes or thought-experiments. Narrative, then, is the depiction of events driven by the intentional behaviour of one or more autonomous agents in a manner that manifests an imagined world which parallels the world of real experience. Expository texts, on the other hand, outline an argument or explanation in order to communicate propositional information directly, for rhetorical or informational purposes (Bruner, 1986; Graesser et al., 1997). Empirical studies have demonstrated that the difference between stories and essays has measurable implications, with regard to comprehension and recall (Graesser et al., 1980; Petros, Bentz, Hammes, & Zehr, 1990; Weaver & Bryant, 1995; Zabrucky & Moore, 1999; Zabrucky & Ratner, 1992), the likelihood of drawing inferences (Singer, Harkness, & Stewart, 1997), the updating of mental models upon second readings (van Oostendorp & Goldman, 1999a), as well as the length and coherence of spontaneous productions by children (McCutchen, 1987). Although more detailed descriptions of what defines literary narratives exist (e.g. Barthes, 1982; Rumelhart, 1975), they lie beyond the scope of this paper.

3. Story comprehension

3.1. Cognitive models of narrative comprehension

Studies of discourse tend to examine goal-based stories more often than any other genre (van Oostendorp & Goldman, 1999b). This is likely a result of the fact that cognitive models used to predict memory for and mental representations of text are most successful with respect to stories (van Oostendorp & Goldman, 1999a). While there exist a number of these models, many differ from one another at a level of detail not useful for comparison with brain areas and their known functions. The discussion which proceeds is strictly intended for relating cognitive models and neuropsychological findings; these theories are thus, by necessity, described in quite broad terms. Readers interested in the details of these frameworks are directed to the source articles or reviews (e.g. Clifton & Duffy, 2001; Graesser et al., 1997).

Although early theories of discourse comprehension focused on the reader's representation of the text itself, most modern models agree on the importance of understanding how readers represent what a text describes. These representations are known as mental models (Johnson-Laird, 1983) or situation models (van Dijk & Kintsch, 1983). Memory-based models such as the minimalist hypothesis (McKoon & Ratcliff, 1992, 1998), however, focus on the automatic memory processes that likely support comprehension at the local level, and don't address strategic processes thought to be necessary for creating global representations. These approaches are not at odds with models

that examine more elaborate processing, the issues of strategic inferencing simply lie outside of their domain. Furthermore, the passive and automatic activation of material from long-term memory described by memory-based theories appears similar to the first step in more elaborate constructionist models (Clifton & Duffy, 2001). The latter, such as Kintsch's Construction-Integration model, describe an initial, automatic, and indiscriminate activation of information relevant to the currently processed word or clause, relatively ignorant of context (Kintsch, 1988). According to these theories, cues held in working memory are used to retrieve information such as elaborative real-world knowledge from long-term storage. Constructionist models distinguish themselves from models such as the minimalist hypothesis, however, in the proposal of a second, more strategic integration process. This mechanism serves to inhibit activated information that is irrelevant to the current context, leaving only that which may aid comprehension to be incorporated into the mental model. Computational models of text comprehension based upon the construction–integration framework attempt to describe in connectionist terms how integration might take place using ideas such as spreading activation and decay (Kintsch, 1994, 2000; Langston & Trabasso, 1999; van den Broek, Young, Yuhtsuen, & Linderholm, 1999). This approach to modelling cognition benefits from what we know of neuronal architecture, but the products are often too detailed in resolution to be properly addressed by neuroimaging and lesion studies. A more general model by Gernsbacher (1997), known as the Structure Building Framework, proposes that readers: (1) lay the foundation for representing new information, (2) map new information onto related previous information, and (3) shift and create new foundations when incoming information is less coherent with previous structures. Zwaan and Radvansky (1998) have proposed a slightly more specific model, the Event-Indexing Model, in which the mental model constructed by a reader is composed of at least five dimensions: (1) temporal, (2) spatial, (3) causal, (4) motivational, and (5) person/object. Coupling the idea that readers track multiple aspects of a narrative with theories of perceptual symbol systems (Barsalou, 1999), Zwaan (2004) has proposed a new model known as the Immersed Experiencer Framework. The primary contribution of this theory is the idea that words automatically activate experiences of their referents. Based on this premise, three steps are proposed to underlie narrative comprehension: (1) words activate broad functional webs that are also activated when the referent is experienced; (2) current webs are articulated by previous webs and vice versa, constraining initially broad activations to currently relevant information; and (3) integration into the current memory representation occurs via the construction of transitions between these articulated webs in ways similar to the modulation of attention. These ideas appear in keeping with the theory of narrative experience as cognitive and emotional simulation previously proposed by Oatley (1999).

3.2. Potential brain regions predicted by cognitive models

Ascribing possible brain areas to support each of these models is a daunting task. This endeavour is made more manageable, however, by examining only those brain areas uniquely associated with story-processing. For the most part, studies of discourse-level language use other lower-level language tasks as a comparison or control. In this way, brain areas engaged during narrative tasks but also active during sentence-level presentations, such as semantic processing or the encoding of stimuli into long-term memory, are somewhat taken into account. It is probable that a great number of brain regions contribute to narrative comprehension. Any network that supports language, memory, and even perception is likely to play some role. This review, however, selectively examines those areas that are engaged during processes specific to discourse-level language. With this in mind, and the obvious caveats notwithstanding, it appears that cognitive models of comprehension describe narrative processes that fall under three broad categories: (1) memory encoding and retrieval, (2) integration, and (3) elaboration or simulation.

While the minimalist hypothesis appears to advocate few memory processes unique to narrative, memory-based researchers agree that more strategic processing occurs under certain conditions (McKoon & Ratcliff, 1998). Assuming the presence of a specific reading goal, for example, the minimalist position defers to theories such as the constructionist model for comment on more global processing. Given the nature of neuropsychological testing, in which readers almost always have a clear goal, how do these latter models predict the use of memory in a manner beyond that engaged during sentence comprehension? The difference appears to lie in the identification of global coherence and the tracking of relations between distant clauses within a text. Maintenance of information over relatively long periods of time is supported by the continued firing of neurons following the removal of eliciting stimuli, and the brain region that best performs this function is the frontal lobe (Rolls, 2000). Appropriately, neurons in the dorsolateral prefrontal cortex (specifically Brodmann's Areas [BAs] 6, 8, and 9/46) have been associated with the cross-temporal and cross-modal processing likely necessary for language processing (Fuster, Bodner, & Kroger, 2000). Other regions in the frontal lobe also appear important, especially upon consideration of the functional areas identified by Moscovitch and Winocour's (2002) Working With Memory model. Processes of strategic memory retrieval most relevant to story comprehension from this model include: (1) the monitoring and manipulation of the contents of working memory (mid-dorsolateral frontal cortex, BAs 9, 46); (2) the specification and/or maintenance of cues for long-term memory retrieval and encoding (ventrolateral frontal cortex, BA 47); and (3) the processes of rejecting (ventromedial frontal cortex, BAs 11, 13, 25) or accepting (anterior prefrontal cortex, BA 10) the products of memory retrieval.

It is deserving of note that a number of other theorists have also recognized the importance of working memory for text comprehension (Baddeley & Wilson, 1988; Just & Carpenter, 1992), particularly the role that inhibitory selection processes might play in the efficient operation of this ability (Hasher & Zacks, 1988; Hasher, Zacks, & May, 1999). As well, the multi-component model of working memory proposed by Baddeley (2000) includes a temporary store known as the episodic buffer that integrates, manipulates, and maintains complex multimodal information. This buffer is also thought to permit the modelling of hypothetical situations, and theoretically forms a foundation for narrative processes (Baddeley & Wilson, 2002). Based on neuropsychological evidence, the functions performed by this component of working memory are thought to be localized in the right frontal lobe (Baddeley, 2000).

The integration and articulation of representations described in constructionist models are expected to engage the selection, monitoring and manipulation processes found in the above-mentioned frontal areas. Of these, the mid-dorsolateral frontal cortex is of interest given its support of temporal ordering, processing of sequential information and temporal integration (Fuster, 2002; Moscovitch & Winocour, 2002). As well, specific frontal areas modulate attention in ways possibly useful for achieving integration through the selective and organized recruitment of other cortical areas. Orbitofrontal regions likely play an important role as a function of their link to inhibition processes; similarly, the anterior cingulate is also likely to be involved due to its association with motivation (Fuster, 2002). The control of attention found in these areas seems specifically related to the shifting stage of the Structure Building Framework, and proposals of language as a modulator of attention embedded in the integration-cum-transition process of the Immersed Experiencer Framework. Also related to issues of integration, a neuroanatomically-based model of narrative comprehension has been offered by Beeman (1993, 1998; Beeman, Bowden, & Gernsbacher, 2000), espousing the importance of right hemisphere networks. Beeman proposes that the right hemisphere appears suited for coarse, distal coding of loose associations whereas the left hemisphere is optimized for more specific coding of immediate and obvious connections. While the right hemisphere aids in activating certain inferences, the left hemisphere is thought to ultimately select and integrate these inferences into the discourse structure. Construction and identification of global coherence is thus likely aided by right hemisphere networks although left hemisphere activation is also predicted by this model.

