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The Brain Basis of Individual Differences in Language Comprehension Abilities

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Abstract

Individual differences in language abilities must be manifest by differences in brain functioning. Thus, comprehensive theories of the biological basis of language should account for systematic variability between individuals. This article is divided into two sections summarizing research on individual differences in the language comprehension network and their theoretical implications. The first section reviews research on individual differences in three network-level characterizations of brain function: neural efficiency, neural adaptability, and functional synchronization. The second section describes some of the implications of this research for theories of language in the brain. The role of the right hemisphere in language comprehension, the brain bases of word knowledge and verbal working-memory capacity, and potential mechanisms underpinning neural adaptability are discussed.

Overview

Individual differences in language abilities are present and prevalent throughout the lifespan, and must ultimately be underpinned by differences in brain functioning. A comprehensive theory of the biological substrates of language comprehension should therefore account for the systematic ways in which individuals differ (e.g., Bates et al. 1995; Cohen 1994). Much of the neuroimaging research to date has shown that language comprehension, like other complex cognitive tasks, results from the collaborative efforts of a distributed and highly interconnected neural network (e.g., Bookheimer 2002; Ferstl et al. 2008; Just et al. 1996; Xu et al. 2005), and that individual differences in language and cognitive abilities have important manifestations at the network level (e.g., Jung and Haier 2007; Prat et al. 2007). This review summarizes results of studies examining individual differences in the functioning of the language comprehension network, and discusses the implications of these findings for theories of the biological basis of language comprehension.

Network-Level Characterization of Comprehension Ability

Good comprehension, like effective cognition, is related to the efficient use of individual components of the language network (e.g., Broca's and Wernicke's areas), to effective communication between components, and to dynamic reconfiguration of the network with changing task demands. The first section of this paper reviews research on the biological basis of language comprehension ability, with an emphasis on network-level characterizations of function. Three facets of function have been shown to underpin good comprehension ability: neural efficiency, neural adaptability, and functional synchronization.

NEURAL EFFICIENCY

One of the best understood links between individual differences in brain function and cognitive abilities is that more-skilled individuals generally accomplish a task more efficiently, using fewer mental resources, than less skilled individuals (Haier et al. 1988; Maxwell et al. 1974; Neubauer and Fink 2009; Prat and Just forthcoming; Prat et al. 2007, 2011; Reichle et al. 2000). The assumption behind efficiency research is that the amount of 'mental resource consumption' that is required to effectively perform a task is reflected by the amount of brain activation observed during the task. Resource consumption can be measured either by the spread of activation in a defined region or set of regions (more focal activation patterns are more efficient), or by the intensity of activation in a defined region (less activation is more efficient).

In their seminal investigation of language comprehension ability, Maxwell et al. (1974) used EEG recordings of 14-year-old boys to test the theory that skilled comprehenders use fewer neural resources. They found that good comprehenders had more efficient neural processes, indicated by significantly lower power throughout the frequency bands, than did poor comprehenders. The relation between increased neural efficiency and improved mental function has been replicated for language comprehension abilities in adults (Prat and Just forthcoming; Prat et al. 2007, 2011; Reichle et al. 2000), and for intelligence and reasoning abilities (for review, see Neubauer and Fink 2009).

One question that arises is whether the relation between comprehension ability and efficient mental processes is specific to language, or whether more efficient brains in general give rise to better computational abilities, with language comprehension being only one instantiation of improved general function. In the experiment conducted by Maxwell and colleagues, individuals were not engaged in a secondary task while EEGs were recorded. However, when EEG recordings were taken from the participants when their eyes were closed, no reliable differences in efficiency were found. The authors surmised that the differences in efficiency were more obvious when information processing was occurring (in the eyes open condition), and would be greatest under conditions in which the subjects were engaged in difficult comprehension processes, although there was no direct test of their proposal (Maxwell et al. 1974).

Subsequent research on individual differences in neural efficiency suggests a more specific relation between skill and efficiency. For example, in a neuroimaging investigation of sentence-picture verification, participants with higher verbal capacities showed more efficient processing in typical language regions (e.g., Broca's area) than did participants with low capacities when they engaged in verbal strategies; whereas, individuals with higher visual-spatial skills showed more efficient processing in typical visual association regions (e.g., parietal cortex) than did individuals with lower visual-spatial skills when they engaged in spatial strategies (Reichle et al. 2000). In other words, the predictive power of skill in a particular domain (verbal versus visuo-spatial) was observed during conditions that evoked that particular type of processing, and in brain regions that subserved the type of process.

