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BEHAVIORAL AND NEURAL RESPONSES TO INDUCED INSTABILITY: THE DYNAMICS OF PERTURBATION AND ADAPTATION DURING LANGUAGE PROCESSING

by

Amy Elizabeth Ramage

A Dissertation Submitted to the Faculty of the
DEPARTMENT OF SPEECH AND HEARING SCIENCES
In Partial Fulfillment of the Requirements
For the Degree of
DOCTOR OF PHILOSOPHY
In the Graduate College
THE UNIVERSITY OF ARIZONA

2001

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As members of the Final Examination Committee, we certify that we have read the dissertation prepared by **Amy Elizabeth Ramage**

entitled **Neural and Behavioral Responses to Induced Instability: the dynamics of perturbation and adaptation during language processing**

and recommend that it be accepted as fulfilling the dissertation requirement for the Degree of **Doctor of Philosophy**

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Final approval and acceptance of this dissertation is contingent upon the candidate's submission of the final copy of the dissertation to the Graduate College.

I hereby certify that I have read this dissertation prepared under my direction and recommend that it be accepted as fulfilling the dissertation requirement.

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SIGNED: Amy Elizabeth Ramage

ACKNOWLEDGEMENTS

I would like to express my gratitude to all of the members of my committee: Drs. Audrey Holland, Elena Plante, Carol Boliek, and Janet Nicol. Each member of this committee has had such a unique contribution to my experience in conducting this study and in writing this manuscript. Thanks go to Audrey Holland for all of her direction and encouragement through joy and tears for the last four years and for the never-ending wonderful ideas in her head. Thanks go to Elena Plante for never doubting that the study could be done and for spending late nights at the scanner working through the minutiae. Thanks go to Carol Boliek for helping me to understand and avoid chaos – may we both remain in stability. And thanks go to Janet Nicol for her willingness to read hundreds of sentences (stimuli and this manuscript) desperately needing her linguistic expertise.

I also must express my thanks to Lew Shapiro and his lab for generously allowing me to use his E-prime license and many of his stimuli. Gratitude also goes to Ken Forster who spent hours teaching me to use DMDX when E-prime was not going to work in the scanner. Also, thank you to Rob Kraemer who assisted in figuring out all of the technical quagmires occurring in the scanner room.

Of course, none of this project would have been possible without the willingness of the subjects to participate. They suffered through being forced into instability and nine of them came back for more. Thanks go to all of them.

Lastly, very special thanks to my family. To my mother Mary Beth who, though she is not sure why I put myself through all of this, has never wavered in her support. To my husband Don who recorded all of the stimuli (three times), dealt with my ups and downs, and served as a sounding board – all without complaining once and while continuing to love me. To my step children Natasha and Colin who understood my love/hate relationship with the computer and put up with me anyway. And to the beast within who has kept it interesting.

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ABSTRACT

The current investigation examined perturbation and adaptation during language comprehension in young normal subjects. Using a dynamic system framework, induced instability was studied by increasing perceptual demand (compressed sentences), syntactic demand, or both. Two experiments were conducted, one behavioral and one using fMRI technology, to explore the relations between brain responses and behavior. This study examines if changes in rate of speech, syntax, or both induce an instability, or perturbation, with subsequent adaptation in which subjects regain a previous stable state. Dependent measures in the behavioral study were accuracy and reaction time based indices of perturbation, adaptation, and stability. Results of the behavioral study demonstrated that language comprehension can be perturbed by changes in syntactic complexity or syntactic + perceptual complexity. Further, it was found that subjects adapted to being perturbed. The more complex the stimulus, the longer it took for subjects to adapt.

The second experiment used fMRI to measure brain activation associated with perturbation and adaptation of language. Several brain regions showed increases in activation with increasing complexity (i.e., perturbation). Some regions (e.g., the superior parietal lobule) appeared more active when the perturbation was perceptual and others (e.g., the left inferior frontal gyrus) more active when the perturbation was syntactic in nature. These regions either

remained active during the adaptation process, or reduced in activation during adaptation suggesting a role specific role in perturbation.

These results suggest that subjects develop and maintain a representation of either the syntactic frame (i.e., via priming), a conscious strategy for accommodating syntactic complexity, or rate normalization schema. Thus, the brain regions that remain active during adaptation may be used to maintain the linguistic or perceptual frame. Within a dynamic system framework, the development of these representations, which occurs over a few items, serves as an attractor to which subjects are drawn each time they are perturbed. Like other complex systems, once instability occurs, there needs to be a strong attractor state to pull subjects into stability that permits appropriate performance to continue.

CHAPTER 1 - INTRODUCTION AND LITERATURE REVIEW

The study of human language must involve a conceptualization of the role of variability in the expression of behavior. Whereas some researchers have suggested that variability impacts human behavior negatively, current models of performance, particularly those in the motor domain (e.g., Kelso, 1995; Schmidt & Lee, 1999), suggest that variability is an important component of learning, the emergence of new behaviors, and the expression of behaviors in multiple contexts. Although studies exploring the role of variability in speech production can be found in the literature (e.g., Sharkey & Folkins, 1985; Ballard et al., 2001), relatively few experiments (e.g., Armstrong, 2001; Evans, 1996) have explored variability during language processing.

The study of performance variability in language has important implications for understanding normal linguistic processing and disordered language. For example, performance in aphasia has been modeled within a resource allocation framework that attempts to account for individual subject variability (e.g., Clark & Robin, 1995; McNeil, 1983; McNeil, Odell, & Tseng, 1991). Similarly, investigators studying specific language impairment in children have tried to capture performance variability using models of attention or working memory (e.g., Campbell & McNeil, 1985; Montgomery, in press). Because little is known about variability of language processing in normal subjects, theoretically motivated, in depth study of normal linguistic variability must be undertaken. Equally important is the need to link behavioral variability in humans with brain activity in order to develop a model that is constrained by the neural systems involved in complex behaviors, particularly language.

One model that captures the substantive nature of variability in many different complex behaviors is that of dynamic systems. The dynamic systems model serves as a conceptual framework for the present study. This chapter begins with a review of performance variability in humans with particular reference to dynamic systems. Next, a review of studies on language processing in normal individuals is presented. Subsequently, there is a review of the functional brain imaging literature in reference to language processing in normal subjects with an emphasis on the brain as a variable complex biological system. Finally, the purposes, research questions and hypotheses for the current experiments, one behavioral and the other neuroimaging, are detailed.

Variability and Dynamic Systems

Variability is an inherent property of all biological systems. In fact, the highly developed human brain is probably one of the most variant of systems given the complexity of its architectonics and physiology. That is, many consider the brain the quintessential complex system (e.g., Kelso, 1995). As well, the output of neural activity is often highly variable, particularly since the resultant behaviors are quite complex. Although variability has often been considered a negative aspect of behavior (performance), current theories state that variability and/or the lack thereof, is critical for understanding the more global issue of how behaviors are learned and how those behaviors are manifest across varying contexts (Evans, 1996; Kelso, 1995; Schmidt and Lee, 1999; Thelen, 1995).

Dynamic systems theory mandates that variability is essential to accurate learning and performance because flexibility is needed to meet constantly changing internal and external demands. It is clear that too little variability can have as negative an effect on performance as too much variability (see for example Schmidt & Lee, 1999 or Folkins, 1985). An example may be when a person with aphasia perseverates and is unable to retrieve a new and appropriate word for a response. Those who embrace dynamic systems as a way to explain human behavior (e.g., Kelso, 1995) suggest that change is a constant, and that response to change is essential. In order to produce reliable, accurate, and repeatable behaviors, including language, the ability to adapt to constant change is critical.

Dynamic Systems as Complex Systems

Dynamic systems theory has its roots in complex system analysis and models of chaos. A dynamic system refers to any system that is made up of interconnected or interwoven parts (e.g., a person, the human body, the brain). Specifically, a dynamic system is defined as any system that is formed from many component parts from which behavior emerges. That is, the behavior of the system is emergent because it cannot be inferred from the behavior of its individual components (Bar-Yam, 1997). Rather, it is the interaction among components that is important. Emergence, in this case, refers to the collective behavior (output) of the individual components. Thus, because emergent properties are collective behaviors, dynamic systems theory asserts that examination of the components independently results in limited understanding. Moreover, in order to operate effectively, there must be coherence among the component parts of a complex system. In summary, because there are multiple parts to a system, each of these parts must operate together and coordinate as a single emergent property in order for a behavior to be accurately produced.

Because the components of a dynamic system are coherent, the system is capable of having many different states. In fact, the "dynamic" aspect of a system refers to its existence in many different states. The existence of various states depends on the internal structure of a system's components at any given time. As a result, a dynamic system is in a constant state of flux and each of its states must be described in order to fully understand the parameters that govern its behavior and their emergent properties. The transition of a system from one state to another is its dynamic property; therefore, any system that is characterized by state changes (e.g., phase shifts) is a dynamic system. For example, a person in motion may be described as a dynamic system and a shift from walking to running may be considered a phase shift (examples related to language processing appear below).

Thus, to understand dynamic systems, it is necessary to understand how the individual components of a system relate to each other. One must be able to classify or describe the elements of a system (and their number), their interactions (and strengths of those interactions), their formation/operation (and the time periods involved), the diversity and variability of the system, the environment and the demands it places on the system, and the activity of the system. The fact that systems are in constant flux or constant variability creates a challenge for studying complex systems. This is because, in most cases, at least one of the variables is unknown and therefore must be predicted or inferred from other parts of the system and their interactions. Another challenge is that the component parts of a dynamic system also are often complex systems themselves. In essence, emergent complexity creates layers of complexity, each needing to be characterized. Language processing is no exception and may be one of the most complex systems found in humans. Because of the constant change in states over time, dynamic systems models seek to explain the temporal evolution of any behavior. Therefore, dynamic system models utilize a series of equations stipulating the temporal evolution of a behavior (x). If x is a continuous function of time, then the dynamic of x is typically defined by a set of first-order ordinary differential equations (Kelso, 1995).

The Terminology of Dynamic Systems

To appreciate dynamic systems from a modeling and/or a conceptual approach, several terms require operational definition. Terms used in dynamic systems theory include: *flexibility* (ability to adjust to changing internal or external conditions), *stability* (ability to persist under various environmental conditions), *instability* (point at which the system is on the brink of changing), *attractor* (a subset of the phase space to which initial conditions reach asymptote as time continues to infinity), *intermittency* (state in which there is no switching from one state to another, but rather the system is poised near critical points where it can spontaneously switch in and out), and *hysteresis* (overlapping regions that exist where, depending on the direction of the parameter change, the system can be in one of several states).

The Variables of Dynamic Systems

In addition to the above, definitions of the variables of interest for studying change within dynamic systems theory are needed. The first variable is the *control parameter*, the variable that promotes instability. Variation in the control parameter causes qualitative changes that lead the system through a variety of possible patterns or states. The *order parameter*, another component of the model, is the dimension on which pattern change occurs. For the person in motion example provided above, velocity is the control parameter (speed of the system) and movement rate is the order parameter (walking vs. running). Thus, as the person increases speed the rate of movement changes from a walk to a run.

Other Examples of Dynamic Systems

Not all dynamic systems are motoric in nature. Attention is a cognitive example of a dynamic system. When a person is performing a task, there is an attentional requirement (unless that task is completely automatic). As task demands increase (control parameter), either because of internal or external distractors, the cognitive system becomes unstable and a change in the attentional demand occurs (order parameter) requiring the system to allocate an increased amount of resources (the emergent property) to the task. A normal system, facing changing task demands, may stay in an intermittent state so that it can easily change the allocation of attention while performing the task and remain in its most efficient state (nearest to an attractor state) most of the time. That is, a normal system will avoid being stuck in a deep attractor well, which would result in the person having difficulty shifting attention.

An important part of the central executor, that controls attention, is located in frontal neural systems. Kamm, Thelen, & Jensen (1990) and Thelen (1995) argue that patients with frontal brain damage may be stuck in a deep attractor well and unable to shift to new states when needed. However, an intermittent state also may be in hysteresis, somewhere between alternating and divided attention, until it settles into the best fit for a new task demand. In all of these examples, system variability is a critical component to understand behavior.

In summary, dynamic systems theory is an approach that can be used to describe the formation, development and stability of patterns or behaviors across a range of different domains including motor control, language and cognitive processing, and brain activity. Specifically, dynamic systems models suggest that patterns or stable behaviors *emerge* as a result of a system's interaction with the internal and external environments. Part of the constraint placed on the system by these environments includes the varying level of demand at any given moment in time. Thus, people need to adapt to constant change (variability). However, variability also is required to develop new behaviors and to express learned behaviors in differing contexts and under differential demands (concepts to be explored later).

Performance Variability and System Stability

Performance variability refers to moment-by-moment change in behavior. When a system is variable, it is unstable; i.e., the greater the variability, the greater the instability. Thus, one can use performance variability as an index of system stability (see Kelso for details, 1995). The dynamic systems approach states that systems and their resultant behaviors fluctuate between stable and unstable states (e.g., Kelso, 1995). The stronger the attractor to a certain state (within limits), the greater the probability that the behavior will be reliable and of use to the person. Essentially, dynamic systems theory suggests that behaviors, such as skilled motor activities or language, emerge from instability in the form of a stable state. The strength of the stability is a function of the attractor that defines the pull to stability. Within this rather simple conceptualization, it is apparent that too much stability (too little variability) may be problematic, as might too much instability (or variability). For example, if an attractor state is too strong, with the result that little or no variability exists, a person may only be able to produce a single behavior. This might be the case in persons with brain damage who perseverate, or might account for the very limited verbal output produced by an individual with global aphasia. If variability is too great, an attractor state may be weak and the emergent behavior may be fleeting or never emerge as a functional entity. Thus, the excessive verbal output of a person with Wernicke's aphasia might in part be due to excessive variability and an inability to maintain a stable state. In either case, the ability to learn new behaviors or express old behaviors in new contexts requires the "right amount" of variability.

Perturbation and Adaptation

Another important concept in dynamic systems models of behavior is *perturbation.* A perturbation is anything that disrupts an ongoing behavior or stable state. In this sense, perturbations are any changes that induce variability. Perturbations can result from changes in the external environment, in the internal state of a person, or as a function of changes in some parameter of a stimulus. For example, if a person is listening to another person talk and suddenly a loud banging sound disturbs the listener, the listener must adjust behavior (attention) in some way to continue adequately understanding the speaker (external environment). Another example is when a professional figure skater hurts her ankle during a jump while performing and continues by making some accommodation to the pain (internal environment).

Critically related to the notion of perturbation, is the concept of *demand*. Demand refers to how much stress is placed on a system by a perturbation. The greater the perturbation, the greater the demand placed on the system or person. Increases in demand stress the system. Changes in complexity of a stimulus can be thought of as perturbations because they change the level of demand during a given activity and stress the performer. Changes in complexity constantly occur. Thus, over time a system is constantly shifting from one stable state to another and dealing with perturbations. For example, a person at work encounters changes in task demand when talking on the telephone and typing at the same time, or when working on a project under substantial time constraints.

Perhaps the most important aspect of human behavior that is yet to be understood is how a person or system *adapts* to changes in demand or to perturbations. Adaptation to change, therefore, is an integral part of day-to-day performance. In other words, humans must constantly adapt to perturbations in order to be able to function accurately and efficiently. It is most critical to know how individuals adapt to perturbations. That is because adaptation determines: (1) whether individuals will be successful in ultimately accomplishing a behavior or learning a new one in the face of perturbation, or (2) if the perturbation will disrupt behavior and not permit the goal to be reached. Dynamic systems theory provides numerous possibilities for response to a perturbation. Consider the following discussion relative to adaptation in a dynamic system framework.

Following a perturbation there must be a response or the system will become chaotic (too variable). The response can either be adaptive (positive) or maladaptive (negative). If a response is adaptive, then there are two possibilities:

1. The behavior may move back to the original stable state (particularly if the attractor is strong) and a given behavior continues appropriately; or
2. The perturbation and subsequent response could represent the emergence of a new stable state that ensures the behavior will be completed accurately.

For example, a person may be walking and suddenly one foot may slip on a curb. In (1), the perturbation may cause a moment of being off balance (instability), but the person will quickly begin walking regularly again on the sidewalk (return to stable state). In (2), the person may be off balance for a short time, but then step off of the curb and begin walking in the street (emergence of a new stable state).

Maladaptative responses to perturbation also can occur. One might be perturbed enough to shift out of a strong stable state and be unable to shift into a new stable state – i.e., remain in a state of instability. Using the above example, the person might continue being off balance. Another maladaptive response could be a shift to a new behavioral state that is inappropriate for the current context. That is, the person may begin walking with one foot on the curb and one on the street (a new, but inappropriate stable state).

Overview of Language Processing

This section provides a brief overview of language processing with a focus on comprehension. Normal language processing involves the access of lexical information that is then organized into various structural relations. These structural or syntactic relations involve the computation of interactions among lexical items. Ultimately, structural relations are combined to form discourse during natural conversation. Several theories have been posed regarding how the lexical, syntactic, and pragmatic sources come together to comprehend a sentence (see for example Frazier, 1987, 1990 for review of the "garden-path" model; Marslen-Wilson & Tyler, 1980 for a review of the "interactive" models; Mitchell, 1994 for a comprehensive review) and all have provided empirical data indicating how increased complexity of language can interfere with its processing.