Both the Event-Indexing Model and Immersed Experiencer Framework predict that an even broader network of activations may occur during story comprehension in conjunction with previously mentioned memory and integration areas. The indexing of persons and motivations purported to take place according to both models implies that areas associated with inferring intentions should be active during story reading. Frith and Frith (1999, 2000, 2001) have noted in a number of reviews that mental inferencing appears to involve the medial prefrontal cortex, particularly the paracingulate cortex located at the most anterior portion of the anterior cingulate, as well as the temporo-parietal junction, located at the superior and posterior portion of the superior temporal sulcus near the superior temporal gyrus; there is also weaker evidence that the temporal poles and amygdala may be involved. Furthermore, the monitoring of spatial relations predicted by these models may lead to activation in hippocampal regions (Rolls, 2000), along with parietal and medial occipital areas, and the posterior cingulate (Grön, Wunderlich, Spitzer, Tomczak, & Riepe, 2000). The Immersed Experiencer Framework, specifically, appears to predict still wider activation, including all primary sensory areas and any part of the brain that might become active during experience with the referents of the words read (Zwaan, 2004). Such activations, however, may not be unique to narrative processing but should also occur during sentence and even single-word processing. A contrary possibility is that the continual activation and articulation of certain sensory or motor networks during discourse comprehension may result in the relatively stronger activation of these areas compared to more micro-level presentations.

Participation of the frontal lobes during narrative comprehension appears to be a common prediction across models. Congruent with this thinking, Grafman (2002) has proposed a theory of prefrontal cortex function that is relevant to story comprehension. According to his model, the prefrontal cortex represents structured, sequential events (known as Structured Event Complexes) that are goal-oriented and schematic. More specifically, Grafman isolates the right prefrontal cortex as the centre of coarse, slower processing of loosely associated information such as that found in the themes and morals of stories. The functions attributed to more specific areas of the prefrontal cortex, such as social event sequences (ventromedial prefrontal cortex) and predictable event sequences (medial prefrontal cortex), all appear relevant for narrative processing.

3.3. Neuroimaging studies of narrative comprehension

While the use of imaging technology to examine story comprehension is made difficult by the temporal nature of stories, there exist a number of interesting and clever experiments on this topic. Fletcher et al. (1995) collected PET data while volunteers read: (1) stories that required the attribution of mental states to characters ("theory-of-mind" stories), (2) stories that did not involve such attributions ("physical" stories), and (3) random sentences (unlinked-sentences). When the physical-story condition was compared to the unlinked-sentences condition, differential activation was observed in the temporal poles (bilaterally, BA 38), the posterior cingulate (BA 23/31), and the left superior temporal gyrus (BA 22/39). Repeating this contrast with theory-of-mind stories in lieu of physical ones led to the

Table 1
Summary of contrasts from imaging studies of narrative comprehension, production and narrative subprocesses

[Study] task–control	Frontal					Motor/parietal			Temporal				Posterior/subcortical			
	MeFG	OF/ACC	SFG	MFG	IFG	PMC	MC	IPa	MTG/S	STG/S	ITG/S	TP	PC	PCC	OC	SC
Comprehension																
P [fle] ToM–US	□								□			☼		■		
P [fle] PS–US									□			☼		□		
P [mag] 2nd–1st present				□									◇	◇		
P [mag] stand.–unus. Story		◇										□				
P [mag] corr. w/comp.		◇													◇	
P [mag] corr. w/mem.			□												◇	
P [mag] rel.–irr. Picture															◇	
P [*maz*] *stories–words*			□						□			☼				
P [nic] moral–semantic				■					■						□■☼	
F [*rob*] *definite–indfnte*	■		■													
F [*stg*] *untitled–titled*				■					■		☼	■[1]				
F [*stg*] *titled–untitled*									□			□[1]				
F [vog] PS–US																
F [vog] ToM–US		■														
F [vog] ToM/SP–US		■				■	■									
F [vog] SP–US		■				■	■			■[2]						
Production																
P [bra] lang.–comp.motor	□			□				□■[3]	☼	□☼			◇	◇■	□■[4]	□■[5]
P [par95] emo. Scpt–CTL	☼	□					■		☼		□				☼	
P [par95] neut. Scpt–CTL	□■		■	☼			■		■				□			
Subprocesses																
F [*cro*] *script–syntax ordr*				□■		□		□[3]								
P [par96] event memb–FD	□	□	□[6]								□[7]	□[7]				
P [par96] temp order–FD	■		■						☼	□						
P [par96] temp order–AC	■															
P [par96] temp order–EM	■		■	■				■[8]	■							

Note: (□) Left, (■) Right, (☼) Bilateral, (◇) Midline. P: PET study, F: fMRI study. (1) Middle temporal sulcus, BA 38; (2) temporoparietal junction; (3) angular gyrus; (4) mesial temporal cortex-lingual, striate cortex, lateral occipital cortex; (5) parahippocampal fusiform; (6) medial superior frontal gyrus; (7) anterior superior temporal gyrus, BA 38; (8) supramarginal gyrus.

same pattern of activation, with the addition of a left medial frontal area (BA 8). Lastly, when theory-of-mind and physical stories were compared, activation was observed in the left medial frontal gyrus, as well as the posterior cingulate and right inferior parietal lobe.[2] The researchers thus concluded that the medial prefrontal region is specifically responsible for the attribution of mental states. They also attributed temporal pole activation to the construction of a story representation during comprehension through the linking of propositions, and left posterior superior temporal activation to discourse-level processing. The final area activated during both story conditions, the posterior cingulate, was hypothesized post hoc to be associated with visual imagery, or possibly the incorporation of information into a burgeoning story structure. It should be noted that the physical stories employed here are somewhat atypical narratives; even simple children's stories often require the

attribution of complex intentions to characters (Astington, 1990).

Vogeley et al. (2001) modified these stimuli slightly to examine the taking of one's self-perspective along with understanding the mental states of characters. Using fMRI, these researchers again compared brain activity associated with reading stories to that observed during the reading of unlinked sentences. When the stories did not entail any mental inference (physical-stories), no significant increases in neural activity were observed compared to the control task. When stories involving mental state inference (with regard to the self, other or both) were compared to this baseline, activation was observed in the right anterior cingulate, right premotor and motor cortex, and right temporoparietal junction (activation varied somewhat according to the type of inference, see Tables 1 and 2). These areas differ from those found previously, most notably in the absence of temporal pole and left superior temporal activation. It is likely, however, that this lack of replication is a function of methodological differences. Vogeley et al. (2001) used a different imaging method and more importantly, a much higher threshold of significance compared to Fletcher et al. (1995). This cannot, however, fully account for the activations

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[2] See also Gallagher et al. (2000), who found activation in the medial prefrontal cortex (BA 8/9), left and right temporal poles (BA 38), and the temporoparietal junction (BA 39/40), during comprehension of theory-of-mind stories and cartoons controlling for activation witnessed during non-theory-of-mind materials.