To investigate the factors related to increased efficiency in good readers, Prat et al. (2010a) conducted a multiple-experiment investigation of individual differences in neural efficiency. Combining data from comparable baseline reading conditions across five neuroimaging investigations, Prat et al. (2010a) conducted a multiple regression analysis of 84 readers, using indices of vocabulary size, working-memory capacity, age, handedness, and sex to predict patterns of activation. They found that the best predictor of efficiency was vocabulary size, with high-vocabulary readers showing reliably less activation, primarily in

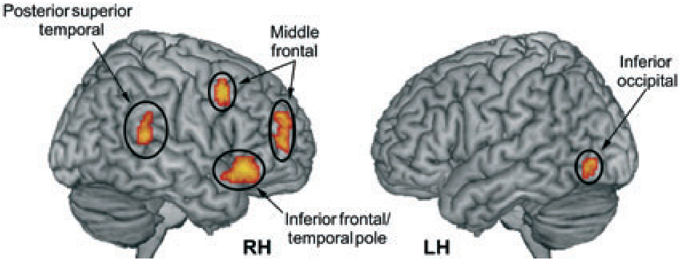

Fig 1. Regions where activation was reliably negatively correlated with vocabulary size, taken from baseline reading comprehension conditions across five experiments, as reported in Prat et al. (2010a).

the right hemisphere (RH) homologs of left hemisphere (LH) language regions, than did low-vocabulary readers. Regions where this reliable negative correlation between vocabulary size and activation were observed are depicted in Figure 1.

One limitation of investigations of efficiency is that comparisons of efficiency can only be made using tasks where performance across individuals can be equated. The importance of controlling for performance can be seen in research using working memory tasks (e.g., McGettigan et al. 2011; Osaka et al. 2003) in which high-capacity individuals, who show better performance on the task, often have higher activation levels in relevant executive areas. For example, Osaka et al. (2003) found greater anterior cingulate modulation in high-capacity individuals than in low-capacity individuals during a listening span task. High-capacity individuals also exhibited better performance on the task. Thus, increased anterior cingulate activation in high-capacity individuals likely reflects an increased involvement of some key cognitive component (e.g., conflict monitoring) for successful task completion. In situations such as this, it is difficult to know whether lower-capacity individuals have less activation because they are not engaging in the task as consistently (e.g., are ‘giving up’ on difficult trials), because they are not employing some appropriate executive strategy (e.g., conflict monitoring), or because of any other number of explanations (e.g., poorer functioning of frontal-parietal networks). As a result, difficult tasks in which significant performance differences are observed between individuals do not lend themselves well to investigations of individual differences in neural efficiency.

Another limitation of efficiency investigations is that differences in efficiency can only be assessed under conditions in which all individuals perform a task without employing different strategies. The importance of controlling for strategies is well illustrated by investigations of inference comprehension. Behavioral research has shown that skilled, or high-capacity readers are more likely to make optional, elaborative inferences (e.g., Just and Carpenter 1992; Long et al. 1994, 1997; St. George et al. 1997) during discourse comprehension than are less-skilled, or lower-capacity readers. Thus, when reading passages that invite elaborative inferences, skilled readers engage in qualitatively different comprehension processes than do less skilled readers. In two investigations of inference comprehension, Virtue and colleagues found a correspondingly larger ‘inference effect’ (indexed by activation in passages that invite inferences minus activation in passages that don’t) in high-capacity readers than in low-capacity readers (Virtue et al. 2006, 2008). In a subsequent investigation of individual differences in inference comprehension that manipulated factors related to the likelihood that causal inferences would be generated, Prat et al. (2011) found that in conditions strongly promoting causal inference generation in all readers (e.g., high coherence and/or high cohesion) negative correlations between reading skill and activation were observed; whereas during the condition in which only skilled readers were likely to generate inferences (low coherence and cohesion), positive correlations between reading skill and activation were observed. Thus, the conditions in which increased activation in more-skilled readers was observed across these three investigations likely reflect different strategies employed across individuals, with more-skilled or higher-capacity-individuals engaging in additional, elaborative inferential processes during discourse comprehension. The efficiency research discussed in this section suggests a possible explanation for differences in the amount of elaboration in which skilled and less-skilled readers engage in. Specifically, it is possible that increased neural efficiency in baseline comprehension processes results in greater availability of resources for the execution of non-essential, elaborative comprehension processes that characterize skilled reading.