At a syntactic level, language processing involves the computation of the geometry of the input and may also involve an analysis of long-distance dependencies. That is, more complex syntactic structures (e.g., object relative structures) require maintenance of lexical activation of the object of a noun when the verb is encountered. Or, the object may need to be reactivated when the verb is encountered. For example, in the sentence *The busboy pocketed the rare coins that the secretary had left* (gap – *the coins*) *on the small plate*, lexical activation for *coins* must be either be maintained or be re-activated to fill the gap after the verb *left*. Filler-gap relations are found in sentence constructions in which noun phrases that have been displaced from their canonical positions leave behind a gap in the representation of a sentence (e.g., "It was the car that the mechanic fixed GAP yesterday."). The noun phrase serving as the object of the verb is re-accessed at the gap in order to co-index the noun with the verb (in the example above, to link "the car" with "fixed"). Most likely, a filler or antecedent is reactivated at the gap position of a sentence (Love & Swinney, 1996; Shapiro, Hestvik, Suzuki, & Garcia, 1998); even when the noun phrase is a semantically implausible filler. The longer the distance is between the antecedent and the gap, the greater the demand when reactivation is necessary.

The English language also is preferentially processed using word order as a cue for parsing (MacWhinney & Bates, 1989). Bates and colleagues have found in numerous studies (e.g., Li, Bates, & McWhinney, 1993) that when syntactic complexity increases, or when atypical grammatical structures are encountered, speakers of English opt for use of the most frequent subject-verb-object ordering. Of course, this strategy is inappropriate for processing of many sentence types.

Whereas sentences can be made more complex with the above manipulations, some manipulations also can facilitate comprehension. One important area of linguistic processing is that of syntactic priming (see Nicol, 1996 for a review). Essentially, syntactic priming is the facilitation in the processing of a sentence because the sentence was preceded by one of similar syntactic structure. (This is important to the current investigation because subjects hear consecutive presentations of similar structures.) Recent investigations into syntactic priming have shown that listening to a structure can prime that structure even when it is a complex sentence (Potter & Lombardi, 1998). In the latter case, the priming was evidenced in production, but it is thought that the priming facilitates access of the structure at a mental level and should therefore be operative for comprehension if the next item has the same or similar structure. Evidence also exists, in this case in written production, for decay of syntactic priming after a few items when those items represent different structures (Branigan, Pickering, & Cleland, 1999).

In sum, it is known that certain syntactic structures are more complex than others. The most simple are those with verbs having few arguments, with no embedded clauses, and that follow the subject-verb-object word order (e.g., *The cat bit the girl*). Manipulation of the frequency or number of semantically related competitors of the nouns used or the number of arguments associated with a verb can make a sentence more complex and can be done without changing the syntax (e.g., *The marine recruits trained for the obstacle course*). Addition of a center-embedded clause creates a long distance dependency between a gap and an antecedent; this also can increase complexity (e.g., *The boy who the mother loved was always on time*). Finally, alteration of the position of subject and object so that the object appears before the subject increases complexity (e.g., *The girl was bitten by the cat*). A combination of the latter two manipulations results in the most complex types of sentences including the object relative (e.g., *The busboy pocketed* *the rare coins that the secretary had left on the small plate*) and object clefts (e.g., *It was the surgeon whom the journalist kissed after the successful heart transplant surgery*) used in this study.

Language as a Dynamic System

As noted above, it is thought that language is variable. This is most pronounced in brain-damaged populations in which variability is seen in every aspect of language from lexical access for production to comprehending the same sentence from one day to the next. However, little is known about the sources of this variability or about how it manifests itself over time. In fact, few studies have explored within subject language variability. It is known, however, that language processing can be disrupted (perturbed) under certain conditions. For example, Dick, Bates, Wulfeck, Utman, Dronkers, and Gernsbacher (2001) found that normal subjects' accuracy to answer questions about just presented sentences was worse for complex sentence structures (object clefts) as compared to simple ones. They reported further that performance decreased substantially when these sentences were compressed to 60% of the original or when the sentences were low-pass filtered (i.e., cut out all information above 600 Hz by 20dB). Exponential decline was found when the sentences were both compressed and low-pass filtered. In fact, under the compression + low-pass filtered condition, normal subjects performed as poorly as patients with aphasia did on the same sentences without stimulus manipulations. These findings suggest that manipulations of syntactic complexity, compression, and low-pass filtering of the auditory signal serve to perturb the language system, resulting in variability and at times, reduced comprehension. However, it is not known how the subjects responded to perturbations over time or whether or not subjects returned to a stable state after the induced instability. That is, adaptation to perturbation was not studied.

One study did provide preliminary information on adaptation to perturbation. Mehler, Sebastian, Altmann, Dupoux, Christophe, & Pallier (1993) investigated the transcription of time compressed sentences (compressed at 40% of the original) and found that normal subjects, while initially showing less accurate responses, adapted to time compression in approximately 10 to 15 seconds with continuous presentation of the stimuli. Further, they found that once subjects were exposed to compression, the adaptation remained for the course of the experiment. That is, the next time they heard compressed speech during a session, they no longer had a need to adapt (indicated by no decreases in accuracy). Within a dynamic system framework, this would indicate that there was no evidence of continued perturbation. Rather, subjects remained in a stable state.

In a more recent study, Pallier, Sabastian-Galles, Dupoux, Christophe, & Mehler (1998) measured listeners responses to time compressed speech. Bilingual subjects listened to sentences in two different languages. The investigators aim was to examine adaptation to compression in both languages. That is, they were interested in whether or not adaptation to compressed speech in one language carried over to the second language. They found that adaptation to compression in one language carried over to the second language, even though subjects had not heard the second language in the uncompressed condition.

Syntactic priming can be considered under a dynamic system framework as well. Essentially, the facilitation of processing after the presentation of a similar syntactic structure suggests that an attractor well is formed by the first sentence and this well may be strengthened by repetition of similar structures, not unlike that found in other systems (see Kelso, 1995). What is not known from the syntactic priming literature is if a change in syntactic structure results in a perturbation and if the result is an interference with sentence processing.

Effect of Temporal Compression on Comprehension of Speech and Language

There have been numerous studies showing a relationship between rapid presentation rate and language comprehension. Temporal processing has been studied from normal as well as from disordered perspectives (see for example Tallal, Miller, & Fitch, 1993; Zimba & Robin, 1998). In particular, temporal manipulations on speech signals have been found to constrain performance in auditory processing (e.g., Bregman, 1990) and speech perception in numerous studies (e.g. Longuet-Higgins & Less, 1984). Moreover, certain investigators have suggested that temporal processing inefficiencies may cause (e.g., Tallal et al., 1993) or contribute to (e.g., Robin, Tranel, & Damasio, 1990) language disorders in children and/or adults. Importantly, temporal constraints change the ability to accurately perceive speech and non-speech stimuli and may serve to perturb language by reducing intelligibility of speech or the ability to comprehend language (e.g., Wingfield & Stine, 1986).

One area of temporal processing related to the current investigation is the perceptual organization of rhythmic, non-speech auditory patterns. It has been shown that the organization of sequences of tones into meaningful perceptual units is related to the frequency at which the stimuli were presented (Royer & Robin, 1986). Interestingly, neurophysiologic data from direct recordings in cats has shown that pattern perceptions in humans can be predicted from the adaptive neuronal response (Robin, Abbas, & Hug, 1990). Essentially, patterns appear to be organized around those elements or neuronal responses that provide the strongest response, and then progressive adaptation to stimulation occurs, independent of pattern starting place. Zimba & Robin (1998) used the neuronal data to show that changing the pattern of adaptation by changing the intensity of a single element (a perturbation) resulted in significant alterations in how subjects reported hearing the stimuli.

Summary

In sum, there is evidence that syntactic and temporal changes can perturb language, speech, and auditory processing. Moreover, data exist which support the notion that adaptation occurs and is critical in perception and comprehension of compressed language. Thus, the study of perturbation and subsequent adaptation during language comprehension has garnered some support in the literature, but requires much greater study to fully appreciate how language may be constrained by perturbation and adaptation.

Brain Activity and Cognitive/Linguistic Processing

To date, no neuroimaging studies have investigated variability during language processing. To some degree, this is due to limitations in the designs used in functional imaging tasks. Because the typical paradigm uses block designs and averages performance across blocks of several items, exploration of variability is difficult at best. Similarly, very few investigations using neuroimaging techniques have sought to uncover patterns of activation or networks of activation that might be interpreted within a dynamic systems framework. However, several investigators have reported on consistent activation patterns with certain types of tasks that may be interpreted as components of a dynamic system.

For example, many studies have attempted to delineate the nature of the regions active during changes in stimulus complexity or related to "resource" or working memory load. Smith and colleagues (1998) reported on dorso-lateral prefrontal cortex (DLPFC; reported as BA 44) using fMRI-imaging techniques during a working memory task ("n-back"). In this task, subjects are asked to indicate when an item (a number or letter) is the same as that seen 2, 3, ...n items previous (n-back task), requiring maintenance of the defined number of items in a list. They reported that the DLPFC activated only when the n-back task increased in difficulty and required maintenance or manipulation of information. More specifically, they reported a monotonic increase in activation of DLPFC as load increased in the n-back task, but only when the task was sufficiently demanding (i.e., when 2- and 3-back conditions were used). These authors interpreted this finding as evidence for the essential role of the DLPFC in maintaining information in working memory. This interpretation is similar to that of D'Esposito and colleagues (1995) who found that bilateral DLPFC became active during dual task conditions although this region was not involved when they were performed alone. These findings also suggest that the DLPFC responds to increasing task difficulty, but is not specifically involved in dual task processing.

Smith and colleagues have recently reinterpreted their previous findings and now suggest that left BA 44, along with left BA 6 (premotor and supplementary motor areas) are involved in the n-back task merely for the subvocal rehearsal that is increasingly required as task demands change (Smith & Geva, submitted). These authors now point to posterior parietal cortex (BA 40) as the essential region for storage and therefore the area that should be active during the increased demands of the n-back task. Diwadkar and colleagues (2000) also found co-modulation of DLPFC and parietal cortex during a working memory task, but the parietal activation was more specific to the visuospatial manipulations of the task. Manoach et al. (1997) also emphasized the close interaction between the DLPFC and the intraparietal sulcus showing increased activation of both regions during their verbal working memory task.

The work of Cohen and colleagues also has indicated that the DLPFC is more likely associated with storage for working memory rather than specifically with task difficulty (Barch, Braver, Nystrom, Forman, Noll, & Cohen, 1997; Braver, Cohen, Nystrom, Jonides, Smith, & Noll, 1997; Cohen, Perlstein, Braver, Nystrom, Noll, Jonides, & Smith, 1997). Using Positron Emission Tomography (PET) scan techniques, Awh and colleagues (1996) reported that verbal working memory is modality independent. Specifically, they claimed that frontal brain regions are active during rehearsal, independent of the modality in which rehearsal occurs. Whereas the exact area responsible for maintenance versus storage remains unclear, it is apparent that DLPFC and possibly also posterior parietal cortex are areas that become involved in a task when demand or difficulty level increase.

Combining language and working memory tasks, Carpenter, Just, Keller, Eddy, and Thulborn (1999) used single event fMRI and showed modulation in levels of activation within a language network (specifically, superior temporal and inferior frontal gyri) to be dependent upon changing syntactic complexity within that domain during a sentence comprehension task. Unfortunately, these authors did not use tasks involving non-language stimuli (e.g., visuospatial) to control for the possibility that their inferior frontal activation, specifically, was involved during processing in other cognitive domains. That is, this area may be sensitive to changes in complexity, independent of the cognitive domain being used at a given time as suggested by the data presented above. They did report, however, that activation occurred in homologous right hemisphere regions (albeit at a lesser degree than on the left). A limitation of the study was that the imaging technique used only seven coronal slices, excluding the full extent of the frontal and occipital regions. This limited the authors' ability to fully appreciate potential networks of brain regions that may work in concert to accommodate the processing conditions.

Further support for the left inferior frontal gyrus' role in processing of linguistic information comes from the work of Rypma and colleagues (1999). These authors found left dominant (i.e., greater signal change) increases in activation of that region during a verbal working memory task in which subjects held three to six letters in memory for identification (versus foils) in a delayed condition. Interestingly, they also found increases in activation of the middle and superior frontal gyri during the same task, but this activation was right dominant. These authors hypothesized that processing taking place in the inferior frontal gyrus must be stimulus dependent whereas that of the middle and superior gyri reflects more general executive processing that is field independent. Manoach and colleagues (1997) also explained their findings of increases in right dorsolateral prefrontal cortex during a similar verbal working memory task as indicating increased attentional demand.

Caplan (1998), using PET techniques, has suggested that Broca's area is specialized for the construction of syntactic form to determine sentence meaning. Likewise, Inui and colleagues (1998) using fMRI reported that the comprehension of Japanese center-embedded and left-branching structures was correlated with activation of Broca's area. More recent studies have indicated that the left inferior frontal gyrus may be divided by functional specificity. That is, these studies have shown that the pars opercularis (BA 44) is more active during syntactic tasks whereas the pars orbitalis (BA 47) is more active during semantic tasks (Dapretto & Bookheimer, 1999; Embick, Marantz, Miyashita, O'Neil, & Sakai, 2000).

Interpreted within a dynamic system framework, the imaging literature points to an ability to create a perturbation of the brain by changing stimulus complexity. Changes in linguistic as well as non-linguistic complexity are able to perturb brain function. Further, the imaging data point to a coordinated network of activity, which would result in emergent properties that guide behavior.

Limitations in the Current Knowledge Base

As is clear from this review, the study of variability in language, the brain and the relation between the two, is in its infancy. Related to brain activity, we know that changes in task complexity in some domains (language and working memory) result in increased activation in specific brain regions. Moreover, some of the data suggest that these regions operate as a network (e.g., the co-modulation of activity in the frontal and parietal regions, Diwadkar et al., 2000). In addition, some of the components of the network may not be process-specific, but rather may respond to changes in complexity relatively independent of task domain.

Behavioral studies of language have shown that when syntactic or perceptual (time compression) complexity increases, there is a concordant decrease in accuracy and slowing of reaction times. However, no data exist specifically examining within subject variability during language processing. Furthermore, few investigations have measured perturbation during sentence processing and even fewer can be found that examine adaptation to perturbation. Finally, no studies could be found that examine the relationship between language, perturbation, adaptation, and the brain. Thus, it is clear that data on perturbation, adaptation and variability in both behavioral and brain activity domains are needed to further explicate language processing in normal subjects.

Purposes of Current Study

Because of the dearth of information on language processing in regard to perturbation, adaptation and variability, a behavioral study (Experiment 1) was designed to provide information on the following:

(a) Perturbation of language comprehension using changes in *linguistic* (syntactic), *perceptual* (time compression), or both with response accuracy and reaction time as indices of performance.

(b) Subjects' adaptation to perturbation by examination of performance over time before and after induced perturbation by the aforementioned changes in complexity.

Once it was found that the experimental manipulations did perturb the language system, a second experiment (Experiment 2, fMRI study) was designed to explore the following issues:

(a) How the brain responds to the linguistic and/or perceptual perturbations by examination of activation levels and patterns of activity in specific regions.

(b) How the brain subsequently adapts to the perturbations by examination of changes in activation levels and/or patterns of activation in specific regions of interest.

For Experiments 1 and 2, the following issues were explored:

(a) Variability in performance or brain activation related to perturbation.

(b) Changes in variability as a result of adaptation to perturbation.

Questions and Hypotheses

The research questions for Experiment 1 were:

(1) During an off-line sentence comprehension task, do changes in syntactic complexity and/or changes in temporal demand as a function of compression result in inaccurate and/or slower responses in normal subjects? The

null hypothesis is that there is no effect and the alternative hypothesis is that there is a decrease in accuracy and/or slower response times when task demand is high.

(2) Does a combination of linguistic and perceptual manipulations create a greater level of perturbation? The null hypothesis is that the combined manipulations are no different than those manipulations alone. The alternative hypothesis is that the combined manipulations result in slower reaction times than either of the manipulations alone.

(3) Does the variability of responses increase when task demand increases (perturbation), indicating instability? The null hypothesis is that the coefficient of variance (described below) does not increase when subjects are perturbed. The alternative hypothesis is that the coefficient of variance increases following perturbation.

(4) Do subjects adapt to perturbations created by the experimental manipulations? The null hypothesis is that subjects do not adapt to the perturbations. The alternative hypothesis is that subjects show adaptation with reaction times returning to baseline levels over time.

The research questions for Experiment 2 are:

(1) When task complexity increases, what is the nature of the hemodynamic response (HR) in normal subjects? The null hypothesis is that there are no changes in brain activation. One alternative hypothesis would be that there are increases

only in those areas active during the baseline condition (H_{a1}). Another alternative hypothesis would be that additional brain regions are recruited to accommodate an increased task demand (H_{a2}).

(2) When task complexity changes, what is the nature of the adaptive hemodynamic response? If H_{a1} is true, then does the increase in those regions return to baseline patterns with adaptation? Or, does the level of activation decrease but to a pattern different than that of baseline? If H_{a2} is true, then do these additional regions return to baseline patterns with adaptation (i.e., no longer involved in the task)? Or, do these additional regions remain active, though to a lesser degree, in a new pattern?

CHAPTER 2 - METHOD FOR EXPERIMENT 1

Participants

Twenty young normal adults (10 males, 10 females) ranging in age from 19 to 35 years participated in this experiment. Subjects were recruited from undergraduate classes at the University of Arizona and the local community. All subjects gave informed consent to participate in the study. Subjects, by their report, met the following selection criteria: spoke English as their first language, were right handed, had no history of neurologic disease or loss of consciousness, had no history of drug or alcohol abuse, did not currently use psychoactive medications, had normal hearing as assessed with pure tone screening (unaided), and had normal vision (aided or unaided) as assessed by reading of newsprint. Many subjects had experience with a second language, but none had greater than two college level courses in that language. Subject characteristics are presented in Table 1.