Table 2
Description of contrasts and acronyms from Table 1

Description	Contrast (target–control)	Acronym	Area
Comprehension			
P [fle] ToM–US	Theory-of-mind stories—unlinked sentences	MeFG	Medial frontal gyrus
P [fle] PS–US	Physical stories—unlinked sentences	OF/ACC	Orbitofrontal/anterior cingulate
P [mag] 2nd–1st present	2nd—1st presentation of stories	SFG	Superior frontal gyrus
P [mag] stand.–unus. story	Standard stories—unusual stories	MFG	Middle frontal gyrus
P [mag] corr. w/comp.	Correlations with increasing comprehension	IFG	Inferior frontal gyrus
P [mag] corr. w/mem.	Correlations with increasing memory	PMC	Premotor cortex
P [mag] rel.–irr. Picture	Relevant picture preceding unusual story—irrelevant picture	MC	Motor cortex
P [maz] stories–words	Stories—single words	IPa	Inferior parietal
P [nic] moral–semantic	Judging shared moral of fables—shared semantic features	MTG/S	Middle temporal gyrus/sulcus
F [rob] dfinite–indfnte	Sentences beginning with definite articles—indefinite articles	STG/S	Superior temporal gyrus/sulcus
F [stg] untitled–titled	Untitled unusual stories—titled unusual stories	ITG/S	Inferior temporal gyrus/sulcus
F [stg] titled–untitled	Titled unusual stories—untitled unusual stories	TP	Temporal poles
F [vog] PS–US	Physical stories—unlinked sentences	PC	Precuneus
F [vog] ToM–US	Theory-of-mind stories—unlinked sentences	PCC	Posterior cingulate cortex
F [vog] ToM/SP–US	Theory-of-mind/self-perspective stories—unlinked sentences	OC	Occipital cortex
F [vog] SP–US	Self-perspective stories—unlinked sentences	SC	Subcortical structures
Production		Study	Citation
P [bra] lang.–comp.motor	American Sign Language and English narrative production—complex motor movements	[fle]	Fletcher et al., 1995
		[mag]	Maguire et al., 1999
P [par95] emo. Scpt–CTL	Imagining an emotional script—generating words or imagining objects from categories of items	[maz]	Mazoyer et al., 1993
		[nic]	Nichelli et al., 1995
P [par95] neut. Scpt–CTL	Imagining a neutral script—generating words or imagining objects from categories of items	[rob]	Robertson et al., 2000
		[stg]	St. George et al., 1999
Subprocesses		[vog]	Vogeley et al., 2001
F [cro] script–syntax ordr	Script-ordering—syntax-ordering	[bra]	Braun et al., 2001
P [par96] event memb–FD	Evaluating event membership—discriminating font of same stimuli	[par95]	Partiot et al., 1995
P [par96] temp order–FD	Evaluating temporal order—discriminating font of same stimuli	[cro]	Crozier et al., 1999
P [par96] temp order–AC	Evaluating temporal order—evaluating actions	[par96]	Partiot et al., 1996
P [par96] temp order–EM	Evaluating temporal order—evaluating event membership		

observed only by the former. As a possible explanation, these regions (motor areas and the right temporoparietal junction) were most associated with the taking of self-perspective, a task unique to this study. For both of these experiments, the reading of unlinked sentences may entail a greater working memory load than linked sentences, since in the former condition readers will likely attempt to make sense of the incoherent presentation (Vogeley et al., 2001). Thus, comparisons with this baseline task may mask activations associated with working memory (e.g. prefrontal areas; Fuster, 2002).

The findings of Fletcher et al. (1995) were more successfully replicated in a study by Maguire, Frith, & Morris (1999), using the same imaging method (PET). These researchers found anterior medial parietal/posterior cingulate (BA 31) activation when subjects were in the process of associating incoming information with prior knowledge in order to create a coherent narrative representation. This activation, however, could also have reflected spatial imagery processes since the researchers used pictures to deliver knowledge frameworks related to the narratives. Left temporal pole (BA 38) activation was also observed and interpreted to reflect the creation of a narrative through the concatena-

tion of sentences. Maguire et al. (1999) also found frontal activation in the ventromedial orbitofrontal cortex (BA 11), which increased as story comprehension grew. Based on the purported role of this region in reward monitoring (Rolls, 2002), the researchers hypothesized that this activation may reflect the rewarding nature of increasing comprehension but not understanding per se. Such a view of orbitofrontal function may be too narrow, however (Schoenbaum & Setlow, 2001). Furthermore, this conclusion by Maguire et al. (1999) is challenged somewhat by findings discussed later (see Section 5.1.3), that associate orbitofrontal activation with selection processes. Activation in this area thus seems consistent with the idea that increased orbitofrontal activation is truly related to comprehension itself, possibly as a result of successful inhibitory selection. Further evidence of frontal involvement was observed in the form of left middle frontal activation (BA 10), which was associated with the repetition and recall of stories, and activation in the left superior frontal gyrus (BA 10) which covaried with memory performance.

Another replication of these findings can be found in a PET study by Mazoyer et al. (1993), that involved presenting the following materials to French speakers: (1) stories in

Tamil which were incomprehensible to the participants, (2) stories in French, (3) lists of French words, and (4) stories distorted by the insertion of nonsense or unrelated words. By subtracting the activation associated with single-words, those areas that are involved in the processing of more macro-level language representations were illuminated. Many of these brain regions coincided with those observed by previous researchers (Fletcher et al., 1995; Maguire et al., 1999). These included the left middle temporal gyrus, the temporal poles, and a left superior prefrontal region (BA 8).

An fMRI study by Robertson et al. (2000), rooted in the Structure Building Framework, exposed participants to multiple series of sentences beginning either with an indefinite article (e.g. *a*, *an*, or *some*) or the definite article, *the*. The latter sets resemble a more coherent and integrated narrative while sentences in the former are interpreted as less related and more independent (de Villiers, 1974). Reading of sentences with definite versus indefinite articles led to differential activation of the right superior and medial frontal gyri. These areas were thus implicated in the identification and interrelation of recurring concepts, that is, the 'mapping' described by Gernsbacher's model. While right-hemisphere activation was marginally higher at all locations, this difference was only statistically significant for more caudal portions of the frontal lobe. The researchers also found that BA 8 was activated for most participants during mapping. It is interesting to note that the materials of this study were very simplistic, and represented in many ways the "physical stories" which were presumed not to tap mental inference (Fletcher et al., 1995; Vogeley et al., 2001). The observation of medial frontal activation in this study thus implies that this region may not only be used for mental inferencing during narrative comprehension, but likely working memory processes as well. Temporal lobe involvement for this contrast cannot be assessed due to the regions of interest (ROI) analysis employed.

The general pattern of frontal and temporal activations witnessed during these studies was also found in other imaging studies related to narrative comprehension, although the specific areas differ slightly. When participants were asked to comprehend the moral of an Aesop's fable, the right inferior frontal (BA 47) and right middle temporal gyrus (BA 21) were activated (Nichelli et al., 1995). Similarly, when activation during reading of an untitled and ambiguous story was compared to that observed during reading of the same story with a title, greater activity was observed in the right middle temporal sulcus (BAs 21, 38), and bilaterally in the inferior temporal sulcus (BAs 19, 20, 37); a right inferior frontal region (BAs 44, 45, 47) was mildly implicated as well (St. George, Kutas, Martinez, & Sereno, 1999). The right hemispheric lateralization of brain activity for both of these studies replicates an earlier attempt at examining narrative processing in the brain using regional cerebral blood flow (Huettner, Rosenthal, & Hynd, 1989).

3.4. Convergent evidence from brain-damaged patients

Although imaging research allows for the identification of quite specific task-associated brain regions, lesion work is much more helpful in localizing the parts of the brain *necessary* for a given function (Cabeza & Nyberg, 2000). Both forms of evidence thus need to be considered. Research on narrative comprehension with brain-damaged populations has consistently illuminated the importance of the right hemisphere (Benowitz, Moya, & Levine, 1990; Moya, Benowitz, Levine, & Finkelstein, 1986; Wapner, Hamby, & Gardner, 1981; cf. Rehak et al., 1992; Wechsler, 1973), although other brain areas have also been identified such as the left anterior temporal lobe including the temporal pole (Frisk & Milner, 1990a,b). What role the right hemisphere plays in this comprehension deficit has not been conclusively determined, although there is evidence that right-hemisphere patients have difficulty drawing inferences due to impoverished activation of semantic information (Beeman, 1993). Wapner et al. (1981) found that individuals with right brain-damage (RBD) recall, and at times justify, bizarre elements of narratives (deliberately inserted by researchers) as accurately as normal information. Controls and other patients generally omit, challenge, or attempt to normalize such information. This finding points to a deficit in recognizing the appropriateness or significance of elements in a narrative for patients with RBD.

Research on these populations has also indicated that the understanding of stories may rely upon the frontal lobes (Novoa & Ardila, 1987). For example, Wapner et al. (1981) found that, among patients with RBD, those who had large lesions in the anterior portion of the brain were most frequently subject to embellishment or confabulation. Hough (1990) found similar comprehension deficits in this population. Her patients with anterior lesions in the right-hemisphere had a tendency to embellish and confabulate, particularly for difficult stories in which the organizing theme was presented last. Intact individuals and those with left brain-damage (LBD) did not exhibit the same pattern. The presence of confabulation appears to provide further evidence of a difficulty with the selection of story-significant elements.