In summary, increased language comprehension ability is manifest in part by more efficient neural processing of linguistic tasks. The resulting efficiency leaves a skilled individual with greater available resources for engaging in additional, non-essential, elaborative processes. The best paradigms for investigating such differences in neural efficiency are those that all participants can perform accurately, employing the same strategies.

NEURAL ADAPTABILITY

Human cognition is characterized by dynamic adaptation to the environment; a cortical network engaged in performing a complex task must be able to adapt to changing information processing demands (e.g., Garlick 2002; Schafer 1982). Understanding differences in language comprehension abilities must involve understanding the interaction among individual characteristics and changing task characteristics. The intersection of participant and task variables has been addressed in investigations of individual differences in neural adaptability, or dynamic configuration of neural networks on an 'as needed' basis with changing task demands. Although a modal set of areas activates for any given task, additional areas are recruited to deal with changes in the level or type of demand. For example, dorsolateral prefrontal cortex becomes activated when comprehension of the latter part of a sentence requires problem-solving processes, at the time that portion of the sentence is being read (Newman et al. 2002).

Neural adaptability is characterized by the coupling between changes in task demands and changes in patterns of brain activation. Such cortical dynamics can be indexed by variation in activation levels which changing task characteristics, reflecting sensitivity of a given region to a particular task demand (e.g., Newman et al. 2002; Prat and Just forthcoming; Prat et al. 2007). Adaptability can also be measured by changes in synchronization between regions with changing task demands, reflecting cortical network reconfiguration with fluctuating task demands (e.g., Prat and Just forthcoming; Prat et al. 2007; Stam et al. 2002).

Research on individual differences in reading comprehension in both children and adults has shown that good comprehenders show greater neural adaptability in the face of changing task demands under a variety of sentence processing conditions (Prat and Just forthcoming; Prat et al. 2007; Yeatman, Ben-Shachar, Glover and Feldman 2010). Specifically, good comprehenders showed greater increases in activation as a function of increased syntactic complexity (Prat and Just forthcoming; Prat et al. 2007; Yeatman et al. 2010), decreased lexical frequency (Prat et al. 2007), and increased sentence length (Yeatman et al. 2010) than did poorer comprehenders.

Such individual differences in neural adaptability may be related to differences in baseline neural efficiency, as resource availability is a precondition for the recruitment of *additional* resources. Another possibility is that differences in adaptability arise from some property of brain function (e.g., better plasticity, improved function of control regions) that underpins cortical dynamics and is somewhat separable from resource availability. According to this view, systematic differences in coupling between changes in the computational demands of a task and changes in cortical activation underpin individual differences in general mental function (e.g., Garlick 2002). These two accounts are not mutually exclusive, as it is plausible that both efficient resource utilization and resource allocation mechanisms are necessary for fluent neural adaptability.

One experiment has directly examined the mechanism behind individual differences in neural adaptability. In a sentence comprehension paradigm, Prat and Just (forthcoming) examined syntactic adaptability (changes in activation observed with changing syntactic complexity) under varying extrinsic working-memory demands. Individuals read sentences presented alone (No Load Condition), sentences preceded by three to-be-remembered words (Low Load Condition), and sentences preceded by three to-be-remembered pronounceable non-word strings (High Load Condition). They found that for all readers, syntactic adaptability decreased as the external working memory demands of the task increased, highlighting the importance of resource availability for neural adaptability. They also found that higher-working-memory-capacity individuals showed greater syntactic adaptability across all working memory loads than did lower-capacity individuals.

Although these results support the notion that individual differences in adaptability are related to individual differences in efficiency, the results in this experiment cannot be fully explained by differences in resource availability. First, when vocabulary size and working memory capacity were allowed to compete for variance in a multiple regression analysis, in the largest differences in neural efficiency were observed as a function of vocabulary size; whereas differences in neural adaptability were found only as a function of verbal working-memory capacity. Scatterplots illustrating neural adaptability (or the lack thereof) across the network as a function of working-memory capacity (a) and vocabulary size (b) are shown in Figure 2.