Design and Procedures

Subjects performed three tasks: the Test of Nonverbal Intelligence-3 (TONI-3; Brown, Sherbenou, & Johnsen, 1997), the experimental task (described below), and the Listening Span Test [LST; a listening version of the Reading Span Test, Daneman & Carpenter, (1980)].

TONI-3 and LST

Because performance on the experimental task (below) may be related to general processing ability, the TONI-3 was selected as a valid and reliable standardized measure of cognitive processing in the nonverbal domain. Success on the TONI-3 requires subjects to develop a nonverbal, visuospatial problem solving strategy in order to complete a design. The strategy used must be flexible as the demands for each item differ. Since a main purpose of the current study was to examine adaptation to perturbation (e.g. subjects' ability to adapt to increased demand), the TONI-3 was selected as a measure of general processing and nonverbal strategy development. The format of the test is a 4 or 6 alternative forced choice paradigm from which the missing portion of a design is chosen. Subjects point to the choice that they believe best completes a particular design. There are 45 total designs on the test. Scoring followed the published guidelines. Raw scores, percentile ranks, and quotients were obtained for each subject.

The LST is an experimental test (not norm-referenced) of verbal working memory. This test was selected because it has been hypothesized that verbal working memory is directly related to language comprehension (e.g., Just & Carpenter, 1992). Scores on the LST [in its original version (the Reading Span Test] have been shown to correlate with performance on tasks of comprehension of syntactically complex sentences (King & Just, 1991). Specifically, it has been

Table 1. Subject Characteristics (n=20)

Subject	Gender	Age	Years of Education	Occupation
1	F	25	18	Student
2	F	25	16	Engineer
3	M	27	16	Engineer
4*	M	35	18	Audiologist
5*	F	20	15	Student
6*	F	34	18	Speech-Language Pathologist
7*	M	19	12.5	Student
8	M	22	13	Auto Body Technician
9*	F	20	13.5	Student
10	F	19	13.5	Student
11*	F	20	14.5	Student
12	M	21	12.5	Student
13	F	21	14.5	Student
14	M	21	15	Student
15*	M	23	16	Student
16*	M	21	15	Student
17	F	27	16	Massage Therapist
18	M	33	19	Lawyer
19	F	29	14	Housewife
20*	M	29	15.5	Student
Mean		24.5	15.1	

* Subjects who participated in Experiment 2

hypothesized that language processing ability is constrained by working memory capacity. Just & Carpenter (1992) have argued that individual differences in language comprehension are due to differences in verbal working memory.

Therefore, it was hypothesized that subjects' response to perturbation in the linguistic domain would be related to their verbal working memory capacity.

In the LST, subjects heard a sentence or group of sentences and were asked to recall the last word of each sentence in the order in which they were presented to them. Each group of sentences represents a level of working memory. There are five repetitions of each level within a set of sentences. Specifically, in the first set, a single sentence was presented and subjects reported the last word of the sentence. This was repeated five times with a different sentence each time. At the next level, a set of two sentences was presented and subjects recalled the last word from each of the two sentences in the order of presentation. There were five trials of two sentences within this set. The sets increased progressively to groups of potentially six sentences. Within each set, five groups of sentences were presented. Criterion to advance to sets of longer groups of sentences was correct responses to at least two groups of sentences (e.g., correctly recalled all of the items for 2 groups of sentences in the 4 sentence set). As described by Daneman and Carpenter (1980), the working memory score on this test represented the number of sentences in the last set to which the subject was able to correctly respond (at the criterion of three correct responses for the first set). If a subject correctly recalled only two sets within a level, then half a point was given (e.g., a 3.5 for the example above). To ensure that subjects processed the sentences, and did not simply listen for and rehearse the last words, subjects were told they would have to answer questions about them. At the end of each set of sentences, questions requiring recognition of concepts presented in the sentences were asked. Accuracy for these questions was recorded, but accurate responses were not required to continue with the task.

All sentences in the LST were syntactically complex. Stimuli were digitally recorded and presented over headphones. Subjects responded verbally and the examiner recorded responses. Within each group of sentences, a constant inter-stimulus interval of 1000 milliseconds was used.

Experimental Task

A sentence comprehension task was administered in which subjects heard a sentence and then determined whether or not a phrase shown on a computer screen was true or false relative to the sentence. For example, a subject heard the sentence "It was the journalist that the surgeon kissed after the successful heart transplant surgery" and then saw the phrase *the surgeon kissed the journalist* on a computer monitor. Subjects then pushed a mouse button to indicate if the phrase on the monitor was *true* (left mouse button) or *false* (right mouse button) relative to the sentence they had just heard. Subjects were instructed as follows: "You will hear a sentence and then see a phrase presented on the screen. You will then decide if the phrase is 'true' or 'false' based on the sentence. Some phrases may not make sense, and if so you should consider them to be false. The answers should be straight forward as it is not the point of the study to trick you. The buttons on the mouse are marked true or false for you. The first set of items is a practice set of five items. There will be approximately 50 items in the five test sets. Are you ready?"

Stimuli. 254 sentences were created representing simple (active, n = 144), object cleft, or object relative syntactic structures (object cleft and object relatives are henceforth referred to as complex sentences, n = 90). The simple sentences were each eight words long and ranged from eight to 16 syllables. The complex sentences were each 15 words long and ranged from 16 to 28 syllables. All experimental stimuli were selected after a validation study was completed showing that they were adequate for the experiment (see Appendix A for results and Appendix B for a list of all experimental stimuli).

Stimulus Preparation. All stimuli were digitally recorded using a trained male speaker. The speaker maintained a fairly constant intensity by viewing a dB meter during production. Stimuli were recorded in a sound isolated room, with a constant microphone-to-mouth distance. Stimuli were edited in Wave (Turtle Beach, Inc.) with amplitude adjustment to maximize signal-to-noise, avoiding peak clipping, and boosts in amplitude were carefully provided for any final sibilants that were less than optimally audible in the original recording.

Procedure. E-prime 1 beta version 5 (Psychology Software Tools, Inc., 2000) was used to present both the auditory stimuli, presented over headphones, and the visual stimuli, presented in large font in the center of a laptop computer screen. Accuracy and reaction time data (RT) were collected as mouse button press responses were made for each item within the E-Prime module. Reaction time accuracy in E-Prime is listed at +/- 3 milliseconds. Subjects viewed a fixation cross in the middle of the screen as auditory stimuli were presented and the visual stimulus appeared at the exact point in time that the auditory stimulus ended. Subsequent stimuli began immediately after a response was given or at 3000 milliseconds (no response), whichever occurred first. Five sessions of the experiment were administered, each containing approximately 50 items (± 2 items) and lasting about seven minutes. Overall, there were 10 blocks of each experimental condition with four to five items in each block. There were 30 blocks of the baseline condition with four items in each block.

Experimental Conditions. Stimuli were presented in one of four experimental conditions as follows:

1. *Simple condition* (low syntactic/low perceptual demand). Subjects listened and responded to simple sentences (actives) with no perceptual manipulation (at an average speech rate of 162 words per minute).
2. *Compressed Simple* (low syntactic/high perceptual demand). Subjects listened and responded to simple sentences (actives) presented at a compressed rate of 70% of original or 228 words per minute.

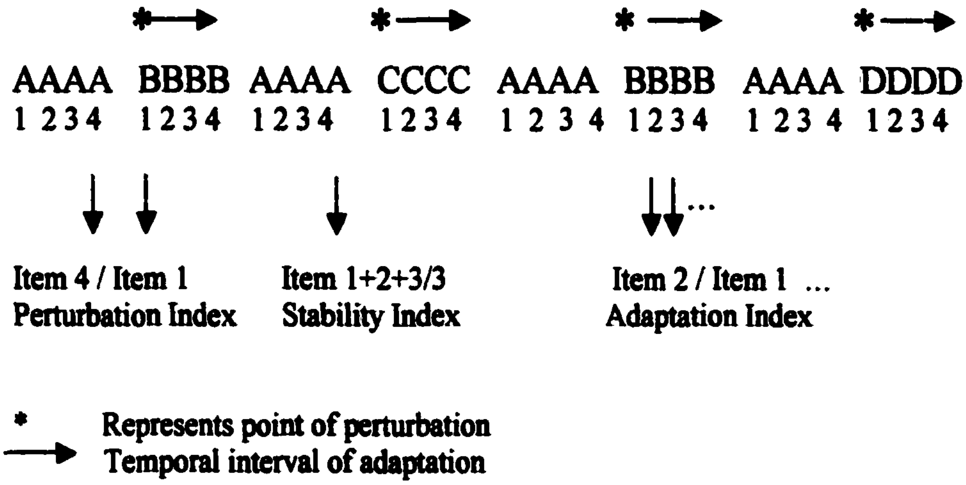
3. *Complex* (high syntactic/low perceptual demand). Subjects listened and responded to complex sentence types (object clefts and object relatives intermixed) presented at an average speech rate of 178 words per minute.

4. *Compressed Complex* (high syntactic/high perceptual). Subjects listened and responded to complex sentences varying in type (object clefts and object relatives intermixed) at 70% compression or an average speech rate 255 words per minute.

Stimuli were compressed using the Wave compression option that adjusts stimuli in the temporal domain only. The 70% compression rate was chosen by having two independent judges listen to the sentences compressed at 60%, 70% and 75% of the original. Based on consensus between the two judges it was determined that the 70% rate created a high level of demand, but remained intelligible. Importantly, these data are in agreement with previous studies showing that comprehension of speech sharply deteriorates at 60% of the original (Schmitt, 1983; De Chicchis, Orchik, & Tecca, 1981).

Stimulus Presentation. To investigate perturbation and subsequent adaptation, a specific presentation order was required. Observations were made at the point of the perturbation and at intervals following it. Figure 1 presents a schematic of the experimental design.

Figure 1. Schematic of stimulus presentation order for Experiment 1.



Key:
A – Simple
B – Compressed Simple
C – Complex
D – Compressed Complex

Data Analyses. Mean accuracy was computed for each stimulus condition for each subject. For the reaction time (RT) analyses, outliers (those that were outside of two standard deviations around the mean) and incorrect items were removed and mean RTs for each stimulus condition were computed for each subject. To normalize data across condition blocks and across subjects, and to allow for exploration of performance according to the dynamic systems hypotheses, a perturbation index and adaptation index was calculated for each block as follows (see Figure 1):

A. Perturbation Index (PI): RT for the last item of a Simple block was considered a basal RT and the RT for the first item of a Compressed Simple, Complex, or Compressed Complex block was considered a perturbation RT. To derive the Perturbation Index, the perturbation RT was divided by the baseline RT. As such, any value greater than 1 represented a perturbation.

B. Adaptation Index (AI): The RT of the first item (point of perturbation) of a Compressed Simple, Complex, or Compressed Complex block was considered basal and each subsequent item was normalized to that value to index adaptation. To derive the Adaptation Index, each item value (item 2, 3, and 4) was divided by the perturbation RT (item 1). As such, any value less than 1 represented adaptation.

Because the dynamic systems framework also considers stability to be a critical condition, a stability index was derived. To obtain an index of stability in the baseline condition, an average of the AIs for items 2, 3, and 4 across Simple blocks were calculated [to be referred to as the Stability Index (SI)]. This value served (1) as a baseline level of stability to then be compared to the PI for determination of amplitude of the perturbation and (2) as an anchor point for comparison of subsequent AI values (i.e., to determine if subjects returned to stability after perturbation). As noted above, both compression and increased syntactic complexity result in poorer performance (perturbation). The above indices were used as ratios to capture performance changes across subjects and standardize the observations by eliminating increased variability from subject basal RTs.

In addition, a critical aspect of this experiment was the examination of individual subject variability. In order to examine variance within subjects, a co-efficient of variation (CV) was calculated (CV = standard deviation/mean) for the SI and PIs only since perturbation theoretically results in instability or increased variability. The CV is a relative index of variability independent of individual subject mean performance.

Experimental Design

A repeated-measures within-subject design was used. The dependent variables were accuracy, the derived indices (SI, PI and AI), and the CV values. The independent variables were stimulus condition (Simple, Compressed Simple, Complex, Compressed Complex) and item position (2, 3,or 4).

CHAPTER 3 - RESULTS FOR EXPERIMENT 1

Results will be reported in the order of the research questions presented in Chapter 1. Prior to this, however, two preliminary analyses are presented. The first set of preliminary analyses examined subject responses in the Simple condition to ensure that they had indeed been stable in this condition. The second set of introductory analyses examined performance over time to determine if any order effects were present. Then, results concerning perturbation are discussed, focusing on the effect of increased syntactic complexity or time compression on subject performance. Next, the additive nature of the experimental manipulations will be reported by examining subjects' performance when stimuli are both syntactically complex and time compressed. Then the issue of variability will be addressed by examining the coefficient of variation in relation to changes in syntactic complexity, time compression, or both. Finally, the results section focuses on subjects' adaptation to changes in complexity. In order to address each of the above issues, the major analyses involved the use of repeated-measures analyses of variance (ANOVAs) with the dependent measures being accuracy and the RT data (i.e., stability index, perturbation index, and adaptation index). In each section, indicated by the major research questions, accuracy data are presented first, followed by analyses of the derived indices. Following the main results is a presentation of the data on the TONI-3 and LST and correlations between the measures of problem solving, working memory, and the derived indices.

It is important to note that repeated-measures ANOVAs assume that the variance of the data for the conditions entered into the test is not different than that of the population for any other conditions (i.e., the sphericity assumption, Jaccard & Becker, 1997). This assumption was violated in all but one of the analyses below. As such, adjusted degrees of freedom (df; Huynh-Feldt epsilon factor adjustment) are reported for those analyses. The use of adjusted dfs reduced the risk of Type I error and therefore increased the robustness of the test. Of note, the F-values and eta^2 did not differ from those values when sphericity was assumed and the adjusted significance values were reported. All analyses were computed using the statistical analysis software SPSS for Windows 10.0.

Preliminary Analysis I: Stability

Because this study is based on a dynamic systems framework, it was important to show that subjects were in a stable state at the outset of the experiment. To establish stability, it was reasoned that the Stability Index (SI) should not differ from the Adaptation Index (AI) for items two, three, and four in the Simple Condition. Recall that in each presentation block, there were four repetitions of stimuli at the same level (i.e., an SI and three AIs per block). The Simple Condition is one in which there is no perturbation, therefore all of the trials in that condition should reflect a stable state. The average SIs across all trials ($n = 30$) was compared to each of the average AIs for the Simple condition. Results indicated a significant main effect for item position [$F(2.108,40.057) = 5.156$, $p =$

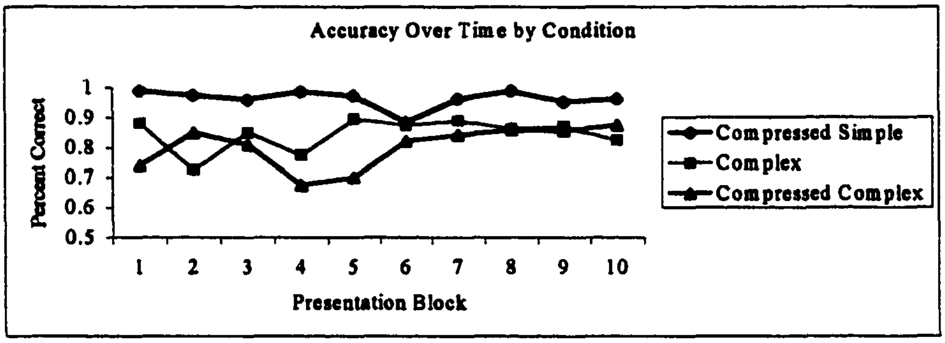
.009, $eta^2 = .213$]; however, the variance for each of the measures entered into the test was very small [SI: mean = 1.05, standard deviation = .06; AI2: mean = 1.07, standard deviation = .07 (t(19) = -3.276, p = .004); AI3: mean = 1.03, standard deviation = .05 (t(19) = 1.740, p = .098); AI4: mean = 1.03, standard deviation = .07 (t(19) = 1.922, p = .07)]. The effect size of the ANOVA was minimal and the lack of variance amongst the variables leads to question about the validity of the test. Whereas the SI differed significantly from AI2, the difference was small and likely was not an important difference. The very low variance across the measures in this condition lent further support to the stability of the subjects' performance.

Preliminary Analysis II: Effects Over Time

Tests of change in performance over time were conducted because subjects were repeatedly exposed to the same type of task. For accuracy, performance on the first half of the blocks was compared to that of the last half using paired t-tests. Performance over time is displayed in Figure 2. Significant differences were found only for the two compressed conditions (Compressed Simple and Compressed Complex) with no other significant comparison. Of note, the direction of the significant differences for the Compressed conditions was in opposite directions. For the Compressed Simple condition, subjects performed significantly more poorly on the last half than the first half of the blocks [1st half = 98%, 2nd half = 95%, t(19) = 2.457, p = .024)], however, performance in this condition was near ceiling and the difference was likely due to a dip in performance in block six.

Conversely, for the Compressed Complex condition, performance significantly improved over time [1st half = 75%, 2nd half = 85%, t (19) = -4.157, p = .001)].

Figure 2. Percent correct performance over time for the Compressed Simple, Complex, and Compressed Complex conditions in Experiment 1.