One study that did not find evidence of confabulation or perseveration amongst frontal patients and amnesiacs, did shed some light on the specific comprehension processes impaired within these groups. Zalla, Phipps, and Grafman (2002) examined normal controls and two patient groups with regard to story comprehension and the ability to draw inferences, either during reading or after a delay. Frontal patients appeared to be impaired at on-line inferencing whereas amnesiac patients may have had slightly more difficulty with delayed inference questions. Importantly, amnesiacs and normals did not differ significantly in their accuracy when drawing inferences on-line. Frontal patients also appeared to have difficulty with sequencing

events during recall, and both groups of patients embellished more than controls. The authors concluded that frontal patients have difficulty establishing inferential cross-temporal links across events, whereas amnesiacs retain the capability to establish local coherence and draw inferences. Whether the latter population can also construct and evaluate global coherence was not addressed by this study, however, and remains an interesting issue for future research.

3.5. Summary and discussion

Across a number of imaging studies on narrative comprehension there is relatively good convergence of findings. The presence of frontal regions is prominent, including medial and dorsolateral (superior and middle) frontal gyri (BAs 8, 10); ventrolateral (BAs 44, 45, 47) and ventromedial regions (BAs 10, 11); and some motor areas. A number of temporal regions are also implicated, including the middle temporal gyrus and sulcus (BA 21); more superior areas such as the superior temporal gyrus (BA 22/39) and temporoparietal junction; as well as inferior temporal regions such as the inferior temporal sulcus and the temporal poles (BA 38). Lastly, the posterior cingulate (BAs 23/31, 31) also appears associated with narrative comprehension. These regions are largely comparable to those identified in a 2003 review of neuroimaging and language (Gernsbacher & Kashak, 2003). Lesion research identified right hemisphere areas as necessary for story comprehension, and possibly right frontal areas specifically, as well as the temporal poles.

Frontal regions hypothesized to support the construction of global coherence as a product of temporal integration, specification and maintenance of cues during encoding/retrieval, as well as selection using acceptance and rejection were all observed. Somewhat surprisingly, areas predicted to support monitoring and manipulation in working memory (BAs 9, 46) were not found, although other areas in the mid-dorsolateral prefrontal cortex were activated. Evidence for integration was also found in areas hypothesized to support the modulation of attention through inhibitory processes and with regard to motivation. A great deal of evidence supported Beeman's proposal that right hemisphere networks are necessary for integration; right hemisphere activation was found throughout frontal, temporal and posterior regions (cf. Robertson, 2000). This observation is congruent with Beeman's empirical demonstrations (Beeman et al., 2000), and the observed right frontal activation is also consistent with both Grafman's theory of prefrontal function and Baddeley's localization of the episodic buffer. Evidence was also found to support the tracking of characters and motivation, as predicted by the Event-Indexing Model and Immersed Experiencer Framework, in the form of theory-of-mind areas like the medial prefrontal cortex, temporoparietal junction, and temporal poles. Partial support for spatial tracking or visual

imagery on the part of readers—also predicted by these two theories—was found in the form of posterior cingulate activation, although hippocampal involvement was absent. While some visual and motor cortex activation was observed, there was not widespread engagement of primary somatosensory areas possibly predicted by the Immersed Experiencer Framework. This may be due, in part, to the brief and simple nature of the presented stories.

It cannot escape notice that the identified frontal areas are also relevant for other processes, such as the encoding and retrieval of episodic and autobiographical memories (Conway, Pleydell-Pearce, Whitecross, & Sharpe, 2002, 2003; Robertson et al., 2000; Tulving, 2002; Wheeler, Stuss, & Tulving, 1997). This similarity may be related to previous research which has demonstrated that readers retrieve personal memories while reading, and that these memories tend to be more actively self-oriented when elicited by stories compared to expository texts (Larsen & Seilman, 1988). There is, in conjunction, another explanation of this overlap considering Tulving's position that episodic memory hinges on the ability to mentally represent and experience oneself across time, known as autonoetic awareness (Tulving, 2002; Wheeler et al., 1997). Projected into the past, this capacity results in a re-experiencing of previous events. However, autonoetic awareness also permits the representation of self-experience in the present and in the future. The latter is similar to representing one's own experience in a fictional context since the future is necessarily without factual basis. Personally experiencing oneself in a story is congruent with the Immersed Experiencer Framework and Oatley's (1999) theory of simulating narrative experience. It is also in keeping with research on the development of imagination, which may provide the basis for the capacity to comprehend narratives (Harris, 2000). There is some evidence that autobiographical memory is more associated with the left prefrontal region (Conway et al., 2002), whereas the findings of this review appear to implicate more bilateral, or right activation. Other research appears to corroborate this observation; one EEG study found that left frontal areas were more implicated during autobiographical imagery, whereas bilateral areas were associated with fictional imagery (Conway et al., 2002). While the retrieval of both autobiographical and imagined memories implicate many similar areas, experienced memories appear to contain more sensory information while imagined events may evoke more schematic or abstract imagery (Conway et al., 2003). Greater right than left frontal activation during narrative comprehension may also indicate a closer parallel with episodic retrieval processes rather than episodic encoding or semantic retrieval, according to the Hemispheric Encoding/Retrieval Asymmetry model (Tulving, Kapur, Craik, Moscovitch, & Houle, 1994). This similarity could reflect actual retrieval processes during reading, or that something like the personal experiencing which composes autonoetic awareness occurs during narrative comprehension. The fact that story-comprehension activates areas which partially parallel those associated

with episodic or autobiographical memory is thus not a shortcoming, but instead an interesting theoretical platform for future research (Rubin & Greenberg, 2003).

4. Story production

4.1. Cognitive models of narrative production

In the 1994 *Handbook of Psycholinguistics*, Garnham (1994) noted that "production has always been a neglected aspect of language processing within psycholinguistics" (p. 1137). Although models for sentence-level production exist, few with regard to discourse are widely discussed. In fact, the 2003 *Handbook of Discourse Processes* (Graesser, Gernsbacher, & Goldman, 2003) contains little mention of production except for a few computational models which, as previously mentioned, are often too detailed to prove useful for mapping brain-process relations. Foltz (2003) asserts, in the same volume, that brain research has not yet risen to the level where it can contribute to models of discourse processing. From another perspective, it could be argued that cognitive models are specified at a level of detail that abjures the possibility of being grounded in current knowledge regarding brain function.

The creation of a cognitive model for discourse production, rooted in brain research, may be a valuable contribution to both psycholinguistics and cognitive neuroscience. This endeavour, however, is bound to encounter more complications than the construction of a comprehension model. Among the specific barriers which face a production theorist is the fact that comparatively little neuroscientific research on the topic exists. Furthermore, production appears more complex than comprehension as the former entails similar processes plus the requirement of semantic selection during generation. The issue of a possible discourse production model is thus withheld until Section 5.2, following a summary and discussion of the interrelation between comprehension and production.

4.2. Neuroimaging studies of narrative production

While the influence and popularity of neuroimaging has grown immensely, there exist few published examinations of narrative production. An innovative PET study by Braun, Guillemin, Hosey, & Varga (2001), however, has made progress in identifying those areas involved in storytelling. Hearing individuals who were native users of both English and American Sign Language engaged in four different tasks: (1) simple oral and limbic motor movements, (2) more complicated movements that resembled communication but were content-free, (3) spontaneous story generation in English, and (4) spontaneous signing of narratives. The researchers were thus able to examine two forms of narrative generation that differ greatly in physical expression. When those activations observed during complex motor

movements were subtracted from those during narrative production (independent of modality), conjunctions (shared activations without magnitude differences) were observed in the medial and superior frontal gyri (BA 9, 10) extending to the frontal pole, bilaterally in the middle temporal gyrus (BAs 21, 39) and superior temporal gyri and sulci (BA 22), the posterior cingulate (BAs 23, 31), and other parietal (BA 39) and occipital areas. Since posterior regions were associated with language but not control movements, the researchers concluded that they were likely responsible for more basic language production and do not contribute to narrative formation per se. The unique method of this study allows for the relatively strong conclusion that the observed pattern of frontal and temporal activations is involved in narrative language production, independent of modality. Moreover, these areas appear to mirror those implicated in comprehension. The findings of this study should be replicated, however, preferably including a comparison with the communication of more micro-level language such as sentences or words.