High-capacity individuals also showed reliably greater syntactic adaptability in prefrontal cortex and in the striatum, although no reliable differences in neural efficiency were detected in these regions. Again, if differences in adaptability are related to differences in baseline efficiency, increased efficiency should have been observed in the regions where increased adaptability was observed. A scatterplot illustrating baseline activation (in black), and increased activation for complex over simple sentences (in white) in the caudate nucleus as a function of working-memory capacity are depicted in Figure 3.

Although resource availability is clearly a precondition for neural recruitment, these data suggest that another facet of brain function may contribute to cortical dynamics, and may also systematically differ between individuals. Further characterization of the mechanisms underpinning individual differences in cortical dynamics is an exciting area for future research, and is discussed in brief at the end of this article.

Taken together, these results highlight the importance of neural adaptability for language comprehension tasks, which are characterized by dynamic information processing. Specifically, individual differences in comprehension abilities are underpinned in part by differences in the coupling between changes in task demands and changes in neural responses, with better comprehenders showing tighter coupling or better adaptability than worse comprehenders.

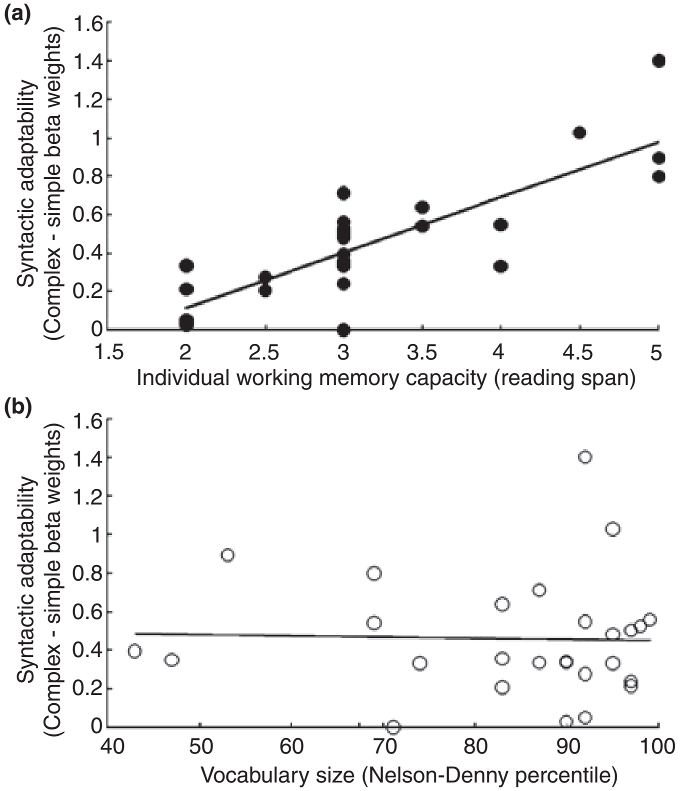

Fig 2. Scatterplots depicting the relation between average syntactic adaptability (mean complex – simple peak beta weights) and (a) individual working-memory capacity and (b) individual vocabulary size.

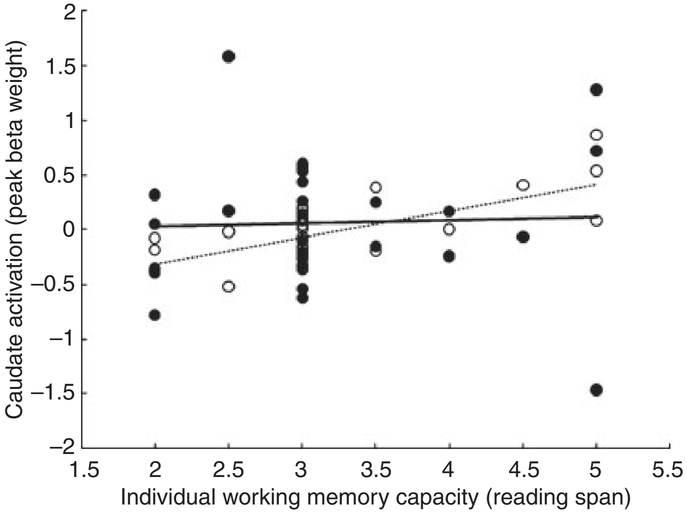

Fig 3. Scatterplot depicting the relation between individual working-memory capacity and syntactic adaptability (complex – simple peak beta in white) and baseline efficiency (simple sentence peak beta weight in black) in the caudate nucleus.