Comparisons of the reaction time indices over time indicated that the Stability Index did not differ from the first 15 to the second fifteen blocks [t(19) = -.795, p = .436]. For the more complex conditions, the perturbation indices were compared across time. The mean data from the first half compared to mean performance of the second half for the perturbation indices (PI) within each of the experimental conditions are reported in Table 2. For the Compressed Simple condition, subjects appeared to be more perturbed over time, with the average perturbation indices for those last blocks being significantly greater than that of the first. No significant differences in the perturbation index over time were found for the Complex or Compressed Complex conditions, though a trend of increasing PIs (greater perturbation) was found for these conditions.

Table 2. Comparison of Perturbation Indices on the First Half and Last Half of the Blocks for Each Condition.

Condition	First Half	Last Half	t	df	P value
Compressed Simple	1.002	1.08	-2.270	19	.035*
Complex	1.25	1.27	-.261	19	.797
Compressed Complex	1.14	1.27	-1.754	19	.096

Given that accuracy and reaction time performance remained constant in the Simple Condition, these data indicate that no learning effect was demonstrated from repeated exposure to the stimuli. Because a stable baseline was found, performance in the Simple Condition can be compared to performance in the other three conditions. Again, note that the Simple Condition is considered as baseline performance and will be referred to as "Baseline" in what follows.

Research Question 1:

Do changes in syntactic complexity and/or changes in temporal demand as a function of compression result in a greater number of inaccurate and/or slower responses in normal subjects?

Accuracy. For the statistical analyses of accuracy (see Table 3) a significant main effect for condition was found [$F(2.215,42.087) = 37.781$, $p < .0001$, $eta^2 = .665$]. Post hoc paired t-tests showed that subjects were more accurate during the Baseline (mean=97%) and Compressed Simple Conditions (mean=95%) than the Complex (mean=86%) and Compressed Complex (mean=82%)

Conditions. However, accuracy did not significantly differ between the Baseline and Compressed Simple or between the Complex and Compressed Complex conditions. This indicated that compression alone did not result in a substantial decline in the accuracy of performance. Rather, these data suggest that the syntactic manipulation was responsible for changes in accuracy.

Table 3. Post hoc paired T-tests results for Accuracy by Experimental Condition in Experiment 1.

Comparisons	df	t	P value
Baseline vs. Compressed Simple	19	1.248	.227
Baseline vs. Complex	19	5.948	.0001
Baseline vs. Compressed Complex	19	6.857	.0001
Compressed Simple vs. Complex	19	7.703	.0001
Compressed Simple vs. Compressed Complex	19	7.341	.0001
Complex vs. Compressed Complex	19	2.666	.015

Note: Bonferroni correction for multiple tests yielded an adjusted alpha of .008

Reaction Time. All statistical analyses are based on the derived values for the stability index (SI), perturbation index (PI) and adaptation index (AI). The values for these indices are presented in Table 4 and the average indices by condition are plotted in Figure 3. This section presents results for the SI and PI. There was a significant difference between the SI and the PIs [F(2.247, 42.693) = 13.807, p < .0001, eta^2 = .421]. Post hoc paired t-tests indicated that subjects were not perturbed in the Compressed Simple condition [t(19) = .352, p = .729], but were perturbed in the Complex [t(19) = -4.166, p = .001] and the Compressed

Complex conditions [t(19) = -4.948, p < .0001]. Thus, compression alone was not sufficient to perturb subjects. Rather, increased syntactic complexity or a combination of compression and increased syntactic complexity was needed to create a perturbation in the subjects studied here.

Table 4. Stability, Perturbation, and Adaptation Indices for Experiment 1.

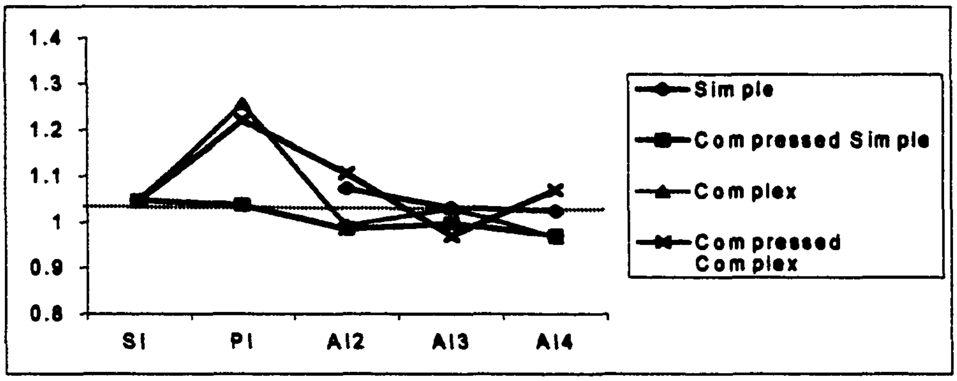
	Simple	Compressed Simple	Complex	Compressed Complex
SI	1.048	▨	▨	▨
PI	▨	1.038	1.257	1.22
AI Item 2	1.075	.986	.993	1.107
AI Item 3	1.032	.998	1.032	.97
AI Item 4	1.03	.972	.968	1.072

Note: Recall that any PI greater than the SI is defined as perturbation.

Accuracy and Reaction Time data for each subject in each condition are shown in Appendix C.

Errors, Outliers, and No Responses. There were 254 items per subject in the study for a total of 5080 items. The average error rate for responses was seven percent (range = .004% to 24%). As well there was a four percent outlier rate (> ± two standard deviations of the mean), and a one percent rate of no responses (responses that were not within the 3500 ms provided).

Figure 3. Graph of the Stability, Perturbation, and Adaptation Indices in Experiment 1.



Note: Stability Index for the group = 1.048. Any PI greater than the SI indicates that subjects were perturbed. Any AI less than one indicates subjects adapted.
·············· Indicates level of Stability Index

Research Question 2:

Does a combination of syntactic and perceptual manipulations create the greatest level of perturbation?

Dick et al. (2001) reported an additive effect of compression and increased syntactic complexity. To determine if this finding could be replicated with the subjects and the stimuli used in this experiment, a separate repeated-measures ANOVA was run to examine the PI in the Complex versus the Complex Compressed conditions. The size of the PI can be considered an index of the amplitude of the perturbation. If there were an additive effect of compression plus increased complexity, it would be reflected in a significantly larger PI for the Compressed Complex condition. Results showed that the PIs for these two conditions did not differ significantly [t(10) = .826, p = .419], ruling out an additive effect of compression + syntactic manipulations.

Research Question 3:

Does the variability of responses increase when task demand increases (perturbation), indicating instability?

The next series of analyses were designed to examine response variability. To standardize variance across different means, the coefficient of variance (CV) was computed for the SI and the PIs. A repeated-measures ANOVA on the CVs showed a significant main effect for condition [F(2.76, 52.441) = 3.791, p = .018, eta^2 = .166]. Post hoc paired t-tests showed that the variance was greater only for the Compressed Complex PI [t(19) = -3.806, p = .001]. No other differences in the CV between conditions were significant.

Research Question 4:

Do subjects adapt to perturbations created by the experimental manipulations?

The following results were analyzed within each condition. Please refer back to Figure 3, which depicts the adaptation to perturbation.

Compressed Simple Condition. Subjects were not perturbed in the Compressed Simple condition and therefore had no need to adapt. Their performance was stable throughout this condition with no significant differences between the PI and AIs [F(2.486, 47.236) = 1.734, p = .181, eta^2 = .084].

Complex Condition. Subjects were perturbed in the Complex condition and showed subsequent adaptation. Statistical tests are shown in Table 5. Post hoc paired t-tests indicated that subjects had adapted by item two of each block. Thus, the PI was significantly higher than AI2 and AI4, but not AI3 (i.e., RTs to items in position three were slower than those of the other items). However, post-hoc testing revealed that AI2, AI3, and AI4 did not significantly differ from one another. These data indicate that subjects adapted to perturbation, especially after item two.

Table 5. Repeated-measures Analysis of Variance for the Perturbation Index compared to the Adaptation Index by item position in the Complex Condition for Experiment I.

Source	df	Mean Square	F	P value	Eta^2
Condition	1.775	.631	9.742	.001	.339
Error	33.724	6.479E-02			

Paired t-tests	df	t	P value
PI and AI2	19	3.649	.002*
PI and AI3	19	2.804	.011
PI and AI4	19	3.803	.001*
AI2 and AI3	19	-.908	.375
AI2 and AI4	19	.820	.422
AI3 and AI4	19	1.570	.133

Note: Bonferroni Correction for multiple tests yielded an adjusted alpha of .008.

Compressed Complex Condition. Subjects were perturbed in the Compressed Complex condition and showed subsequent adaptation [F(3, 57) = 9.316, $p < .0001$, eta^2 = .329]. Post hoc t-tests indicated that subjects adapted by item three (see Table 6). That is the PI was significantly different from AI3. The PI also differed significantly from AI4. Again, AI2, AI3, and AI4 did not significantly differ from one another.

To summarize the adaptation findings, subjects appeared to adapt following perturbation. In the Complex Condition adaptation was apparent by item 2 and for the Compressed Complex condition by Item 3.

Table 6. Repeated-measures Analysis of Variance for the Perturbation Index compared to the Adaptation Index by item position in the Compressed Complex Condition for Experiment 1.

Source	df	Mean Square	F	P value	Eta^2
Condition	3	.194	9.316	.0001	.329
Error	57	2.082E-02			

Paired t-tests	df	t	P value
PI and AI2	19	2.921	.009
PI and AI3	19	4.687	.0001*
PI and AI4	19	2.998	.007*
AI2 and AI3	19	2.454	.024
AI2 and AI4	19	.740	.469
AI3 and AI4	19	-2.109	.048

Note: Bonferroni Correction for multiple tests yielded an adjusted alpha of .008.

TONI-3 and LST

Scores for the TONI-3 and LST are presented in Appendix D. Subjects' scores were within the normal range on the TONI-3 (mean quotient = 115, standard deviation = 16). Subjects also performed within normal on the Listening Span Test as compared to normal performance on the Reading Span Test in previous studies (mean span = 4.4, standard deviation = .6; Just & Carpenter, 1992). In addition to the LST score, total number of words recalled and percent correct responses to the recognition questions are reported. Pearson correlations were computed between the scores for these tests and data from the experiment. Those data included (1) whether or not subjects were perturbed (PI for each condition) and (2) whether or not subjects adapted to being perturbed (AI2, AI3, or AI4 for each condition). An a priori correlation of 0.5 was adopted as the minimal level for associations to be interpreted as meaningful (Cohen & Cohen, 1983). No correlations met this criterion (ranged from .021 to .438), indicating little relation between performance on the TONI-3 or LST and how much subjects were perturbed or were able to adapt (see correlations in Appendix E).

CHAPTER 4 - METHOD FOR EXPERIMENT 2

Participants

Nine of the 20 subjects in Experiment 1 (5 males, 4 females) participated in Experiment 2 (please see demographic information in Table 1, p. 46). As such, they met the same selection criteria found in Chapter 2, Experiment 1, Method (p. 44). In order to be selected for Experiment 2, subjects had to demonstrate accuracy above 80% on the Compressed Complex Condition in Experiment 1. Furthermore, to ensure that subjects were perturbed by the experimental manipulations, only those subjects performing worse than 95% correct on the Compressed Complex condition were included. Additionally, subjects were asked about tendencies toward claustrophobia and were administered a metal screen to rule out any safety issues related to metal in the body and MRI and were excluded as appropriate. Subjects were informed of all risks and benefits of participation in this experiment and informed consent was obtained specific to this experiment (see consent form in Appendix C). Subjects were informed of scanning procedures before the study began (e.g., shown the scanner, told briefly about how it works, etc.). Data from one of the nine subjects in this experiment (subject 11) were excluded due to excessive head movement[1].

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[1] When fMRI data were registered, correction values obtained for roll, pitch, and yaw were greater than 1.

Design and Procedures

Experimental Task

The same experimental task and stimuli used in Experiment 1 were used (see Chapter 2, Method, Experiment 1). However, items that were in the compressed conditions in Experiment 1 were switched to the non-compressed conditions and vice versa for the non-compressed items in order to minimize any possible learning of stimuli effects. Additionally, the visual stimuli presented for responses were changed so that items that were true for a subject in Experiment 1 were false in Experiment 2. Distance in time between testing in Experiment 1 and 2 ranged from two weeks to three months. Information about within subject change in performance from Experiment 1 to 2 is presented in Chapter 5.

Subjects held a computer mouse with "true" and "false" response buttons in their right hand. Accuracy and RT data were collected. Scanner noise was an additional constant factor in Experiment 2.

It was necessary to add an additional condition for Experiment 2. A control task was included to allow for identification of brain activation associated with peripheral processing due to motor responses in button pressing, listening to a speech signal, and looking at visual information. For the control task, subjects heard sentences that were the same length as those in the Simple Condition saying, "you will now please push the *true/false* button." Subjects then saw either "push the true button" or "push the false button," in the goggles used to present visual stimuli in the scanner (see below) and pushed the corresponding mouse button.

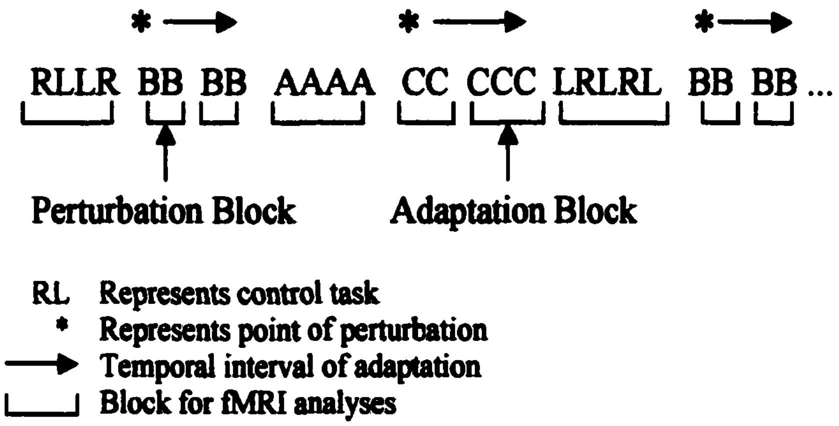
As in Experiment 1, there were five blocks of stimuli with the addition of the control task. Each block lasted approximately nine minutes.

Procedure. In order to assure timing fidelity for stimulus presentation and response latencies, DMDX software (Forster, 2001; not E-Prime) was used to present the stimuli and collect accuracy and RT data. Auditory and visual stimuli were presented over a headphone and goggle system (Resonance Technologies, Inc.) specifically designed for safe use in the scanner. The quality of the auditory presentation was identical to that for the E-Prime system since the same sound files were utilized with both. Printed phrases were presented on the screen in large font. Because glasses cannot be worn in the scanner, corrective lenses that were affixed to the goggles were provided for subjects needing them (Subject 12).

All scans were conducted at the Arizona Health Sciences Center at the University of Arizona. Cerebral activation [as reflected by measures of the hemodynamic response (HR)] was measured using blood oxygenation level-dependent (BOLD) contrast in a 1.5 Tesla GE Signa (General Electric Medical Systems) MRI scanner. Parameters for the single-shot spiral gradient-echo image acquisition protocol (Glover, Tokarcauk, & Bowtell, 1995) were: relaxation time, TR=3000 ms; echo time, TE=40 ms, field of view, FOV = 22 x 22 cm^2; acquisition matrix, 64x64; slice thickness = 5mm. Twenty-one slices (1mm inter-slice gap) covering the entire brain were obtained in the axial plane. Fast spin echo, T1-weighted axial images were obtained using the same slice thickness and alignment as the functional scans. High resolution, Spoiled GRass T1-weighted sagittal images (256x256 acquisition matrix with 1.5 mm slice thickness, 124 slices) were obtained for anatomical localization. Total time in the scanner was approximately 60 minutes per subject.

The same stimulus order used in Experiment 1 (and illustrated in Figure 1, p. 52) was used with the addition of timing parameters to allow for analyses in a block design. Using the block design, the first two items in an experimental block (i.e., a block of items within the Compressed Simple, Complex, and Compressed Complex conditions) were averaged as a measure of perturbation. The last two to three items were averaged as a measure of adaptation with the assumption that by the third item in a block, the subject had adapted to the perturbation. Between each perturbation and adaptation block, a rest period of 3000 ms was imposed to allow for relaxation of the HR associated with the perturbation. Please see Figure 4 for a schematic of the stimulus presentation and block design.

Figure 4. Schematic of block design for Experiment 2.



Note: Between each block was a 6000 ms delay to allow for the HR response associated with a perturbation block to return to baseline prior to measuring the HR in the adaptation block.

Data Analyses. Data were analyzed using the Analysis of Functional Neuroimaging software (AFNI version 2.23; Cox, 1999) for reconstruction of structural and functional images. Images were extracted, reconstructed, and co-registered in 3-dimensional space and linear trends in the data were removed. Models of the HR were created to represent each of the experimental conditions over time. Changes in signal intensity were correlated with these models on a voxel-by-voxel basis. Lags of 0-6 seconds were added to the onset of each of the model waves to allow for individual variation in the HR and the model that provided the best fit to the data for each voxel was used. "Activated" voxels were those for which a correlation coefficient was greater than .31 ($r^2 = .10$) and only activation that was present for three or more contiguous voxels was considered. The combined use of the .31 thresholds and 3-voxel clusters resulted in an overall Type I error rate of less than .05 per subject.