A neuroimaging study in which participants imagined emotional or nonemotional plans found areas of activation similar to those of Braun et al. (2001), although it did not deal directly with actual expression (Partiot, Grafman, Sadato, Wachs, & Hallett, 1995). During unemotional mental simulation, activity was observed in the right superior and middle frontal gyri (BA 8), left middle frontal gyrus (BA 9), right and left medial frontal gyri (BAs 6 and 10, respectively), the right middle temporal gyrus (BA 39) as well as the inferior parietal cortex (BA 40) and precuneus. The mental simulation of an emotional plan resulted in left (BA 9) and right medial frontal gyri activation (BAs 8, 9), cingulate activation (left anterior [BA 32/34], and bilateral posterior [BA 31]), and activation in the middle temporal gyrus (bilateral anterior, right posterior [BA 21]) and inferior temporal gyrus (BA 20). While the mentally-simulated plans were never expressed, it seems likely that similar processes are involved in acts of narrative production.

4.3. Convergent evidence from brain-damaged patients

The brain areas indicated by imaging studies of production have also been associated with production deficits in brain-damaged patients. A number of researchers have found that those with RBD exhibit impaired narrative production (Davis, O'Neil-Pirozzi, & Coon, 1997; Joanette, Goulet, Ska, & Nespoulous, 1986; cf. Bloom, Borod, Santschi-Haywood, Pick, & Obler, 1996; McDonald, 1993), while those with LBD do not (Bloom, 1994; Ulatowska, Freedman-Stern, Weiss-Doyel, & Macaluso-Haynes, 1983). Evidence of right hemisphere responsibility is joined by some support for frontal cortex contributions to narrative production (Novoa & Ardila, 1987), although the two aetiologies are at times difficult to separate (McDonald, 1993). One study that examined a sub-group of patients with closed-head trauma—those who suffered frontal

lobe damage—found tentative evidence for this relation (Chapman et al., 1992). These individuals demonstrated distinct impairments in episodic narrative structuring and macro-level story abstraction, even in comparison to the average performance of the remaining participants who all had severe injuries.

Research on patients with less focal damage has also been illuminating. A large number of studies detail the discourse production impairments of patients with traumatic brain injury (TBI); unfortunately, interpreting these studies is very difficult, especially with regard to localization of function (Coelho, 1995). There is some evidence, however, that executive functioning is related to performance on storytelling tasks in this population. Higher scores on the Wisconsin Card Sort Task—an oft-used measure of frontal-lobe functioning—by TBI patients is associated with composite measures of discourse performance (Tucker & Hanlon, 1998), the number of episodes generated (Coelho, 2002; Coelho, Liles, & Duffy, 1995) and decreased sentence-length but increased sentence-complexity (Coelho, 2002). In children with TBI, this association has been demonstrated even when verbal ability is taken into account (Brookshire, Chapman, Song, & Levin, 2000). Another measure of frontal ability, verbal fluency, is also related to discourse production in children (controlling for general verbal ability) (Brookshire et al., 2000).

Curiously enough, evidence for an association between memory and discourse production from patient populations has been mixed. A couple of studies have found no relation between measures of working memory and discourse performance (Caspari & Parkinson, 2000; Chapman et al., 1992). One of these studies, however, examined only a single amnesiac patient (Caspari & Parkinson, 2000). Examination of a much greater number of TBI patients did find that verbal memory was related to discourse production; this association, however, was not significant when partial correlations controlling for verbal ability were examined (Brookshire et al., 2000).

A thorough investigation of patients with focal lesions by Kazmarek (1984) strongly supports the possibility that story production relies on the frontal lobes and furthermore, that different subprocesses may be associated with specific, differentiable regions. The speech behaviour of six groups of patients were examined: those with (1) left dorsolateral frontal lesions, (2) left orbitofrontal lesions, (3) right frontal lobe lesions, as well as (4) posterior aphasics, (5) posterior brain-damaged nonaphasic patients, and (6) controls. Frontal patients had great difficulty organizing the information that they wished to communicate. Such individuals were plagued by perseverations, digressions, confabulations, and the use of stereotyped phrases. These patients also had difficulty initiating stories and were unable to re-tell any of the narratives, despite unimpaired sentence-level language abilities and intact memory for the stories. When lesions were restricted to the right hemisphere, patients over-employed trite phrases while attempting to create a story. Those with left dorsolateral lesions tended to perseverate on statements initiating the story, which they were then unable to continue or complete. In contrast, patients with left orbitofrontal lesions had difficulty controlling the progression of their narratives, often following arbitrary associations, resulting in confabulation. Kazmarek concluded that the left dorsolateral frontal lobe is necessary for the sequential organization of linguistic information while the left orbitofrontal lobe allows for the directed development of the narrative. Another interpretation could be that the left dorsolateral area is responsible for causal-temporal ordering, while the left orbitofrontal acts to select appropriate elements and suppress irrelevant associations.

4.4. Summary and discussion

Imaging studies of production converged with respect to activation in the medial, and dorsolateral (middle and superior) frontal gyri (BAs 6, 8, 9, 10), areas near the temporoparietal junction on the left (BA 22) and right side of the brain (BA 39/40), and the posterior cingulate (BAs 23, 31). Research on lesion patients also confirmed the participation of the frontal lobes and right hemisphere areas. Thus, while there is less data pertaining to production relative to comprehension, agreement between studies does exist. In light of this smaller body of evidence, however, discussing the nature of story production is best left to follow an examination of its relation with story comprehension.

5. Comparing narrative comprehension and production

A number of identical areas appear to be involved in both narrative comprehension and narrative production. Research using brain-damaged patients indicates that right hemisphere areas, particularly right frontal, are necessary for producing and comprehending discourse. The reviewed imaging studies found that both processes involved the medial and dorsolateral regions of the frontal cortex, temporal regions including the temporoparietal junction, and the posterior cingulate. Although other parallels in brain activation exist, these tend to be less consistently observed. Few regions appear to be associated uniquely with comprehension or production, although no study of narrative production has identified activation in the temporal poles. This area is hypothesized to be responsible for discourse-level processing such as the concatenation of sentences. Theoretically, such a process would also be useful for production so it is difficult to explain this divergence. More studies of story expression are required to confirm this possible difference. In sum, the parallel brain regions identified using both neuroimaging and patient data imply that story comprehension and production are closely linked.

There is a good theoretical reason why narrative comprehension and production should be related. Ignoring the debate on how these aspects of language may be similar

at more micro-levels (Heim, Opitz, Müller, & Friederici, 2003), at the level of narrative the ability to organize the meaning of connected sentences in order to form a holistic representation for either understanding or communication seems to be a shared necessity. It is proposed that selection and causal-temporal ordering may underlie this construction and commonality.

5.1. Selection and causal-temporal ordering in comprehension and production

If stories are, in part, a coherent causal-temporal ordering of select information, it can be argued that a person must possess the ability to distinguish between story-significant and story-insignificant elements in order to construct or comprehend narratives. Similarly, the capacity to properly sequence these events with regard to time and influence appears to be of fundamental importance for both functions. The measure that appears to most adequately tap both abilities is known as the Story Arrangement Task (SAT), in which participants are asked to order a number of sentences or pictures so that they form a coherent narrative. In some versions of this task, irrelevant items are included and respondents must select those congruent with the narrative being formed.

5.1.1. Neuroimaging studies of selection and ordering

In an fMRI study by Crozier et al. (1999), brain-scans were taken while healthy individuals engaged in script and sentence-ordering tasks. Participants were asked to detect: (1) errors in a sequence of words, (2) errors in the sequence of a familiar script (such as getting dressed before taking a shower), or (3) the presence of double-consonants in a series of non-words. During the script-ordering condition, the following three brain areas were implicated (with syntax-ordering as a control): (1) the right and left middle frontal gyrus (BA 8), (2) the left supplementary motor area (BA 6), and (3) the left angular gyrus (BA 39). Crozier et al. (1999) hypothesized that the middle frontal gyrus (BA 8) is involved in the temporal ordering of events, while activation of the latter two areas may have resulted from mental simulation of the motor tasks described in the scripts. The fact that such activations were observed after controlling for those areas involved in the ordering of words demonstrates that distinct brain regions are responsible for the construction of stories compared to those required for syntax-level ordering.