FUNCTIONAL SYNCHRONIZATION

To function optimally, the various anatomically distinct, but functionally integrated, nodes of a neural network must be able to communicate effectively and to synchronize their processes. In a language task, this means that the areas that execute subcomponent processes (e.g., semantic retrieval and syntactic parsing) must collaborate to synthesize the information that is necessary for comprehension. Collaboration is reflected in fMRI studies by the correlation of activation time series in a given region with activation time series of another region. The extent to which the activation levels of two regions rise and fall in tandem is taken as a reflection of the degree to which the two regions are functionally connected (Friston 1994). Indices of *functional connectivity* provide useful characterizations of network-level activity. For example, functional connectivity increases with learning, at the same pace as increases in performance, indicating that system coordination is an important facet of its effectiveness (Buchel et al. 1999).

Research on functional connectivity has provided new insight into the nature of individual differences in comprehension ability. In a working memory task, Otsuka and Osaka (2005) found that younger individuals had higher functional connectivity and performed better on the task than did older individuals. Prat et al.'s (2007) investigation of individual differences in sentence comprehension extended these results in young adults, to show that higher-working-memory-capacity individuals had better network synchronization than did lower-capacity individuals. They found that functional connectivity between the key regions in the LH language network (including between Broca's and Wernicke's areas) was higher in readers with better working-memory capacities than in readers with worse working-memory capacities during sentence comprehension.

Reduced connectivity between components of the language comprehension network has also been implicated as a source of processing difficulty in individuals with developmental language impairments. For example, reduced functional connectivity between the angular gyrus and the left temporal lobe has been observed in individuals with dyslexia (e.g., Horwitz et al. 1998; Pugh et al. 2000), especially during phonologically demanding tasks (Pugh et al. 2000). Similarly, reduced functional connectivity between frontal and posterior regions has been observed in individuals with autism during a variety of language comprehension tasks (e.g., Just et al. 2004; Kana et al. 2006). Taken together, increased connectivity in high-capacity comprehenders and reduced connectivity in language impaired populations illustrate the importance of effective communication between regions of the language network for intact comprehension.

Characterization of functional connectivity is particularly appropriate for evaluating the response of a cortical network to changing task demands. For example, as task demands increase, functional connectivity also tends to increase (e.g., Diwadkar et al. 2000; Prat et al. 2007), reflecting the need for tighter coordination in more demanding conditions. Interestingly, across a variety of reading comprehension tasks, Prat and colleagues found that *modulation* of synchronization with changing task demands varies as a function of working-memory capacity, with high-capacity readers showing the greatest modulation (Prat and Just forthcoming; Prat et al. 2007). When demands increased, high-capacity readers were more likely to maintain or increase synchronization, whereas low-capacity readers tended to show decreased synchronization with increasing demands (Prat and Just forthcoming; Prat et al. 2007). These results highlight the importance of dynamic, adaptable network synchronization for effective comprehension.

In summary, research on the brain basis of comprehension ability shows that individual differences are reflected by the amount of activation necessary for executing a task (efficiency), by fluctuations in activation with changing task demands (adaptability), and by integration of processing between brain regions (synchronization). The research converges to show that network-level descriptions of brain function are necessary for accurately characterizing comprehension ability.

Theoretical Implications

The ability to relate variability in patterns of brain activation to differences in cognitive capabilities is useful; however, the ultimate goal of individual differences research is to use this data to inform theories. This research has important implications for both better understanding the individual and better understanding the phenomenon being studied. Below, the implications of individual differences in the neural basis of language comprehension are discussed with respect to three broader scientific questions.

WHAT IS THE ROLE OF THE RIGHT HEMISPHERE IN LANGUAGE COMPREHENSION?

Individual differences in neural efficiency are often manifested by differences in RH activation, and variability in RH contributions as a function of comprehension ability has been observed in a variety of language paradigms. For example, in a series of divided-visual-field experiments investigating discourse representation, Prat, Long, and Baynes (2007) found that less skilled readers showed evidence of sentence-level (propositional) and discourse-level (topic) representations in both the RH and LH, whereas skilled readers showed only LH representation at both levels. In an fMRI investigation of lexical ambiguity, Mason and Just (2007) found greater RH activation in low-working-memory-capacity participants than in high-capacity participants. These differences in RH activation are of particular interest because the role of the RH in language comprehension remains controversial.