Activated clusters were examined for each subject to eliminate obvious artifact (e.g., susceptibility artifacts, areas that were outside of the functional images, large vessels). Masks were then made for each activated cluster for each subject allowing for further analyses specific to those regions. Masks represented a volume that was active in at least one condition. These masks were then applied to the data for each condition yielding the intensities for voxels within each masked region (i.e., sub- and super-threshold data) for comparison by condition. These intensity values are the least squares fit for each voxel time series to the model wave and therefore are indicative of the strength of the relation to that model (Cox, 2001). In addition, the percent of the voxels represented in a mask that were super-threshold was computed for each condition. These data, put together, give information about whether the region increases in intensity, amount of brain active, or both for each condition. Percent signal change also was computed for each of these voxels (1-[intensity in the Simple condition/intensity in another condition]) allowing for comparison by condition as compared to baseline. Only regions in which at least three subjects showed activation were retained for the region analyses.

Experimental Design

Repeated measures within-subjects ANOVAs were used to analyze the behavioral data collected during scanning as well as the fMRI data. The behavioral data were analyzed exactly as in Experiment 1. For the fMRI data, the dependent variables were the number of voxels active above threshold and the percent change in hemodynamic response in a region. The independent variables were fMRI block (perturbation block, adaptation block) and stimulus condition (Simple, Compressed Simple, Complex, and Compressed Complex).

A priori Hypothesized Regions of Interest

The regions hypothesized to be involved in the perturbation blocks and/or the adaptation blocks, as highlighted in Chapter 1, are those that have been shown in the literature to either be involved in language processing or cognitive processing with increasing complexity. Those regions include: the temporal lobes, the inferior and middle frontal gyri, and the superior parietal lobules.

CHAPTER 5 – RESULTS FOR EXPERIMENT 2

Behavioral Results

Results are reported in the same format as Chapter 3, with responses to the research questions presented in Chapter 1. First, preliminary analyses on stability and performance over time are examined. The main analyses begin with the response of the nine subjects to the perturbation while in the scanner. Changes in performance with the varying conditions are then reported in reference to their performance in Experiment 1. Next, variability associated with changing task demand is reported. Finally, adaptation to perturbation is explored.

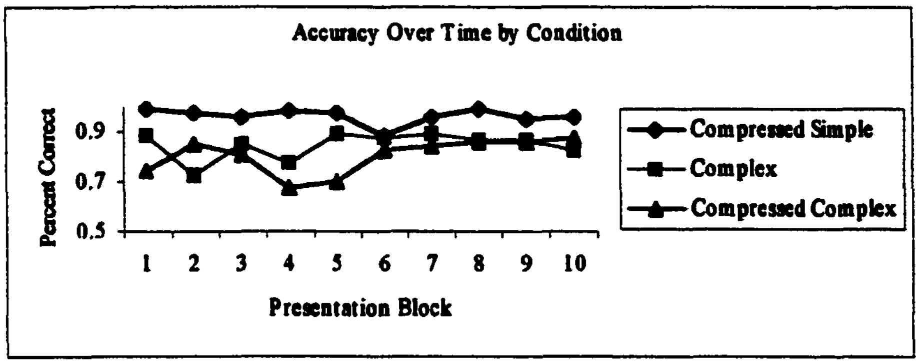
Preliminary Analysis I: Stability

As in Experiment 1, it was important to show that subjects were stable in the Simple Condition. The SIs across all 30 blocks of the Simple Condition were compared with the AIs for items two, three, and four in those blocks. There was no significant difference between these measures [F(1.826, 14.610) = .291, p = .732, $eta^2 = .035$], indicating that subjects were stable (SI mean = 1.06, standard deviation = .07; AI2 mean = 1.07, standard deviation = .08; AI3 mean = 1.05, standard deviation = .08; AI4 mean = 1.07, standard deviation = .09).

Preliminary Analysis II: Effects Over Time

Performance was examined for changes related to exposure to the task. Accuracy for the first half of the items was compared to the second half of the items for each condition. No significant differences were found between the first and second half of the items in the Simple (first ½ = 92%, last ½ = 94%), Compressed Simple (first ½ = .95%, last ½ = 95%), or Compressed Complex (first ½ = 72%, last ½ = 77%) Conditions. Subjects did show improvement in performance over time in the Complex Condition [first ½ = 74%, last ½ = 85%, t(8) = -3.177, p = .013]. Accuracy over time is displayed in Figure 5.

Figure 5. Percent correct performance across time in each condition for Experiment 2.



Comparisons for derived indices for RT are now presented. As in Experiment 1, no significant difference was observed for the Stability Index in the first and last half of the experiment [t(8) = -1.754, p = .117]. Additionally, no significant differences were observed over time for the Perturbation Indices in the other conditions (see Table 7). These data indicate that subjects performance did not changes as a function of exposure to the material while in the scanner.

In summary, these results indicate that the performance of these subjects remained stable in the Simple Condition across items and that this condition may be considered baseline performance. These subjects also showed steady performance in the more complex condition with no differences in the PIs over time.

Table 7. Comparison of Perturbation Indices on the First Half and Last Half of the Blocks for Each Condition in Experiment 2.

Condition	First Half	Last Half	t	df	P value
Compressed Simple	1.05	1.09	-.655	8	.531
Complex	1.22	1.22	-.005	8	.996
Compressed Complex	1.38	1.35	.287	8	.781

Research Question 1:

Do changes in syntactic complexity and/or changes in temporal demand as a function of compression result in a greater number of inaccurate and/or slower responses in normal subjects?

Accuracy. A significant main effect for condition was found for accuracy [F(1.555, 14.884) = 30.989, $p < .0001$, $eta^2 = .795$]. Post hoc paired t-tests revealed that accuracy for the Baseline Condition (mean = 95%) did not differ significantly from the Compressed Simple (mean = 97%) or Complex (mean = 88%) Conditions, but was greater than that observed in the Compressed Complex Condition (mean = 80%; see Table 8). Performance in the Compressed Simple Condition differed significantly from the Complex and Compressed Complex Conditions. Finally, subjects were more accurate in the Complex than the Compressed Complex

Condition. These results demonstrate that the syntactic manipulation perturbed these subjects. In addition, the compression + syntactic manipulation had the largest impact on accuracy.

Table 8. Post hoc paired T-tests results for Accuracy by Experimental Condition in Experiment 2.

Comparisons	df	t	P value
Baseline vs. Compressed Simple	8	-1.444	.187
Baseline vs. Complex	8	2.282	.052
Baseline vs. Compressed Complex	8	15.715	.0001
Compressed Simple vs. Complex	8	4.323	.003
Compressed Simple vs. Compressed Complex	8	13.918	.0001
Complex vs. Compressed Complex	8	3.490	.008

Note: Bonferroni correction for multiple tests yielded an adjusted alpha of .008

Reaction Time. The Stability, Perturbation, and Adaptation Indices are reported in Table 9 and average indices across conditions are plotted in Figure 6. To determine whether or not subjects were perturbed, comparisons were made between the SI and the PIs for each condition. A significant difference was found between these indices [F(2.839, 22.713) = 16.187, p < .0001, eta^2 = .669] indicating that subjects were perturbed in this experiment. Post hoc paired t-tests showed that, like in Experiment 1, subjects were not perturbed in the Compressed Simple Condition [t(8) = -.633, p = .544]. Subjects also were not significantly perturbed in the Complex Condition [t(8) = -2.895, p = .020 – Bonferroni correction indicates that significance is at the .008 level]. Subjects were perturbed in the Compressed

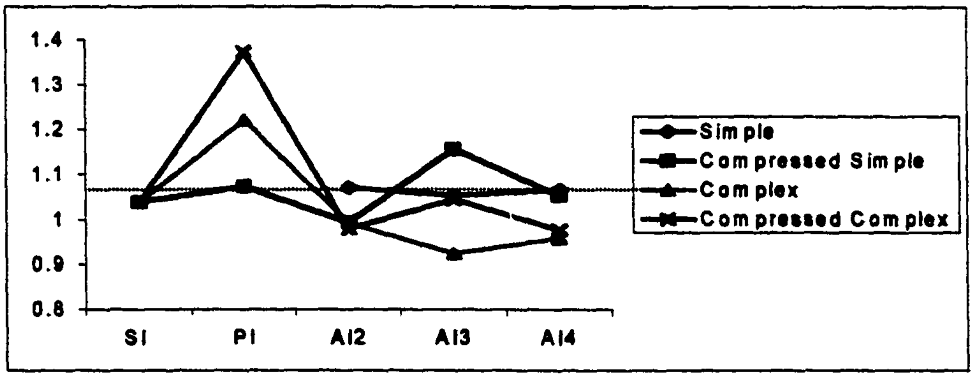
Complex Condition [t(8) = -6.119, p < .0001]. The compression + syntactic manipulations resulted in the greatest degree of perturbation in Experiment 2.

Table 9. Stability, Perturbation, and Adaptation Indices for Experiment 2.

	Simple	Compressed Simple	Complex	Compressed Complex
SI	1.063			
PI		1.073	1.222	1.37
AI Item 2	1.071	.99	.992	.979
AI Item 3	1.053	1.157	.926	1.044
AI Item 4	1.07	1.053	.958	.977

Note: Recall that any PI greater than the SI indicates perturbation.

Figure 6. Graph of the Stability, Perturbation, and Adaptation Indices for the Group in Experiment 2.



.... Indicates level of stability

Accuracy and Reaction Time data for each subject in each condition are shown in Appendix F.

Errors, Outliers, and No Responses. The average error rate for responses was eight percent (range = .4% to 13%; mean = 20.9 errors). As well there was a three percent outlier rate (> ± two standard deviations of the mean, mean = 7.9 outliers), and a four percent rate of no responses (responses that were not within the 3500 ms provided, mean = 11.9 no responses).

Research Question 2:

Does a combination of syntactic and perceptual manipulations create the greatest level of perturbation?

As in Experiment 1, the PI was used to gauge the size of the amplitude of perturbation. If an additive effect of syntactic and perceptual manipulations existed, then a significant difference would be found between the PI for the Compressed Simple and the Compressed Complex Conditions. Indeed, a significant difference was found between these conditions [$t(8) = -5.826$, $p < .0001$], indicating that when subjects were in the scanner, there was an additive effect of compression plus increased syntactic complexity that was not found in Experiment 1. However, the PI for the Complex versus the Compressed Complex did not differ significantly [$t(8) = -2.413$, $p = .042$] suggesting that the difference reported above was most likely due to the change in syntactic complexity rather than purely to the compression.

Research Question 3:

Does the variability of responses increase when task demand increases (perturbation), indicating instability?

The coefficient of variance (CV) was used to standardize the variance across subjects and to explore response variability. No significant difference was found for the variance between conditions [F(3,24) = .657, p = .586, eta^2 = .076].

Research Question 4:

Do subjects adapt to perturbations created by the experimental manipulations?

The following results were analyzed within each condition. Please refer back to Figure 6, which depicts the adaptation to perturbation.

Compressed Simple Condition. Subjects were not perturbed in this condition and therefore had no need to adapt; therefore no further analyses were performed.

Complex Condition. Subjects also were not significantly perturbed in the Complex Condition. Since subjects showed a trend toward perturbation (see Figure 6), examination of adaptation was conducted. It is interesting to note that subjects did show an adaptive response. That is, the PI was significantly higher than the AI for item 4 [t(8) = 3.550, p = .008].

Compressed Complex Condition. Subjects were perturbed in this condition and showed subsequent adaptation [F(3,24) = 11.239, p < .0001, eta^2 = .584]. Post hoc paired t-tests showed that subjects adapted by item 2 (see Table 10) and remained stable thereafter (i.e., AIs for items two, three, and four did not differ significantly).

Table 10. Repeated-measures Analysis of Variance for the Perturbation Index compared to the Adaptation Index by item position in the Compressed Complex Condition for Experiment 2.

Source	df	Mean Square	F	Significance	Eta^2
Condition	3	.322	11.239	.0001	.584
Error	24	2.869E-02			

Paired t-tests	df	t	Significance
PI and AI2	8	5.828	.0001*
PI and AI3	8	3.765	.006*
PI and AI4	8	6.252	.0001*
AI2 and AI3	8	-.606	.562
AI2 and AI4	8	.072	.945
AI3 and AI4	8	.701	.503

* Significant at Bonferroni Correction adjusted alpha of .008.

To summarize the behavioral results from Experiment 2, subjects only were significantly perturbed in the Compressed Complex Condition. Subjects adapted to this perturbation by item two and remained stable after being perturbed. Although subjects were not significantly perturbed in the Complex Condition, they showed a trend of being perturbed and importantly demonstrated an adaptive response.

Comparison of Performance from Experiment 1 to Experiment 2

Paired t-tests were calculated to compare accuracy and reaction time measures from Experiment 1 to Experiment 2 for the nine subjects participating in Experiment 2. For accuracy, subjects performed more poorly in Experiment 2 than in 1 only for the Simple [t(8) = 3.381, p = .010] and the Compressed Complex [t(8)

= 7.902, $p < .0001$] Conditions. No significant differences were observed for accuracy or the SI and PIs across the two experiments.

Brain Activation Results

In this section, the functional Magnetic Resonance Imaging results are reported. For the statistical analyses reported here, alpha was set at .05. Most analyses involved six comparisons (values from each condition compared to one another in the perturbation or the adaptation blocks) requiring a Bonferroni correction of alpha = .008 for statistical significance. Because the study was exploring processes not yet investigated in neuroimaging (i.e., adaptation to perturbation), findings are reported in the tables that met the .05 level of significance for alpha, but only those comparisons meeting the .008 requirement are discussed as statistically significant.

Results are presented in the order in which the research questions were given in Chapter 1. First, brain regions in which activation is associated with increases in task demand are presented. Issues related to whether or not increases are observed in areas associated with the baseline task or in new regions specific to increased demand are addressed. Second, the nature of the adaptive response is explored. Subsumed in each of these topics will be descriptions of analyses performed for the intensity data and for the percentage of voxels active within a region by condition. The number of voxels active served as an indicator of where and how much activation occurred. The dependent variable for these analyses was the percent of the voxels encompassed in the region of interest that were active (i.e., correlated with the model wave at .31 or greater). The intensity data served as indicators of the strength of the activation within a region. The dependent variable here was the average intensity (across the time series) for each voxel encompassed in the region of interest. Analyses for each region were computed only for the subjects for whom the region showed activation above threshold in any condition, however the activation may not have been significantly different from the Baseline condition. The numbers of subjects showing activation in the regions included in the analyses are reported in Table 11.

Table 11. The numbers of subjects showing activation per region during any condition.

Region (total number of participants = 8)	Number of Subjects	
	Left	Right
Middle Temporal Gyrus	7	5
Superior Temporal Gyrus	5	4
Inferior Frontal Gyrus	6	5
Middle Frontal Gyrus	6	8
Superior Frontal Gyrus - Lateral	4	7
Superior Frontal Gyrus – Medial	6	6
Angular Gyrus	6	5
Supramarginal Gyrus	7	4
Superior Parietal Lobule	5	4
Cerebellum	5	7
Fusiform Gyrus	8	7
Occipital Lobe	8	6

Importantly, the activation in the Simple Condition differed little, if any, from that of the control task (i.e., no activation above threshold was observed in clusters of three+ voxels in the Simple Condition as compared to the Control for any subject). As such, the Simple condition was considered baseline for all of the following analyses and will be referred to as "Baseline."

Research Question 1:

When task complexity increases, what is the nature of the hemodynamic response (HR) in normal subjects?

The results of analyses of the voxel and intensity data for brain regions significantly active for perturbation blocks are presented in Table 12. For these analyses, repeated measures ANOVAs were used to compare either the percent of voxels active data or the intensity values from perturbation blocks in each condition (Baseline, Compressed Simple, Complex, and Compressed Complex) for each region. Additionally, comparisons were made between hemispheres for each region.

All of the regions thought to comprise the "language network" (Michael, Keller, Carpenter, & Just, 2001) were active including the inferior frontal gyri and the superior/middle temporal gyri. Overall, the regions that appeared to be involved in the perturbation blocks of the task included the left superior temporal gyrus, the left inferior frontal gyrus, the middle frontal gyri, the left medial superior frontal gyrus, the left angular gyrus, the left supramarginal gyrus, the left superior parietal lobule and the left occipital lobe. Regions showing increases in number of voxels active or in intensity specifically during the more complex conditions were the left inferior frontal gyrus, the left angular gyrus, and the left superior parietal lobule.

Temporal Lobes

No significant main effect of condition was found for the number of voxels active in the left [F(3,12) = 4.778, p = .020, eta^2 = .544] or the right [F(3,9) = 1.549, p = .268, eta^2 = .341] superior temporal gyrus. However, a main effect for condition was found for the left middle temporal gyrus [F(3,18) = 3.929, p = .026, eta^2 = .396] with an increased number of voxels active in the Compressed Complex Condition [t(6) = -4.425, p = .004].

For intensity, the right middle and superior temporal gyri were not significantly more intensely activated than Baseline levels for any condition in the perturbation blocks. In contrast, main effects for condition were found for left middle and superior temporal gyri. The left middle temporal gyrus was significantly more intense compared to Baseline [F(3,18) = 7.156, p = .002, eta^2 = .544] only during the Compressed Simple [t(6) = -4.706, p = .003] and the Complex [t(6) = -4.605, p = .004] Conditions. The left superior temporal lobe showed significantly higher intensities than Baseline in all conditions in the perturbation blocks [F(3,12) = 7.385, p = .005, eta^2 = .649; Compressed Simple: t(4) = -5.120, p = .007; Complex: t(4) = -4.956, p = .008; Compressed Complex:

Table 12. Brain regions significantly active during Perturbation blocks by condition using either the percent of the voxels that where active within a region of interest or the intensity data for the analyses.