An earlier PET study provided evidence that the selection processes of narrative function differ from those for the ordering of events (Partiot, Grafman, Sadato, Flitman, & Wild, 1996). Scans were taken while participants engaged in four different tasks, identifying: (1) the presence of a unique font for script-event items, (2) anomalous actions for a given action-script, (3) anomalous events for a given script, and (4) script-events that did not conform to the logical order for a given script. Activation for the first task was subtracted from the latter three to highlight those areas in-

volved in the particular function of interest: action-selection, event-selection, or event-ordering. Action-selection is not discussed as this task involved very basic scripts, such as the components of 'speaking/talking.' Selection of anomalous events within a script (e.g. 'put on swimsuit' for the script of 'attending a wedding') led to activation in the left medial frontal gyrus (BAs 9, 6), left anterior cingulate gyrus (BAs 24, 24/32), and the anterior part of the left superior temporal gyrus (including the temporal pole, BA 38). Event-ordering resulted in activation of the right medial and superior frontal gyri (BA 8), left superior temporal gyrus (BA 22), and bilateral middle temporal gyrus. When activation associated with action-selection was used as a control, only the medial frontal activation remained. Subtracting the activation associated with event-verification highlighted the following areas: right superior (BA 8), inferior (BA 44) and medial frontal gyri (BA 8), right supramarginal gyrus and the right superior temporal gyrus (BA 39). Not surprisingly, examination of response latencies for each condition suggest that selection precedes organization. The researchers concluded that frontal activation is uniquely associated with true event-ordering as temporal lobe involvement generally disappears when action- or event-verification is taken into account.

5.1.2. Convergent evidence from brain-damaged patients

Convergent evidence from research on brain-damaged populations supports the results of the imaging studies reviewed above. Investigations have demonstrated that individuals with RBD experience difficulty ordering information to create a coherent story (Schneiderman, Murasugi, & Saddy, 1992; Wapner et al., 1981), although one study found that RBD patients are impaired on pictorial-sequencing but not the verbal version of the SAT (Huber & Gleber, 1982).

Studies also indicate that the frontal lobes are necessary for organizing story information. For example, Sirigu et al. (1995) asked patients with prefrontal damage to generate stories describing how they would accomplish a particular goal, which ranged in complexity from preparing for work to starting up a beauty salon. Frontal patients exhibited greater difficulty in ordering actions, defining boundaries of scripts, and evaluating the importance of events correctly, compared to intact individuals and those with posterior damage. Sirigu et al. (1996) later replicated their findings using a variation of the SAT, in which participants had to arrange actions for a script in the absence or presence of: (1) a theme sentence, and/or (2) distractor actions unrelated to the script-goal. Once again, patients with lesions in the prefrontal cortex had difficulty ordering events, respecting script boundaries and benefiting from the presence of a theme-sentence. They also failed to discard events that were unrelated to the goal. Prefrontal patients thus appear to have an impaired understanding of causal-temporal relations and a reduced ability to select goal-relevant items.

A subsequent study by Sirigu et al. (1998) provided additional evidence that different brain regions are implicated

in story-level versus sentence-level ordering. While patients with Broca's area lesions had difficulty ordering words to form sentences, they were able to perform the script task used previously. In contrast, prefrontal patients generally exhibited the opposite pattern: proper formulation of syntax, but impaired story-ordering. These specific individuals had lesions located farther to the anterior of the left hemisphere, including BA 45 and part of 46. In some cases, damage extended to BAs 10, 9, 11, and part of 8.

Work by other investigators influenced by Grafman's (2002) theory, as well as early observations by Le Gall et al. (1993a, b), have provided strong evidence for a dissociation between the ability to order and the ability to select narrative elements. Allain, Le Gall, Etcharry-Bouyx, Ghislain, & Jean (1999) examined 23 patients with frontal damage and compared their performance on script-ordering tasks to 10 individuals with posterior damage and 10 normal controls. Only the frontal patients had difficulty with the tests. More importantly, two distinct groups emerged within the latter population. Eight patients were prone to sequencing errors and judging which actions were most important to achieving the desired outcome. However, these same individuals had no difficulty discarding items that were not at all relevant to the overall script. A second group of 11 patients exhibited the exact opposite pattern of impairment. These individuals were able to organize, order and evaluate the importance of actions in a script, but they failed to discard aberrant items. Finally, four patients performed as well as controls. The authors were somewhat successful in identifying those brain areas associated with each pattern of deficit. Through regression analysis, Allain et al. (1999) found that damage to the left prefrontal, left premotor and rolandic region, and the left paraventricular region was associated with sequencing errors. Post hoc subgrouping comparisons confirmed this finding. In contrast, intrusion (or selection) errors were related to the left lateral frontal region (left paraventricular) and the left posterior orbital region. This latter finding, however, was not confirmed by post hoc analyses. The results of this study were replicated 2 years later using a larger population of patients (Allain et al., 2001). Once again the two patterns of behaviour within the group of frontal patients was observed and the previous neuroanatomical findings were largely affirmed. Specifically, left or bilateral frontal damage was more associated with ordering errors with one analysis singling out the left paraventricular. Errors associated with selection processes were most prevalent amongst those with orbitofrontal lesions.

5.1.3. Summary and discussion

The available imaging research on the temporal organization of story-events converged on the importance of the prefrontal cortex, specifically parts of BA 6, and the middle and superior (medial and dorsal) frontal gyri located in BA 8. Lesion work provided confirmatory evidence that the lateral prefrontal cortex appears to house causal-temporal ordering processes. This data further indicated that order-

ing may be located in the anterior left hemisphere (BAs 45/46, 10, 9, 11, 8), or more specifically a bilateral or left lateral frontal area, perhaps the left paraventricular. This latter estimation appears in keeping with previous findings by Kazmarek (1984), and the script-ordering areas (BAs 6, 8) identified by Crozier et al. (1999) are very near this paraventricular region. It is encouraging that in one patient study, 7 of the 12 who exhibited errors in narrative organization had lesions that involved BAs 6 and 8 (Allain et al., 2001).

With regard to the selection of relevant events, imaging data implicated left medial prefrontal areas (BAs 6, 9) including the anterior cingulate (BA 24, 24/32), as well as the left temporal pole (anterior superior frontal gyrus, BA 38). Lesion research was corroborative with respect to prefrontal localization as patients with damage in this area, particularly the orbitofrontal region (BAs 10 11, 12, 13, 47), were most impaired in this regard. These findings are also consistent with a previous observation by Kazmarek (1984).

It appears that the selection and ordering of story-events may partially account for the shared activation in lateral and medial frontal areas during narrative comprehension and production. The temporoparietal junction and posterior cingulate, however, were also common to comprehension and production but do not appear to be strongly associated with selection or ordering. Since the temporoparietal region is involved in theory-of-mind (Frith & Frith, 1999, 2000, 2001), as is a medial frontal area also common to comprehension and expression, mental-inferencing may help compose the common ground between these two processes. During the comprehension of stories, this network may be used to infer the mental states of characters; during production, these areas may help produce realistic, intentional characters as well as predict how one's production will influence the beliefs and comprehension of a receiver (Alexander, 2002). The posterior cingulate is often activated during episodic memory retrieval (Cabeza & Nyberg, 2000), and may play a role in visuospatial processing or the emotional modulation of memory for text (Maddock, Garrett, & Buonocore, 2003). This area could thus contribute to the encoding of emotional material during narrative comprehension, and spatial imagery and/or the retrieval of episodic information during both expression and understanding.

5.2. Modelling production in light of comprehension and proposed subprocesses

The processes identified above for narrative expression do not appear to be sufficient for forming a cognitive model of discourse production. They are useful, however, for describing this ability in terms of our current neuropsychological understanding (see Section 7.2). One possible starting point for cognitive psychologists interested in production is its strong relation to narrative comprehension. As stated earlier, the memory processes used to create an integrated model of text during comprehension may also play a role in creating a representation of the target story-to-be-expressed

during production. Issues regarding the actual physical realization of spoken or written discourse are unlikely to differ from those necessary for sentence-level expression, and theorists may benefit from a focus on the creation of a holistic production which defines discourse-level expression. Other issues include the fact that storytelling, versus other genres of expression, likely involves some knowledge of basic story-structures, an awareness of audience expectations, and an understanding of what constitutes believable behaviour for a fictional character. As well, content-source variables must be considered to a greater degree relative to comprehension. It is very likely that the act of re-telling a familiar story differs from telling a novel story prompted by a picture, which differs from telling a story based on one's past experience, which also differs from telling a story related to you by someone else. In contrast, one set of processes can likely be used to comprehend all of these productions. It could be that the only things common to many forms of storytelling are the sort of memory processes employed during comprehension, and perhaps mental-state attribution.