Although it is generally accepted that the RH contributes to discourse-level reading comprehension, the nature of its contribution remains uncertain. For example, some neuropsychological research suggests that the RH is involved in various types of inferential processes (Beeman 1993; Brownell, Potter, Bihrle and Gardner 1986), while other investigations fail to find deficits in RH-damaged patients, even when attempting to replicate previous studies (McDonald and Wales 1986; Tompkins 1991; Tompkins, Fassbinder, Lehman Blake, Baumgaertner and Jayaram 2004). Similarly, some neuroimaging studies of healthy controls report RH contributions to inferential processes (e.g., Kuperberg, Lakshmanan, Caplan and Holcomb, et al. 2006; Mason and Just 2004; Sieborger, Ferstl and von Cramon 2007; Virtue et al. 2006, 2008), whereas others do not (e.g., Ferstl and von Cramon 2001). In addition, a recent meta-analysis of discourse comprehension studies found no evidence for unique RH contributions to inferential processes (Ferstl et al. 2008).

The combination of inconsistent attempts to characterize RH language function and the prevalence of individual differences in RH activation during language tasks, suggests that conventional theoretical frameworks may lack consideration of an adaptive, ‘as needed’ role of the RH in language processes. Prat and Just have proposed a dynamic RH spillover hypothesis, which describes the conditions that predict RH participation in language comprehension processes (Just and Varma 2007; Prat and Just 2008; Prat et al. 2011). Briefly stated, the hypothesis is that: (1) the RH serves as a resource reserve for language processing with similar but coarser-grained and less efficient capabilities than the dominant LH homologs; and (2) the RH becomes increasingly engaged when the processing demands of a language task outstrip the resources available in LH such that some of the residual processing spills over into RH.

The idea that lateralized processes 'spill over' into the contralateral hemisphere with increased difficulty is not a new one. For example, Just et al. (1996) found increased RH activation during sentence comprehension when syntactic complexity increased. A recent experiment by Mitchell and Ross (2008) showed that prosodic processes (normally lateralized to the RH) drew increasingly upon LH homologs as complexity increased, illustrating that spillover of processing occurs from RH to LH as well.

Individual differences research is central to this theory because it predicts that recruitment of the RH varies systematically across people, depending on an individual's capabilities and on the amount of demand imposed by the task relative to the available resources. According to this view, the LH language areas are consistently evoked in most people for a given language task, whereas RH contributions are more variable between participants and tasks and are therefore more difficult to characterize at the group level. This difficulty should be surmountable with the application of a theoretical framework that provides a systematic account of the individual differences in RH involvement in language processing.

WHAT CAN INDIVIDUAL DIFFERENCES IN THE BRAIN TELL US ABOUT READER CHARACTERISTICS?

Behavioral research has consistently demonstrated that both word knowledge (generally indexed by some measure of vocabulary size or verbal fluency) and fluid information processing abilities (generally indexed by some measure of working-memory capacity) are highly correlated with indices of comprehension ability (e.g., Bell and Perfetti 1994; Daneman and Merikle 1996; Just and Carpenter 1992; Long et al. 1994, 1997, 2008; Perfetti et al. 1979). While verbal working memory capacity and word knowledge have been extensively correlated with comprehension ability, the constructs measured and the developmental trajectories of these two characteristics of readers are quite different. For example, verbal working memory capacity has been viewed as a general characteristic of fluid information processing ability that peaks in early adolescence (e.g., Gathercole 1999; Gathercole et al. 2004) and then decreases after young adulthood (e.g., Horn and Cattell 1967; Stanovich et al. 1995). Indices of verbal working memory capacity are highly correlated with indices of non-verbal working memory capacity as well as with more general measures of reasoning and fluid intelligence (e.g., Engle et al. 1999; Kyllonen and Christal 1990). Until recently, working memory capacity was believed to be a rather impermeable characteristic of an individual that was unaffected by experience with particular tasks (see Jaeggi et al. 2008 for recent studies showing improvement of working memory capacity with specialized training and Chein and Morrison 2010 for studies showing improved fluid processing abilities). Word knowledge, on the other hand, is acquired through experience with language; it continues to grow with reading experience throughout the lifespan, though the rate at which it grows varies as a function of other intellectual capabilities (Cunningham and Stanovich 1997; Stanovich and Cunningham 1992).