Region	% Voxels Active in Region during Perturbation Blocks						Intensity in Region during Perturbation Blocks					
	Left			Right			Left			Right		
	CS	C	CC	CS	C	CC	CS	C	CC	CS	C	CC
Middle Temporal Gyrus		*	**				**	**	*			
Superior Temporal Gyrus	*		*				**	**	**		*	*
Inferior Frontal Gyrus	*	*	**				*	*	**	*	*	
Middle Frontal Gyrus	*	**	**	**	**	**	**	**	**	*	**	**
Superior Frontal Gyrus - Lateral										**	**	
Superior Frontal Gyrus – Medial	**	**	**	**	*	**	**	**	*	*	*	*
Angular Gyrus			*				*	*	**			
Supramarginal Gyrus		**	*				**	**	**			
Superior Parietal Lobule	*	*	**				**		**			
Cerebellum							*		*	*		*
Occipital Lobe	**	*	**				**	*	*			

* Significant at alpha = .05

** Significant at Bonferroni corrected alpha = .008

Key: CS = Compressed Simple; C = Complex; CC = Compressed Complex

t(4) = -5.296, p = .006]. These data suggest that though the left middle and superior temporal lobe regions are active during the processing of linguistic stimuli, they are not necessarily sensitive to increases in perceptual or syntactic demand.

Further, whereas the intensity data indicated that the left temporal regions showed changes that were strongly associated with task demands, the voxel data indicate that this increase in intensity did not involve larger areas of activation.

Frontal Lobes

Inferior Frontal Gyri. The left inferior frontal gyrus revealed a main effect for condition for the number of voxels active above threshold [F(3,15) = 8.258, p = .002, eta^2 = .623]. Post hoc paired t-tests showed that the difference in number of voxels only was significant in the Compressed Complex Condition [t(5) = -6.506, p = .001]. A main effect for condition also was found for the intensity of the left inferior frontal gyrus during perturbation blocks [F(3,15) = 5.549, p = .009, eta^2 = .526]. Post hoc paired t-tests showed that, like the voxel data, the intensity was significantly higher in the most complex condition, the Compressed Complex Condition, than in the other conditions [Compressed Complex: t(5) = -8.707, p < .0001]. By contrast, the right inferior frontal gyrus analyses resulted in no significant differences between Baseline and the other conditions for the voxel data [F(2.043, 8.17) = 2.868; p = .113, eta^2 = .418] or the intensity data [F(3,12) = 3.498, p = .05, eta^2 = .467; Compressed Simple: t(4) = -3.450, p = .026; Complex: t(4) = -3.316, p = .029; Compressed Complex: t(4) = -2.493, p = .067]. These data suggest that the left inferior frontal gyrus is differentially involved in processing when perceptual and syntactic demands are greatest.

Middle Frontal Gyri. One a priori hypothesis was that regions involved with increasing complexity are the middle frontal gyri (i.e., the dorsolateral prefrontal cortex described in Chapter 1). For both the left and right middle frontal gyri, a main effect of condition was found for the number of voxels active [left: F(3,15) = 6.322, p = .006, eta^2 = .558; right: F(3,21) = 5.653, p = .005, eta^2 = .447]. For these regions, increased numbers of voxels above threshold were found for all conditions except the Compressed Simple Condition in the left hemisphere [t(5) = -3.357, p = .020]. The left middle frontal gyrus also was significantly more intensely activated than Baseline during all of the conditions in the perturbation blocks [F(3,15) = 7.511, p = .003, eta^2 = .600; Compressed Simple: t(5) = -4.232, p = .008; Complex: t(5) = -4.269, p = .008; Compressed Complex: t(5) = -7.609, p = .001]. The right middle frontal gyrus was significantly more intense only in the complex conditions [F(3,21) = 4.959, p = .009, eta^2 = .415; Complex: t(7) = -3.895, p = .006; Compressed Complex: t(7) = -3.876, p = .006]. These data suggest that a larger area of the middle frontal gyri became involved more intensely active in tasks of increasing complexity, but may not be particularly lateralized for type of stimulus (e.g., syntactic versus perceptual changes in complexity).

Superior Frontal Gyri. A significant main effect for condition was found for the medial aspect of the left superior frontal gyrus [F(3,18) = 8.440, p = .001, eta^2 = .584] with significant increases in numbers of voxels active above threshold in all three conditions [Compressed Simple: t(6) = -5.132, p = .002; Complex: t(6)

= -5.687, p = .001; Compressed Complex: t(6) = -4.754, p = .003]. A main effect of condition also was found for the medial aspect of the right superior frontal gyrus [F(3,15) = 3.595, p = .039, eta^2 = .418] with significantly more voxels active during the compressed conditions [Compressed Simple: t(5) = -5.118, p = .004; Compressed Complex: t(5) = -4.402, p = .007].

For the intensity data, a significant main effect of condition for the medial aspect of the left superior frontal gyrus [F(3,18) = 7.447m p = .002, eta^2 = .554] also was found. Post hoc paired t-tests showed that this region was active during the Compressed Simple [t(6) = -4.177, p = .006] and the Complex [t(6) = -7.790, p < .0001] Conditions, but not during the Compressed Complex Condition [t(6) = -3.706, p = .010]. The same pattern held for the lateral aspect of the right superior frontal gyrus [F(3,15) = 4.189, p = .024, eta^2 = .456; Compressed Simple: t(5) = -4.391, p = .007; Complex (t(5) = -4.845, p = .005; Compressed Complex (t(5) = -2.304, p = .069].

The areas of the superior frontal gyri that were active included the supplementary motor area (left) and the premotor area (right), which were likely associated with the button press response. However, because the button press also was involved in the control task, these data suggest a possible interaction between the increased cognitive demand of the task and the motor planning of the response.

Parietal Lobes

Superior Parietal Lobules. Another a priori region of interest was the superior parietal lobule. For the left superior parietal lobule, an increase in number of voxels above threshold was observed only for the Compressed Complex Condition [t(4) = -8.968, p = .001]. No significant increase in number of voxels was found for the right superior parietal lobule. The left superior parietal lobule also was more intense when subjects were processing compressed speech and not increased syntactic demand as there was no increase in this region for the Complex Condition. The main effect for condition found for the left superior parietal lobule [F(3,12) = 7.871, p = .004, eta^2 = .663] was due to significantly higher intensity than Baseline only during the Compressed Simple [t(4) = -5.042, p = .007] and the Compressed Complex [t(4) = -5.743, p = .005] Conditions. The right superior parietal lobule analyses revealed no significant intensity differences from Baseline levels in any of the conditions [F(3,9) = 2.640, p = .113, eta^2 = .468]. Activation of the left superior parietal lobule (both the area active and the strength of the activity) was task specific (no increases in intensity on the right related to increased syntactic demand) and associated with the perceptual manipulations in this experiment.

Angular and Supramarginal Gyri. Other regions of the parietal lobe that showed increased numbers of voxels or intensities were the left angular and supramarginal gyri. No increases in the number of voxels active in the angular gyri were found [left: $F(3,15) = 4.409$, $p = .021$, $eta^2 = .469$; right: $F(3,9) = 3.515$, $p = .062$, $eta^2 = .539$]. However, the left angular gyrus was significantly more intense during the Compressed Complex Condition [$t(5) = -7.224$, $p = .001$]. The right angular gyrus was not significantly involved during perturbation blocks [$F(3,12) = 1.535$, $p = .256$, $eta^2 = .277$].

For the left supramarginal gyrus, main effects for condition for number of voxels active were observed [$F(3,18) = 9.103$, $p = .001$, $eta^2 = .603$]. There were significantly more voxels active in the left supramarginal gyrus during the Complex Condition only [$t(6) = -5.137$, $p = .002$]. Conversely, this region was significantly more intense than Baseline during all of the conditions [$F(3,18) = 14.104$, $p < .0001$, $eta^2 = .702$; Compressed Simple: $t(6) = -7.940$, $p < .0001$; Complex: $t(6) = -7.241$, $p < .0001$; Compressed Complex: $t(6) = -4.564$, $p = .004$]. The right supramarginal gyrus was not significantly active during any condition [$F(3,9) = 2.139$, $p\ .165$, $eta^2 = .416$]. Of interest, the left angular and supramarginal gyri are typically associated with integration of sensory information related to language (e.g., Geshwind & Kaplan, 1962) and were likely active in the experimental tasks in the scanner due to the need to integrate auditory and written stimuli in order to make a response. In both regions, the increases observed were more related to the strength of the activation as opposed to the amount of area active.

Other Regions

The other regions showing significantly more voxels above threshold or higher intensities than Baseline were the cerebellum, the fusiform gyri, and the occipital lobe. Of these regions, only the occipital lobes were strongly associated with the task. A main effect of condition was found for this region [F(3,21) = 4.189, p = .018, eta^2 = .374] with significantly more voxels above threshold for the Compressed Simple [t(7) = -4.088, p = .005] and Compressed Complex [t(7) = -3.813, p = .007] Conditions than in Baseline. A main effect of condition for the intensity data also was found for the left occipital lobe [F(3,21) = 5.611, p = .005, eta^2 = .445]. Post hoc analyses indicated that this region was significantly more intense only in the Compressed Simple Condition [t(7) = -7.855, p < .0001]. These findings lend support to the hypothesis that, as the task becomes more difficult, regions involved in the baseline task show increases in activation. The occipital lobe is likely involved in all conditions to some extent, including the Baseline condition, given the need to read the phrases presented on the screen.

In sum, when task demand increased, brain regions traditionally associated with language processing (left inferior frontal gyrus, superior/middle temporal gyri) as well as regions found to be associated with working memory (middle frontal gyri) increased in intensity. Areas of the parietal lobe also showed increased activity associated with increasing task demand (left angular gyrus, supramarginal gyrus, and superior parietal lobule).

To summarize, the hemodynamic response associated with perturbation blocks was investigated for each condition by region. The regions showing increases in intensity and/or number of voxels above threshold by condition are presented in Table 13.

Table 13. Summary of regions showing increased numbers of voxels and/or intensity for each condition during the perturbation blocks.

Compressed Simple	Complex	Compressed Complex
left middle temporal gyrus	left middle temporal gyrus	
left superior temporal gyrus	left superior temporal gyrus	left superior temporal gyrus
		left inferior frontal gyrus
left and right middle frontal gyri	left and right middle frontal gyri	left and right middle frontal gyri
left and right superior frontal gyri	left and right superior frontal gyri	left angular gyrus
left angular gyrus		left supramarginal gyrus
left supramarginal gyrus	left supramarginal gyrus	left superior parietal lobule
left superior parietal lobule		left occipital lobe
left occipital lobe		

No regions showed particular sensitivity to increases in syntactic complexity alone, but the left inferior frontal gyrus and the left angular gyrus showed significantly higher intensities only in the Compressed Complex Condition.

The medial aspect of the right superior frontal gyrus, left superior parietal lobule, and the left occipital lobe were the only regions that revealed either increased intensity or number of active voxels during the compressed conditions, suggesting some specificity to the perceptual demand of the task.

Research Question 2:

When task complexity changes, what is the nature of the adaptive hemodynamic response?

The results of analyses of the voxel and intensity data for brain regions significantly active for adaptation blocks are presented in Table 14. For these analyses, repeated measures ANOVAs were used to compare either the percent of voxels active data or the intensity values from perturbation blocks in each condition (Baseline, Compressed Simple, Complex, and Compressed Complex) for each region. Additionally, comparisons were made between hemispheres for each region.

The areas making up the "language network" also were involved during adaptation, but to different degrees than for the perturbation blocks. Some regions appeared to be as active in the adaptation blocks as they had been in the perturbation blocks suggesting that they were involved in the task regardless of block type (i.e., the left superior temporal gyrus, the left supramarginal gyrus). Other regions were active only during the adaptation blocks including the left lateral superior frontal gyrus, the right angular gyrus and the right fusiform gyrus.

Further, regions that were involved only in the more complex conditions during the perturbation blocks were no longer active in those conditions for adaptation (e.g., the left inferior frontal gyrus).

Temporal Lobes

The left middle and superior temporal gyri showed significant main effects for condition for number of voxels active [middle: F(3,18) = 4.544, p = .015, eta^2 = .431; superior: F(3,12) = 7.201, p = .005, eta^2 = .643]. For both regions, significant increases in the number of active voxels were observed only in the Compressed Complex Condition [middle: t(6) = -4.100, p = .006; superior: t(4) = -6.273, p = .003]. This is the same pattern that was found for the number of voxels in the perturbation blocks for the left middle temporal gyrus. No increase in number of active voxels had been observed for the left superior temporal gyrus during perturbation blocks.

For the intensity data, statistical analysis also revealed a main effect of condition for the left middle temporal [F(1.708,10.250) = 6.179, p = .020, eta^2 = .507] and superior temporal [F(3,12) = 8.889, p = .002, eta^2 = .690] gyri. For the left middle temporal gyrus, post hoc paired t-tests revealed intensity levels significantly above Baseline only for the Complex Condition [Compressed Simple: t(6) = -3.785, p = .009; Complex: t(6) = -5.281, p = .002; Compressed Complex: t(6) = -3.772, p = .009]. The left superior temporal gyrus showed significantly greater intensities only for the compressed conditions [Compressed Simple: t(4) = -

Table 14. Brain regions significantly active during Adaptation blocks by condition using either the percent of the voxels that where active within a region of interest or the intensity data for the analyses.

Region	% Voxels Active in Region during Adaptation Blocks						Intensity in Region during Adaptation Blocks					
	Left			Right			Left			Right		
	CS	C	CC	CS	C	CC	CS	C	CC	CS	C	CC
Middle Temporal Gyrus	*	*	**				*	**	*			
Superior Temporal Gyrus	*		*		*	**	**	*	**	*	*	*
Inferior Frontal Gyrus	**	**	*				*	*				
Middle Frontal Gyrus	*	**	**				*	**	**	**	*	*
Superior Frontal Gyrus - Lateral		**	*					**	**			
Superior Frontal Gyrus – Medial	**	*	**				**	*	*			
Angular Gyrus	**		**	*		*	**		*	*	**	
Supramarginal Gyrus	*	*	**	*			**	**	**			
Superior Parietal Lobule	*						**	*				
Fusiform Gyrus	*		*	**		*	*		*	*		*
Occipital Lobe	**	*	**	*		**	**	*	*	*		*

* Significant at alpha = .05

** Significant at Bonferroni corrected alpha = .008

Key: CS = Compressed Simple; C = Complex; CC = Compressed Complex

5.590, p = .005; Complex: t(4) = -4.616, p = .010, Compressed Complex: t(4) = -7.741, p = .001]. Though these areas were also active during perturbation there were differences during adaptation. Specifically, the left middle temporal gyrus no longer demonstrated increased intensity in the Compressed Simple Condition. However, intensities remained above Baseline for the Complex condition. Interestingly, the opposite pattern was observed for the left superior temporal gyrus, which remained active during the compressed conditions, but was no longer active in the Complex Condition.

Frontal Lobes

Inferior Frontal Gyri. A significant main effect for condition was present for the number of voxels active in the left inferior frontal gyrus [F(3,15) = 7.805, p = .002, eta^2 = .610]. However, in the adaptation blocks the significant increases in numbers of active voxels were found in the Compressed Simple [t(5) = -5.545, p = .003] and the Complex [t(5) = -4.720, p = .005] Conditions, not the Compressed Complex Condition which had shown this effect in the perturbation blocks. Likewise, whereas the left inferior frontal gyrus showed significantly higher intensities in the Compressed Complex Condition during perturbation blocks, once subjects had adapted to the increased complexity, it was no longer significantly different from Baseline [F(3,15) = 3.936, p = .030, eta^2 = .440]. No increases in numbers of voxels [F(3,12) = 2.666, p = .095, eta^2 = .400] or intensity [F(2.985, 11.941) = 3.476, p = .051, eta^2 = .465] were found for the right inferior frontal gyrus.

Middle Frontal Gyri. Significant increases were observed in number of voxels active in the left middle frontal gyrus [F(3,15) = 9.559, p = .001, eta^2 = .657] in the Complex [$t(5) = -10.270$, $p < .0001$] and Compressed Complex [$t(5) = -5.368$, $p = .003$] Conditions. This also was the case for the perturbation blocks. No increase in numbers of voxels in adaptation blocks was observed for the right middle frontal gyrus, which differs from the perturbation blocks in which significantly more voxels were active for all conditions in the right middle frontal gyrus.

For the intensity data, significant main effects for condition were observed for both the left [$F(3,15) = 6.399$, p .005, $\text{eta}^2 = .561$] and right [$F(1.740,12.181) = 3.513$, $p = .033$, $\text{eta}^2 = .415$] middle frontal gyri. Post hoc paired t-tests showed increased intensity in the left middle frontal gyrus during the Compressed Simple [$t(5) = -4.721$, $p = .005$] and Complex [$t(5) = -7.312$, $p = .001$] Conditions, but not the Compressed Complex [$t(5) = -3.714$, $p = .014$] Condition. For the right middle frontal gyrus, significantly increased intensity was found only for the Compressed Simple Condition [$t(5) = -3.666$, $p = .008$].

These data show that, for the left middle frontal gyrus, intensities for the Compressed Complex Condition no longer differed from Baseline, but the number of voxels above threshold did. For the right middle frontal gyrus, the pattern was notably different from that of the perturbation blocks. During perturbation, intensities for the Complex and Compressed Complex Conditions were significantly greater than Baseline. During adaptation, only the Compressed Simple Condition showed intensities significantly greater than Baseline. Further, whereas the number of voxels active was higher in all conditions during perturbation, no significant change in numbers of voxels still existed in adaptation.