6. Summary of the neuropsychological substrates of narrative

When the current state of the imaging literature is considered along with lesion and patient research, it is possible to pinpoint some neural substrates of narrative processes and subprocesses. The imaging studies reviewed are summarized in Table 1, with the first column containing each study, its contrast, and the imaging method used; studies that employed ROI analyses are italicized. Contrasts are typically subtractions, consisting of target task activations compared with control condition activations, although activations correlated with a behaviour are also listed. Subtractions are listed as "Task–Control." The remaining columns describe in what neuroanatomical structures the activations are located, and how this activation is lateralized. Rarely activated structures are grouped in broader categories (e.g. subcortical activations), areas with no activations are omitted (e.g. medial temporal), and in some cases categories are collapsed to ease interpretation (e.g. middle temporal gyrus and sulcus). All of the contrasts are further described in Table 2, although interested readers are encouraged to consult the original publications. Table 2 also explains the acronyms used for the neuroanatomical structures listed in Table 1. Available activations are plotted according to the coordinates proposed by Talairach and Tournoux (1988) in Figure 1. Whenever possible, activations are plotted as medial or lateral according to the description provided by the researchers; in all other cases, activations 12 mm or less from the mid-line are plotted on the medial surface. Activations that fall directly on the mid-line ($x = 0$) are plotted bilaterally. Some studies did not provide co-ordinates for activations, specifically those employing a ROI analysis, and these activations are absent from the figure (viz., Crozier et al., 1999; Mazoyer

et al., 1993; St. George et al., 1999). Upon inspection, however, these omitted activations appear to conform to the general pattern observed. Activations from available studies of narrative processing appear to cluster in five regions, which are described below along with some speculation regarding the processes associated with each. It may well be, however, that the pattern of interactions between these areas will prove more enlightening; future researchers should thus consider utilizing data-analytic techniques that reveal such relations (cf. Grady, McIntosh, Rajah & Craik, 1998).

6.1. Medial prefrontal cortex

Both comprehension and production are associated bilaterally with the medial prefrontal cortex. Based on the available imaging research it appears that ordering and selection processes engage this area, and are likely partially responsible for the shared activations observed. Selection, however, is more strongly associated with this region as it alone benefits from both convergent lesion evidence and congruent observations from other theorists (e.g. regarding the inhibition function of this area; Cabeza & Nyberg, 2000; Fuster, 2002; Moscovitch & Winocour, 2002). The medial prefrontal cortex is also likely responsible for sponsoring another narrative subprocess, namely theory-of-mind. There exists both theoretical support for the idea that mental-inferencing plays a role in narrative-processing, and evidence for the engagement of this cortical area during theory-of-mind tasks.

6.2. Lateral prefrontal cortex

According to the available imaging data, lateral prefrontal activation for narrative understanding and expression appears largely right-hemispheric, corroborating other work using lesion patients. This region of cortex, particularly the dorsolateral portion (BAs 6, 8), appears to be important for the ordering of events within a narrative. Consistent with this idea, other theorists have associated this area with cross-temporal ordering (Fuster, 2002; Fuster, Bodner, & Kroger, 2000), and the working-memory processes that likely underlie this process (Moscovitch & Winocour, 2002). The lateral prefrontal cortex may also be involved in other working-memory functions, such as cue-maintenance for long-term memory retrieval. Although this region of cortex has been associated with episodic memory retrieval, the activations observed during narrative processes appear to be posterior to those associated with such retrievals (Cabeza & Nyberg, 2000, see Fig. 10). Some evidence suggests that the motor cortex is also activated during comprehension. Mental simulation of the actions depicted within the story may be responsible, particularly if the narrative is self-oriented.

The fundamentally goal-centred nature of stories is a good match for the many goal-based functions attributed to the frontal lobes. Researchers have identified a number of such processes, including: (1) the formation and execution of
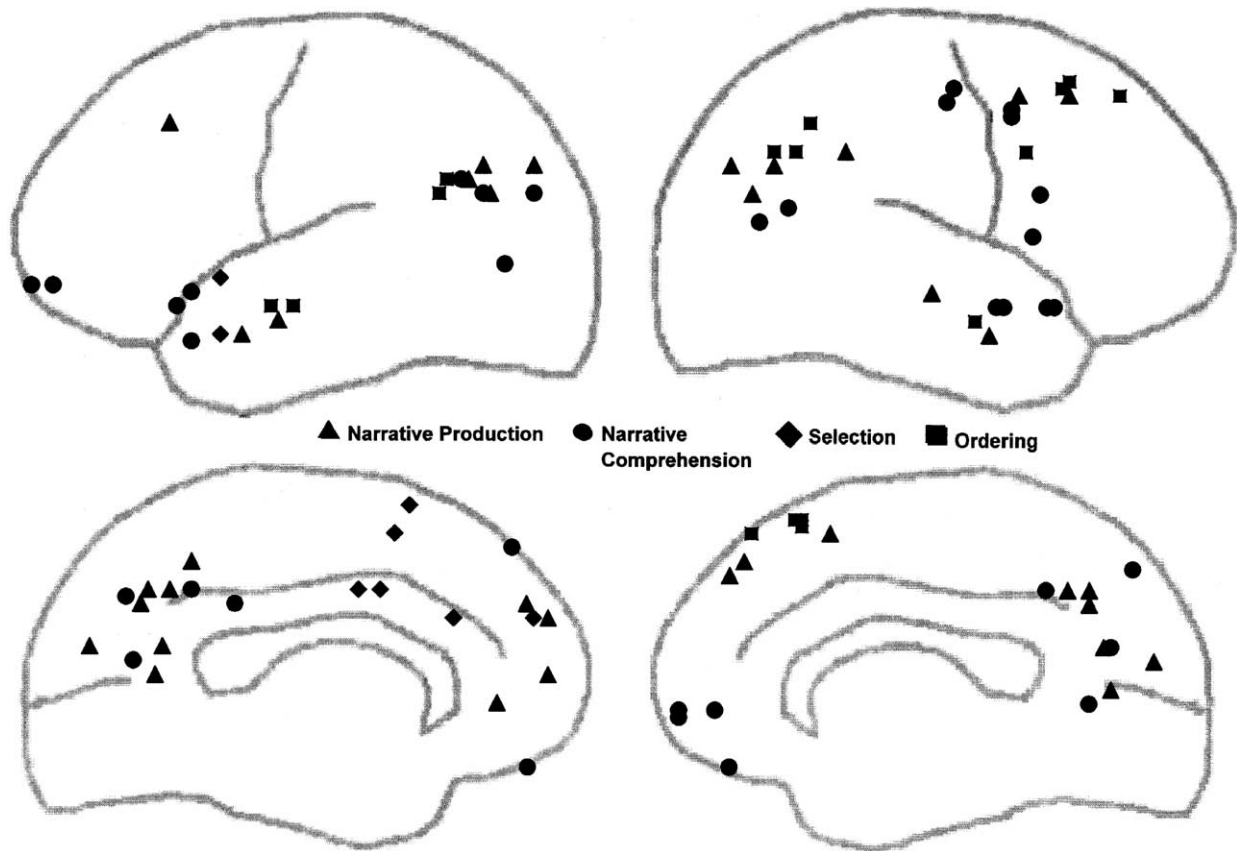
Fig. 1. Reported peak activations for studies of narrative comprehension, narrative production, selection and ordering. *Note*: In the case of one orbitofrontal activation, plotted co-ordinates fell just outside of the diagram. This peak has been moved to the closest surface.

plans for action, (2) goal-oriented working memory, and (3) the temporal organization of speech, behaviour and logic (Fuster, 2000).

6.3. Temporoparietal region

Story comprehension and story production are associated bilaterally with a region at the juncture of the temporal and parietal lobes. Event-ordering activations are also found in this area, although there is no evidence from lesion work that this area is necessary for the successful execution of this process. Furthermore, some imaging researchers have concluded that temporal areas are not uniquely engaged during such tasks. A more likely candidate process for this region is the attribution of mental-states. Along with the medial prefrontal cortex, the temporoparietal junction is one of the most frequently identified cortical regions for mental-inferencing. The competing possibility that this area is responsible for basic language functions is undermined upon comparing the observed activations to those depicted in a meta-analysis of lower-level language (Cabeza & Nyberg, 2000, see Figs. 6 and 8). Temporal lobe regions linked to simple semantic processing do not appear to overlap with those observed for story processes. It is possible,

however, that the temporoparietal junction is related to some aspect of sentence or cross-sentential processing, as others have theorized (Fletcher et al., 1995; Mazoyer et al., 1993).