Based on the separability of these components of comprehension, one can imagine different trajectories by which an individual might obtain a certain level of proficiency (or lack thereof) in a reading comprehension task. For example, someone with an average working-memory capacity who is a voracious reader may obtain the same level of proficiency as another individual with high working-memory capacity who does not read frequently. Research on the neural characterizations of language experience and fluid information processing offers some insight into understanding how these two scenarios may result in different profiles of brain activation for readers of the same proficiency level.

Multiple lines of research converge to suggest that individual differences in efficiency may be related to differences in language experience. The relation between efficiency and experience with a particular task is nicely illustrated in training paradigms. For example, practice with novel mirror reading paradigms results in reduced activation in the right superior parietal regions involved in the mental transformations required for the task (Kassubek et al. 2001; Poldrack and Gabrieli 2001; Poldrack et al. 1998). With respect to language comprehension processes, in two analyses where individual word knowledge (as indexed by vocabulary scores) and working memory capacities (as indexed by reading span scores) were allowed to compete for variance, word knowledge was a better predictor of neural efficiency than was working memory capacity (Prat and Just forthcoming; Prat et al. 2010a). The relation between print exposure and word knowledge has been well established (Cunningham and Stanovich 1997; Stanovich and Cunningham 1992). Thus, it is plausible that the observed reduction of activation in high comprehenders results from increased experience with or exposure to language comprehension tasks.

Increased efficiency with experience can also be observed developmentally. Electrophysiological research has shown that young infants (about 13 months old) show differences in brain responses to familiar versus novel words in a highly distributed manner, whereas the differences between familiar and novel words in slightly older infants (about 20 months old) are more focally distributed, primarily in the temporal and parietal regions of the LH (Mills et al. 1997). In addition, Mills and colleagues found that vocabulary size was an important predictor of efficiency of word representations, with higher vocabulary 20-month-olds showing more focal differences between known and unknown event-related potentials, than did infants of the *same age* with smaller vocabularies (Mills et al. 1993). Thus, these results suggest that the increased efficiency in older infants is related more to language proficiency and experience than to chronological age. A similar pattern of increased efficiency with language experience can be observed in bilinguals. Research on bilingually developing toddlers has shown that infants show greater efficiency in the language for which they exhibit better proficiency, as indexed by larger productive vocabularies (Conboy and Mills 2006). In adults, patterns of activation for an individual's first language (L1) and second language (L2) tend to show that L1 is more focally represented than L2, but that proficiency in L2 (more so than age of acquisition) is the primary factor that is related to the degree of focalization of L2 distribution (for review, see Abutalebi 2008). Taken together, this research suggests that language experience results in more efficient processing of language, and that this increased efficiency is reflected by less, or more focal, patterns of brain activation.

Increased efficiency with language experience does not necessarily imply that individual differences in neural efficiency are explained entirely by differences in experience. It is plausible that differences in the rate of becoming efficient also exist, such that skilled comprehenders need less experience with a particular type of task in order to become efficient than do less skilled comprehenders. Neubauer et al. (2004) investigated this possibility in an electrophysiological experiment, measuring neural efficiency in a novel pattern completion task in individuals with varying intelligence, measured by the German Leistungs-Prüf-System. They found no efficiency differences in the baseline exposure to the task; however, following training, more intelligent individuals showed more efficient patterns of activation than did less intelligent ones. In addition, the rate at which activation decreased with training was greatest in the most intelligent individuals. Their results suggest that given the same amount of exposure to a task, more intelligent individuals have greater increases in efficiency than do less intelligent individuals. Thus, the increased efficiency observed in skilled comprehenders is likely the result not only of experience with language, but also of an increased ability to *benefit* from language experience.