Superior Frontal Gyri. Patterns of activation also changed for the superior frontal gyri during adaptation compared to perturbation. Significant main effects were found for the lateral [F(3,9) = 12.207, p = .002, eta^2 = .803] and medial [F(3,18) = 7.313, p = .002, eta^2 = .549] aspects of the left superior frontal gyrus for number of voxels above threshold. Recall that these frontal brain regions had shown no significant changes in number of active voxels in the perturbation blocks. A significant increase in active voxels was observed only in the Complex Condition for the lateral aspect [t(3) = -6.546, p = .007] and in the Compressed Simple [t(6) = -6.117, p = .001] and Compressed Complex [t(6) = -5.772, p = .001] Conditions for the medial aspect. No significant effects were found for the right superior frontal gyrus [lateral: F(2.267,11.334) = .929, p = .451, eta^2 = .157; medial: F(3,15) = 3.034, p = .062, eta^2 = .378].

For intensity, only the analyses for the left superior frontal gyri revealed significant main effects for condition in the adaptation blocks [lateral: F(3,9) = 9.621, p = .004, eta^2 = .762; medial: F(3,18) = 4.999, p = .011, eta^2 = .454]. The lateral aspect of the left superior frontal gyrus had significantly higher intensities during the Complex [t(3) = -7.084, p = .006] and Compressed Complex [t(3) = -10.370, p = .002] Conditions than in Baseline. The medial aspect of the left superior frontal gyrus had significantly higher intensities only during the

Compressed Simple [t(3) = -5.607, p = .001] Condition. This region also had shown increased intensities during the Complex Condition during perturbation. No significant main effects were found for the right superior frontal gyrus [lateral: F(3,15) = 1.250, p = .327, eta^2 = .200; medial: F(3,15) = 1.426, p = .274, eta^2 = .222] indicating no role of this region during adaptation; even though this region was active for the Compressed Simple and Complex Conditions during perturbation.

Parietal Lobes

In the parietal lobes, significant main effects were found only for the left angular [F(3,15) = 14.841, p < .0001, eta^2 = .748] and left supramarginal gyri [F(3,18) = 9.455, p = .001, eta^2 = .612] for the number of voxels active. In the left angular gyrus, increases in active voxels were observed for the Compressed Simple [t(5) = -5.998, p = .002) and the Compressed Complex (t(5) = -8.548, p < .0001] Conditions. In the left supramarginal gyrus, increases were observed only for the Complex Condition [t(6) = -3.917, p = .008].

For the intensity data, significant main effects of condition were found for the left [F(1.477,7.384) = 9.064, p = .013, eta^2 = .644] and right angular gyri [F(3,12) = 5.389, p = .014, eta^2 = .574], the left supramarginal gyrus [F(3,18) = 14.075, p < .0001, eta^2 =.701], and the left superior parietal lobule [F(3.725, p = .042, eta^2 = .482]. For the left angular gyrus, post hoc paired t-tests showed a significant increase in intensity compared to Baseline for the Compressed Simple

Condition only [t(5) = -8.252, p < .0001]. Intensities for the right angular gyrus significantly increased only for the Complex Condition [t(4) = -6.118, p = .004]. The intensities for voxels in the left supramarginal gyrus were significantly increased from Baseline for all conditions, as they had been in the perturbation blocks [Compressed Simple: t(6) = -4.921, p = .003; Complex: t(6) = -4.502, p = .004; Compressed Complex: t(6) = -5.069, p = .002]. For the left superior parietal lobule, significantly increased intensities were observed only for the Compressed Simple Condition [t(4) = -5.433, p = .006], and were no longer observed for the Compressed Complex Condition [t(4) = -1.913, p = .128].

Other Regions

For the voxel data, significant main effects for condition were found for the right fusiform gyrus [F(3,18) = 6.496, p - .004, eta^2 = .520] and the occipital lobe bilaterally [left: F(3,21) = 4.189, p = .018, eta^2 = .374; right: 3,15) = 5.070, p = .013, eta^2 = .503]. Significant increases in numbers of voxels above threshold for the right fusiform gyrus were observed only in the Compressed Simple Condition [t(6) = -5.101, p = .002]. The left occipital lobe showed significant increases for the Compressed Simple [t(7) = -4.088, p = .005] and the Compressed Complex [t(7) = -3.813, p = .007)] Conditions. The right occipital lobe had significantly greater numbers of active voxels only for the Compressed Complex Condition [t(5) = -5.515, p = .003]. The fusiform gyrus and right occipital lobe were not active during the perturbation blocks.

For the intensity data, a significant main effect for condition was found for the left occipital lobe [$F(3,21) = 12.531$, $p < .0001$, $eta^2 = .642$]. Post hoc paired t-tests indicated significantly increased intensities only in the Compressed Simple Condition [$t(7) = -9.419$, $p < .0001$], similar to the perturbation blocks.

To summarize, the hemodynamic resonse associated with adaptation blocks was investigated for each condition by region. The regions showing increases in intensity and/or number of voxels above threshold by condition are presented in Table 15.

Table 15. Summary of regions showing increased numbers of voxels and/or intensity for each condition.

Compressed Simple	Complex	Compressed Complex
	left middle temporal gyrus	
left superior temporal gyrus		left superior temporal gyrus
left inferior frontal gyrus	left inferior frontal gyrus	
left and right middle frontal gyri	left middle frontal gyrus	left middle frontal gyrus
left superior frontal gyrus-medial	left superior frontal gyrus-lateral	left superior frontal gyrus-lateral
left angular gyrus	right angular gyrus	left angular gyrus
left supramarginal gyrus	left supramarginal gyrus	left supramarginal gyrus
left superior parietal lobule		
right fusiform gyrus		
left occipital lobe		left and right occipital lobe

For adaptation, the only regions showing sensitivity to syntactic complexity alone were the left middle temporal gyrus and the right angular gyrus (active only in the Complex Condition). Regions showing increases in activation associated only with the compressed conditions were the left superior temporal gyrus, the medial aspect of the left superior frontal gyrus, the left angular gyrus, and the left occipital lobe. One remarkable difference between the perturbation and adaptation blocks was the absence of increased intensity or number of active voxels in the right frontal regions.

Percent Change in Intensity

Another dependent variable used for Experiment 2 was the percent change in intensity valued for each condition as compared to Baseline. These values allow for direct comparison within each subject between perturbation and adaptation blocks in each condition (as opposed to comparing only to Baseline). However, great individual variability was observed between conditions. Only the following were significant for all subjects:

1. A significantly greater signal change was observed between the Compressed Simple perturbation and adaptation blocks for the left occipital lobe [$t(7) = -3.45$, $p = .011$; Bonferroni correction here is .016 with three comparisons – perturbation and adaptation blocks within the Compressed

Simple, Complex, and Compressed Complex conditions] indicating significantly more intensity in the adapted state.

2. A significantly greater signal change was observed between the Compressed Complex perturbation and adaptation blocks for the medial aspect of the left superior frontal gyrus [t(6) = 3.359, p = .015] indicating significantly more intensity in the perturbed state.

Individual Performance

The purpose of this section is to explore the individual variability of brain responses and their relation to behavior. To do so, the behavioral performance of each subject along with their fMRI results were examined. First, the experimental manipulations that served to perturb each subject and whether or not adaptation occurred are discussed. Then, brain regions showing active voxels (defined as correlated with the model wave at .31 or higher in three or move contiguous voxels) during at least one condition are presented. Any differences in percent signal change from Baseline that were considered substantial are discussed. For this section, a substantial change is defined as a change of greater than 30%. This criterion was chosen since typical physiologic flux is approximately 20% (e.g., Schmidt-Neilsen, 1990). Finally, a discussion of the individual patterns and brain behavior relations ensues. Note that detailed descriptions of each subjects' performance (Appendix G) and changes in the percent signal intensity by region between perturbation and adaptation blocks for each condition by region (Appendix H) are graphically displayed in the Appendices.

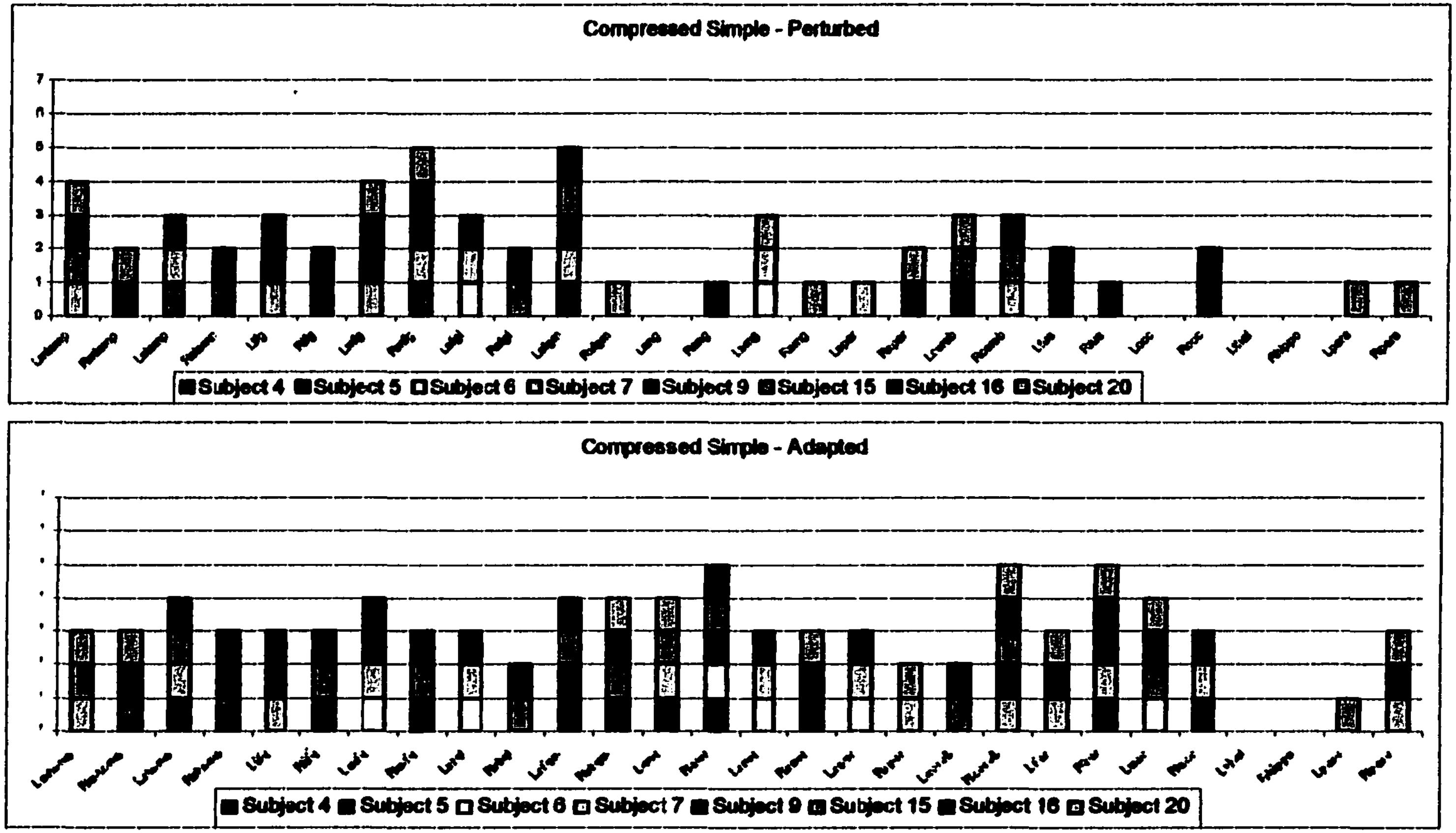
Presence of perturbation and adaptation by condition in Experiment 2 for each subject is presented in Table 16. All but one of the subjects was perturbed in the Complex and Compressed Complex Conditions, but only subject 6 adapted in both conditions. Most of the subjects showed adaptation only in the Compressed Complex Condition. Subject 9 was not perturbed in any condition. However, inspection of her data (Appendix G) reveals that her performance was extremely variable in all of the conditions and that she was not stable at the outset of her participation in the study.

Brain regions in which subjects showed activation of greater than 30% above Baseline are presented in Figures 7 (Compressed Simple), 8 (Complex), and 9 (Compressed Complex). No clear patterns of brain activation associated with perturbation or adaptation were evident across subjects. However, the hypothesized regions in the temporal lobes (middle and superior gyri) and the frontal lobes (inferior and middle gyri) were active in most subjects (Appendix G). Four subjects showed activation in the left inferior frontal gyri during perturbation. Only 2 demonstrated activation during adaptation during the Compressed Complex condition (Figure 9).

Table 16. Presence of perturbation and/or adaptation by condition for each of the subjects in Experiment 2.

Subject	Perturbed in Experiment 2			Adapted in Experiment 2		
	CS	C	CC	CS	C	CC
Subject 4 (35 year old male)		X	X		X	
Subject 5 (20 year old female)		X	X		X	
Subject 6 (35 year old female)		X	X		X	X
Subject 7 (19 year old male)		X	X			X
Subject 9 (20 year old female)						
Subject 15 (23 year old male)			X			X
Subject 16 (21 year old male)	X	X	X			X
Subject 20 (29 year old male)		X	X			X

Figure 7. Subjects showing greater than 30% change in intensity by region in the Compressed Simple Condition.



Key: mtemp – middle temporal gyrus, stemp – superior temporal gyrus, ifg – inferior frontal gyrus, mfg – middle frontal gyrus, sfgl – superior frontal gyrus (lateral aspect), sfgm – superior frontal gyrus (medial aspect), ang – angular gyrus, smg – supramarginal gyrus, spar – superior parietal lobule, cereb – cerebellum, fus – fusiform gyrus, occ – occipital lobe, thal – thalamus, hippo – hippocampus, para – parahippocampus

Figure 8. Subjects showing greater than 30% change in intensity by region in the Complex Condition.