6.4. Anterior temporal region including temporal poles

All of the story processes and subprocesses examined are involved bilaterally with the anterior temporal lobes including the polar region (BA 38). Although activations associated with ordering and selection are found here, no evidence from brain-damaged patients indicates that this region is necessary for such functions. In conjunction, temporal areas may not be uniquely involved with ordering according to the available imaging research. Conversely, lesion evidence demonstrating narrative comprehension impairments following damage to this area does exist, implying that the poles support some other necessary process. Two likely candidates are theory-of-mind and the concatenation of sentences or propositions; both abilities have been associated with the temporal poles and appear necessary for story-processing. Although no activations associated with narrative production fall directly within the polar region, production does appear to be related to areas just slightly

posterior. As with the temporoparietal region discussed above, comparison with a recent meta-analysis of language activations reveals that this area is not involved in simple semantic processes (Cabeza & Nyberg, 2000, see Figs. 6 and 8).

6.5. Posterior cingulate cortex

Comprehension and production are associated bilaterally with the posterior cingulate, and this common activation is not attributable to selection or ordering processes. A variety of functions could lie within this area, as it has been tied to the association of new information with a schema or prior knowledge, visuospatial imagery, episodic retrieval, and the emotional modulation of memory processes. The latter three possibilities all seem congruent with the concept of autonoetic awareness, as a self-experiencing of a depicted fiction likely involves imagery and episodic memory processes that may well be affective in nature. It is possible that this area is directly involved in a simulation aspect of story processing, imbuing comprehension and production with realistic elements such as personal experience and related imagery.

7. General discussion

Narrative neuroscience is still a new area, but the preceding review has demonstrated that a number of brain structures are consistently activated during particular story processes. Furthermore, these brain areas appear to be unique to narrative-processing, separate from those identified for word and even sentence-level operations. Imaging studies that employ rigorously-controlled stimuli and control conditions, such as those by Robertson et al. (2000) and Crozier et al. (1999), reveal that story-processing activations are not the same as those for sentence-processing. Similarly, lesion research such as that by Kazmarek (1984) and especially Sirigu et al. (1998) demonstrate a double dissociation between syntax- and script-level abilities. This work converges with a great deal of evidence that many aphasics appear to have intact discourse-level abilities despite gross syntactic impairments (see Alexander, 2002; Rubin & Greenberg, 2003, for reviews). Both lines of evidence, imaging and patient, indicate the importance of right hemisphere areas in sharp contrast to the traditional portrayal of left lateralized language processes (i.e. Broca's and Werniche's areas). Lastly, when compared to a recent review of the imaging literature, it is clear that the full pattern of activation for narrative processes differs from those for attention, imagery, word recognition and production, working memory, episodic encoding and retrieval, and semantic retrieval (Cabeza & Nyberg, 2000). Further implications of this review with respect to cognitive and neuropsychological models are discussed below, along with directions for future research.

7.1. Cognitive models of comprehension and production

As predicted, it is very difficult to unequivocally accept or reject specific cognitive models of discourse comprehension based upon evidence from brain research. The processes described by these models can rarely be discriminated at the level of specificity addressed by neuroimaging and lesion research. As it stands, the broad prefrontal activation associated with comprehension supports a wealth of cognitive models that propose an important role for working memory, both as a repository for long-term memory cues as well as an executive processor that inhibits irrelevant retrievals and modulates other neural networks. The advantage of considering the reviewed research, however, is that the validity of such claims has on some level been addressed and confirmed. Specific areas of the brain appear to support the types of memory processes (e.g. inhibition and temporal sequencing) necessary for constructing a model of what is described by a text. Moreover, newer models that propose more elaborate processing during comprehension, such as the Event Indexing Model and Immersed Experiencer Framework, also receive support in the form of evidence for the tracking of characters and motivation, imagery, and the mental simulation of actions. In order for neuroscience to fully address these models, however, experiments must be designed to test their specific predictions.

Almost all studies of comprehension have used stories as stimuli. As a first step toward future research, it would be interesting to examine whether the reading of expository texts results in engagement of the same brain areas as narrative texts. One hypothesis is that those structures uniquely associated with theory-of-mind will not be engaged when reading a discursive text free from intentional characters. Another fruitful avenue of investigation would be to contrast models that predict a rich sensory experience during reading with those that contend that a more abstract representation results. In order to do so, however, longer, more ecologically-valid story stimuli that are tightly controlled with regard to content must be incorporated into imaging research. The association between narrative comprehension and episodic memory is also interesting. If reading fiction involves a sort of autonoetic awareness, how does an impairment in this capacity affect the ability to appreciate a story's global coherence? Perhaps relatively simple stories can be comprehended, while deficits may become increasingly visible as stories require more insight or elaborative real-world knowledge. As well, the difference in laterality of frontal activation for real and imagined experiential recall seems worthy of further investigation.

Understanding narrative production remains a very difficult and somewhat neglected problem for neuroscience and cognitive psychology. This review has demonstrated, however, that communicating a story appears closely linked to the same brain regions used to understand stories. Cognitive models of comprehension should thus make an effort to explain how proposed processes could also support the

production of discourse. As with studies of comprehension, the majority of production studies, including those on brain-damaged populations, examine the expression of narratives. Investigating whether the production of expository discourse engages different areas of the brain than narrative discourse seems a good direction for future work. Previous research on intact children demonstrating differences in discourse production as a function of genre provide an encouraging basis for this endeavour (McCutchen, 1987). Different methods for eliciting discourse production (e.g. cues, recall, spontaneous generation) should also be examined more closely.

7.2. Neurologically-based models of comprehension and production

Overall, the neurologically-based models of comprehension were greatly supported by the extant literature. Right hemisphere activations were prominent throughout numerous studies, corroborating Beeman's assertion that these networks are necessary for comprehending macro-level language. Specific predictions of this model, with respect to semantic nets, typically could not be addressed by the research reviewed although Kazmarek (1984) did observe the overuse of trite constructions in RBD patients. One potential challenge to this model, however, is the common observation of confabulation amongst such patients. Despite their damage, RBD individuals appear both capable of and prone to drawing loose associations between activated semantic elements in a narrative. As a possible explanation, damage to the right hemisphere may not totally obliterate broad semantic nets, allowing for the continued drawing of some loose associations. This damage could simultaneously impair inhibition processes proposed to take place while the left hemisphere engages in selection, thus resulting in the integration of inappropriate inferences. Hypothetically then, the majority of studies that report confabulation amongst RBD patients should include individuals with medial prefrontal damage. Unfortunately, making this discrimination is very difficult when reviewing the literature (McDonald, 1993).

Grafman's model was also well-supported by the reviewed research; right prefrontal activation was witnessed during most story-processing tasks. Furthermore, this theory can easily account for the shared activations witnessed between comprehension and production. Structured Event Complexes likely activate associated script-information in similar ways regardless of whether this information is marshalled to comprehend incoming information, or to produce outgoing information. This right prefrontal activation is also supportive of Baddeley's proposed localization of the episodic buffer. Like Grafman's theory, the integration, maintenance and manipulation of multimodal information hypothetically achieved by this buffer can easily accommodate both narrative production and comprehension.

Based on the reviewed brain areas, a relatively simple neurologically-based portrait of comprehension and produc-

tion can be proposed. As discussed above, working memory processes in the medial and lateral prefrontal cortex can be used to select and sequence information that is either being comprehended or prepared for production, in order to produce a representation of what is being described, or a representation of a story-to-be-expressed. This could be achieved in concert with areas that may modulate attentional focus in the narrative (either comprehended or produced), through the selection processes of the orbitofrontal cortex and anterior cingulate for example. Posterior regions of the cingulate may be responsible for the retrieval of elaborative information such as personal experience, in order to enrich comprehension or add realism to a produced story. This area may also contribute visuospatial imagery and perhaps modulate memory as a function of affect elicited by the narratives. Furthermore, the medial prefrontal cortex, temporoparietal junction, and temporal poles may allow for the understanding of characters' mental states—be they described by the self or others. Mental-inferencing may also be used to understand one's audience during production. Anterior temporal regions such as the temporal poles also likely support macro-level language processes like the concatenation of sentences, perhaps in conjunction with the temporoparietal junction.

8. Conclusions

This review has summarized the neuroimaging and lesion research pertaining to story comprehension and production, and examined the selection and sequencing subprocesses proposed to underlie both. While the gap between cognitive and neuropsychological models remains, it has perhaps been diminished somewhat by this review. It is clear that each approach has something to offer the other, and a mutually beneficial union is certainly not out of the question. Further research, particularly imaging studies using healthy participants, needs to be completed before a clearer picture of the relation between narratives and neuroanatomy can emerge. Current investigations, however, have manifested some interesting and interpretable consistencies related to frontal, temporal and cingulate function, and different story processes. At the very least, this review has hopefully succeeded in demonstrating that pursuing such knowledge is both valuable theoretically and empirically viable.

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