In contrast, individual differences in adaptability and synchronization seem to primarily reflect more general fluidity in information processing that underpins complex cognitive tasks (e.g., Garlick 2002; Schafer 1982; Shucard and Horn 1973). In two studies conducted by Prat and colleagues, increased neural adaptability was found as a function of increased working-memory capacity (Prat and Just forthcoming; Prat et al. 2007), but not as a function of increased word knowledge (Prat and Just forthcoming). Research showing that high-working-memory-capacity readers are able to dynamically recruit neural networks with changing task demands may, therefore, reflect improved general information processing abilities in these individuals. One prediction that can be derived from this hypothesis is that the experientially dependent neural efficiency results should be observed only in learned language tasks, whereas the relation between working-memory capacity and neural adaptability should also generalize to novel tasks and to a broader range of cognitive domains.

The results described herein suggest that individual differences in language experience are primarily manifested as differences in neural efficiency, whereas individual differences in fluid information processing abilities are manifested as variability in neural adaptability and synchronization. In addition, increased efficiency with experience tends to be related to a specific class of tasks, whereas increased adaptability and synchronization in high-capacity readers seems to be a more general facet of information processing in the brain. Although these psychometric properties tend to be correlated in individuals, the separable neural instantiations of them should allow researchers to disentangle the contributions of experience (or skill) from those of fluid abilities (or giftedness) to performance on any given task. Conversely, through experimental manipulation, one should be able to determine whether difficulty with a particular task is primarily related to general intellectual difficulties or more specifically to a lack of sufficient practice. I view this as an exciting avenue for future research.

WHAT ARE THE MECHANISMS UNDERPINNING NEURAL ADAPTABILITY?

Investigations of individual differences in language comprehension have shown greater adaptability in high-capacity comprehenders (Prat et al. 2007; Prat and Just forthcoming; Yeatman et al. 2010); however, the mechanism behind this adaptability is still poorly understood. One potential clue can be gleaned from the fact that the largest and most consistent adaptability effects tend to be observed in prefrontal regions and in the striatum (Prat et al. 2007; Prat and Just forthcoming). These regions frequently activate in neuroimaging investigations of working memory (e.g., Braver et al. 1997; Lewis et al. 2004; Rypma et al. 1999) and seem to be especially important when language comprehension processes involve a large amount of cognitive control (Crinion et al. 2006; see Friederici 2006 for a review; Mason and Just 2007).

Theories proposing that the striatum serves a general role in routing information throughout the cortex (Gurney et al. 2001; O'Reilly and Frank 2006; Stocco et al. 2010) offer a potential explanation for individual differences in cortical adaptability. Although these theories differ in their proposed mechanisms, the consensus among them is that the striatum functions like a gate, receiving input from all the cortical regions, providing output to the prefrontal cortex, and selecting which signals should pass between cortical regions to limit interference and ensure that selected representations will transfer to appropriate cortical centers. Thus, greater recruitment of both striatum and prefrontal regions with increased syntactic complexity across two studies may show more effective routing of signals in high than low-working-memory-capacity readers. This hypothesis is supported by the fact that increased synchronization between the striatum, prefrontal cortical regions, and the LH language regions was also observed with increasing syntactic complexity, more so in high-capacity readers than in low-capacity readers (Prat and Just forthcoming). In light of these theories, individual differences in adaptability may be related to the ease with which relevant information can be dynamically transferred to cortical processing centers. This ability is central to language comprehension as well as to other tasks that require maintenance and manipulation of information, such as working-memory capacity and fluid intelligence.

Summary

This review provides evidence that individual differences in the brain can be systematically understood. This information can inform theories about the neural underpinnings of complex cognition in general, and language comprehension abilities, specifically. This review shows that language comprehension abilities are underpinned by a dynamic, distributed brain network, and that efficiency, adaptability, and synchronization of the network relate to the effectiveness of its computations.

Short Biography

Chantel Prat's research investigates the nature of biological constraints on information processing, with an emphasis on the neural correlates of individual differences in language comprehension abilities. Her current research employs the combination of fMRI, TMS, DTI, and behavioral paradigms to investigate the neural basis of individual differences in language and cognition. She earned her PhD at the University of California, Davis, working with Debra Long on investigations of individual differences in representation of discourse in the two hemispheres, and trained subsequently at the Center for Cognitive Brain Imaging with Marcel Just, conducting investigations of network-level characterizations of cognitive capacity. She is currently an Assistant Professor at the University of Washington, Seattle, with appointments in Psychology and at the Institute for Learning and Brain Sciences. Dr Prat was recently awarded the Society for Text and Discourse's Tom Trabasso Young Investigator Award for 2011.

Note

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