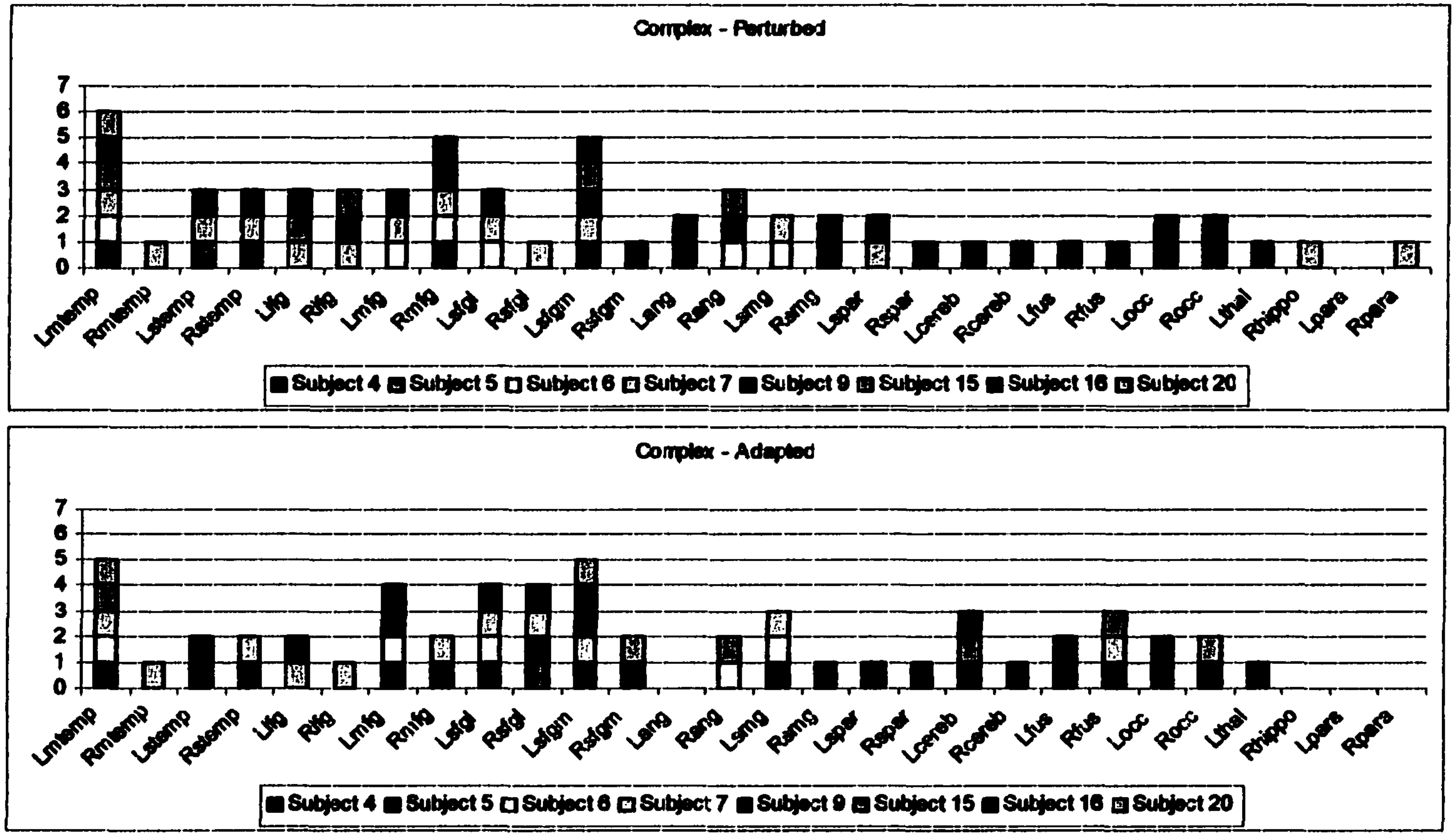
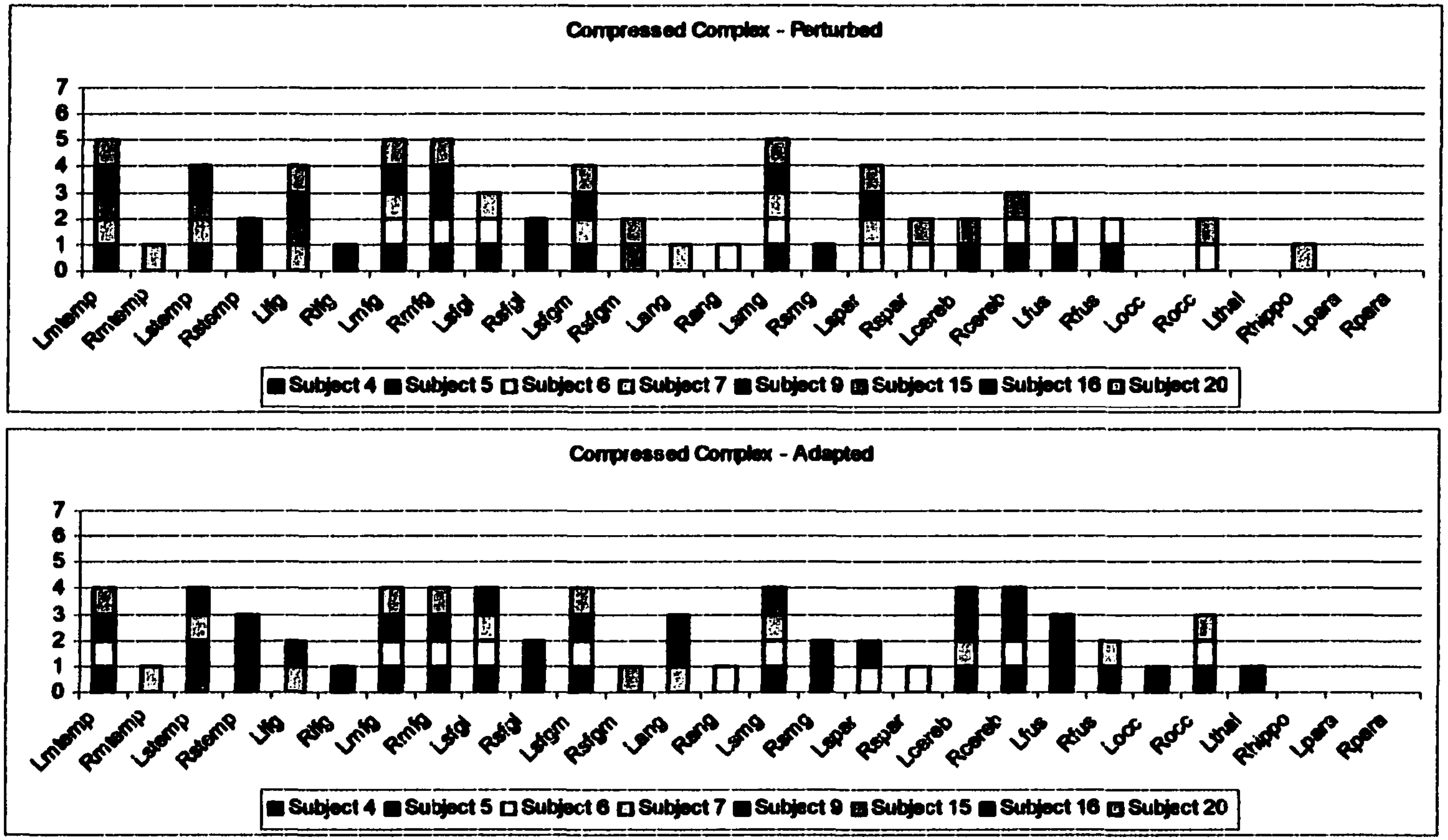


Figure 9. Subjects showing greater than 30% change in intensity by region in the Compressed Complex Condition.



CHAPTER 6 – DISCUSSION

This chapter is organized around the main questions and the dynamic system framework presented in Chapter 1. First the behavioral results from Experiment 1 are discussed followed by an exploration of the fMRI results from Experiment 2. The final section is a discussion of the relation between the behavioral and brain responses. Issues related to shortcomings of the current study and future directions are discussed within each section.

Experiment 1

Summary of Main Findings

There were three main findings for Experiment 1 providing strong support for the initial hypotheses regarding perturbation and adaptation. First, it was found that increases in syntactic complexity created a perturbation in that subjects performed more poorly when first encountering the increased demand of object cleft or object relative sentences. One hypothesis that was not supported was that compression of simple sentences would perturb subjects. However, a combination of compression and increased syntactic complexity did perturbed subjects, but no strictly additive effects of both compression and increased complexity were found (i.e., subjects were not more perturbed in the Compressed Complex Condition than they had been in the Complex Condition). However, it should be emphasized that the combined task demand led to greater instability and a longer time to adapt.

It also was the case that subjects adapted to perturbation. Following a decrease in performance (increased reaction times as indicated by the Perturbation Indices), subjects returned to baseline performance (stability) by item 2 (Complex Condition) or item 3 (Compressed Complex Condition). Below each issue is discussed in more detail. First a discussion of the use of the derived indices and the initial finding that first half performance was in some conditions significantly different than second half performance ensues.

Derived Indices

Before discussing the results it seems reasonable to comment on the derived indices used in the current experiment given that the Stability Index (SI), the Perturbation Index (PI), and the Adaptation Index (AI) have never been used before. Though other investigators have used ratio values to index performance, this is the first utilization of ratios of reaction time (RT) values to reflect changes in demand associated with perturbation and adaptation. As well, the use of a stability index is a new measure.

These indices appear to reflect the stability of performance and the increases and decreases in stability associated with changing demand and in a unique manner (that could not have been possible with raw RT values alone). A clear benefit of the derived indices is that they normalize data across subjects so that basal differences in RT are essentially washed out and cross-subject comparisons can be made under reduced noise inherent in raw RT data. In other words, the typical between-subject variability associated with RT data was essentially removed by using ratio-based indices. The indices allowed for a comparison between conditions by assuming that within a dynamic system (i.e., constantly changing), the relative differences between conditions and stimuli are more important than the absolute differences.

Change Across Time

Accuracy improved over time for the Complex and Compressed Complex conditions, but the PIs increased over time indicating greater levels of perturbation. These data do not suggest a learning effect per se, but rather a response continuum within a dynamic system. At first glance, these data suggest that there may have been a speed-accuracy trade off. That is, subjects may have produced slower RTs in the more complex conditions as they increased accuracy over time. However, this explanation may not be compelling given that raw RTs in the Compressed Simple Condition were actually faster than those found in the Simple condition even though the PIs for the Compressed Simple condition increased over time.

The more likely explanation is that the PIs increased over time in the more complex conditions because subjects had to pay more attention. That is, although accuracy increased, the demands placed on subjects' attention as they continued in the task increased. The expense of the increased demand was to create an increased perturbation over time. Essentially, the dynamics of the situation resulted in increasing demand over time, as shown by the increased PIs, even though the raw

RTs were faster than in baseline. Recall that attention is probably a control variable in a dynamic system. As such, increases in attention will result in changes in stability and subsequently perturbation.

In summary, though there were changes over time, these changes were probably not the result of learning. Learning would have resulted in consistent increases in accuracy and decreases in RT, which did not occur. Rather, it is more likely that any changes over time were the result of subjects' inability to maintain a constant level of attention and their response to these fluctuations. Thus, the changes over time also can be interpreted within the dynamic systems model in which subjects were constantly adapting to internal changes.

Perturbation

It has been shown that increases in syntactic complexity often reduce performance in normal subjects and persons with aphasia during comprehension tasks such as the one used in the current study (e.g., Caplan, 1987; Just & Carpenter, 1992; Miyake, Carpenter, & Just, 1995). It also has been found that time compression reduces comprehension and thus can be considered a perturbation (Mehler et al., 1993; Pallier et al., 1998). The results of the current study support and extend previous observations in that increases in syntactic complexity resulted in clear decrements in performance as indexed by a derived value, the Perturbation Index (PI).

Of particular interest is the finding that compression alone did not perturb subjects in this experiment as measured by the indices. This finding differs from the Dick et al. study (in press), which clearly documented time-compressed decrements in performance on language comprehension tasks. It is unclear why the subjects in this study were not perturbed by compression alone although there are different possible interpretations for this finding. One explanation may be that the study reported here used the derived indices versus the raw RT values used in the other study. However, accuracy, a common measure across studies, did not significantly differ between the Simple and Compressed conditions either.

A more plausible explanation is that the blocked presentation mode used here differed from Dick and colleagues (2001). Those investigators used random stimulus presentation. However, in order to study adaptation in this study, a blocked presentation was necessary. Blocking stimuli may have resulted in making the task more stable and therefore simpler overall than when a totally random mode is utilized. If this was the case, then the demand placed on subjects by compression alone during blocked presentations may not have be enough to perturb these young healthy subjects. Support for this hypothesis comes from the attention literature. Robin and Rizzo (1992) found that RTs to stimuli that were presented in a blocked manner were faster than those presented in a random manner. Indeed, when blocked presentation modes are used, little if any attention effects are found given that the task demands are substantially reduced (Posner, 1978). Future work should examine the effect of presentation mode on performance.

The finding that compression under blocked presentation did not perturb subjects can be encompassed by dynamic system theory. If presentation mode changes the demand, then this finding suggests that blocked presentation modes result in a stronger attractor or a deeper well. In other words, blocked presentation of stimuli creates a stronger stable state. Random presentation modes by virtue of increasing task demand induce instability and thereby alter performance. Thus, compression alone under the blocked presentation mode of the current study was not enough to create an instability that was enough to perturb performance or cause a release from a strong attractor. Further, once the strong attractor had been developed in a block of compressed stimuli, subjects were more likely to be drawn back to that attractor when compression was presented to them repeatedly. This explanation is in line with the findings of Pallier and colleagues (1998) who found that once bilingual subjects had been exposed to compressed speech in one language, they were quicker to adapt to the faster rate when also presented in another language.

That perturbation (higher PIs than SIs) increased during changes in syntactic complexity and syntactic complexity plus compression conditions is noteworthy. While it is known that object cleft and object relative sentences are more difficult for subjects to comprehend than simple sentences, it was not known if the demand placed on the language system would be enough to create a perturbation. That the initial encounter with a more demanding syntactic structure led to a significantly increased PI, suggests that such linguistic changes create enough instability to pull one away from an attractor state.

Most studies on language processing have not examined individual variability. Thus, the examination of individual variability through use of the coefficient of variance (CV) provides hitherto unavailable information on within subject fluctuation in performance. Performance in the Complex Compressed Condition was most unstable as indicated by the significantly higher CV than in all other conditions. Hence, unlike other studies, this study provides evidence that changes in syntactic complexity or changes in compression combined with syntactic complexity result in greater individual variation.

The notion that language may be viewed as a dynamic system in a state of constant flux differs from most models of adult speech and language disorders in the field of speech-language pathology. Specifically, disorders like aphasia were traditionally thought to be invariant in the sense that performance variability was a distinguishing symptom when differentiating aphasia from apraxia (e.g., McNeil, Robin, & Schmidt, 1997). Indeed, the distinction between motoric versus linguistic errors are often made on the basis of variability. That is, if verbal output is variable the deficit is more likely thought to be motoric in nature given that language is rule-governed and in some theoretical frameworks, less variable. However, because language *is* variable, such arguments relative to aphasia are difficult to understand. Given that all complex systems like language and motor speech programming are variable, stability alone cannot be used to differentiate among disorders. More studies like the current one, examining individual variability during language processing, are needed, particularly in groups of subjects with neurogenic speech or language disorders.

The findings from Experiment 1 can be related to performance in aphasia in a number of ways. Though future work is needed to study the effects of perturbation in persons with aphasia, certain predictions can be offered within a dynamic systems framework. It has been hypothesized that persons with aphasia have a reduced capacity or inefficient processing system in regard to language processing (Clark & Robin, 1995: McNeil, Odell, & Tseng, 1991; Murray, Holland, & Beeson, 1997). If this is the case, then individuals with aphasia are more likely to be perturbed by changes in syntactic complexity or compression. Indeed, a wealth of data exists that shows decrements in aphasic performance related to increased syntactic demand (see Caplan, 1987 for review) and/or increased temporal demand (e.g., Robin, Tranel, & Damasio, 1990; Tallal & Newcomb, 1978). It may be that persons with aphasia have a weakened attractor (a shallow well) or border closer to instability. One can predict that changes in compression that did not affect the PI of the normal subjects in the current study, would indeed show increases in aphasia. As well, it may be that the ability to adapt to a constantly fluctuating system may be extremely difficult in aphasia. Thus, once perturbed, it may take a long time for the person with aphasia to settle into a stable state.

Adaptation

Perhaps the most important aspect of the current study was the study of adaptation. Review of the extant literature suggests that this is among the first to examine how subjects adapt to being perturbed by changes in linguistic complexity *and* compression. The basic result was that subjects did adapt to perturbation in the Complex and Compressed Complex Conditions.

The only previous literature providing any information about adapting to language stimuli is that of Mehler and colleagues (1993). These investigators explored subjects' perception of compressed speech and found that once subjects had been exposed to compressed speech for about 15 seconds, they adapted to this manipulation. Dupoux and Green (1997) extended these findings by examining the effect of even greater amounts of compression on the comprehension of the stimuli. They compared performance when the stimuli were compressed at 38 and 45% of the original rate. Subjects were presented sets of four to five sentences (compound active sentences) and were asked to write each one down as best they could. These authors found that subjects had adapted to the compression in the 45% compression condition by the second set of sentences (after about five sentences) but did not adapt until the third set in the 38% compression condition (after about 10 sentences; adapting in this case was improved accuracy for writing the sentences). Whereas the compression rate in the present study was less than that of the Dupoux and Green study, their data lend support to the idea that even when the change in complexity is only in the rate of speech, subjects can take longer to adapt when the complexity is great. These authors attribute the ability to adapt to highly compressed speech to short-term adjustment to the speech or rate normalization. However, they also noted that subjects must develop some long-term stored representation for adjusting to the compression so that when they hear it again they are not perturbed again. This long-term representation may be likened to being primed to listen to speech at a particular rate.

No previous work has investigated whether or not subjects adapt to increased syntactic complexity. The syntactic priming literature suggests that once subjects have heard a structure, they are more likely to comprehend the next structure they encounter using the same parsing strategy, even when that strategy is complex (Potter & Lombardi, 1998). It may be the case that the recurring object cleft and/or object relative sentence types primed the subjects in this study. However, the sentence types varied across conditions (simple versus complex conditions) and within the complex conditions in an attempt to control for this possibility. Furthermore, whether or not subjects were primed may be an indicator of how the "language system" organizes itself in a dynamic manner to process stimuli with increasing syntactic complexity. Being primed may be an essential part of developing a stable state when a system is perturbed by difficult linguistic structures.

Further, on a more conscious level, subjects likely developed strategies to assist them in understanding the sentences. Subjects often reported, after participating in Experiment 1, that they had begun to determine the subject and object of each sentence before responding approximately half way through the experiment. Reports included either developing a visual image of the action taking place in each sentence or determining "who did what to whom." Development of these strategies should take time, a few items, because the sentence types varied from item to item.

In Experiment 1, subjects took longer to adapt in the Compressed Complex Condition than they did in the Complex Condition. If it is the case that subjects must develop a long-term representation for processing fast speech (as suggested by Dupoux & Green, 1997), then performance in the Compressed Simple Condition should have shown greater effects of perturbation. However, that condition involved the processing of simple sentences and the compression rate was not very high (i.e., the speech was not as fast as that of Dupoux & Green). If it is the case that subjects must develop a representation for processing complex sentence types (as a function of being primed), then they should improve in their ability to process them over time. This was not the case in Experiment 1, as performance in the Complex Condition did not significantly improve over time. However, if it is the case that, when bombarded with both fast and syntactically complex sentences, subjects must develop and maintain representations for processing fast speech and representations for processing complex sentences, then they should take longer to improve their performance. This was the case for the Compressed Complex Condition in Experiment 1, as performance significantly improved in the second half of the experiment. Therefore, it may be that in order to adapt to increased complexity, at least of the type used in this experiment, one must develop representations for processing information at that level. Further work is needed to explore whether or not this is the case and whether or not the inability to learn and generate these representations may play a role adaptation to perturbation in patient populations.

Working Memory and Language Processing

There have been different accounts of the role of working memory in language processing, the most prominent of which is the Capacity Constraint theory of Just and Carpenter (1992). This model focuses on the central executor and states that linguistic computations and storage draw from the same pool of resources. This model makes the assumption that language processing (sentence comprehension) is constrained by an individual's working memory capacity. Though there have been different instantiations of this model, the basic prediction is that language processing should be related to working memory capacity. The basic premise of the CC model is that processing and storage demands draw from the same limited pool of resources.

In the current experiment, it was predicted that the degree of perturbation or amount of adaptation would be related to working memory capacity, since the CC model would predict that as demand became high (perturbation occurs), subjects with lower WM capacities would be more likely to make more errors or to show greater changes in RT (higher PIs). As the limited capacity system becomes stressed, there should be a greater degree of perturbation and/or a lesser degree of adaptation. Contrary to this prediction, no relations were found between WM capacity and any of the behavioral indices in the current study. It may be that the measures chosen did not appropriately measure working memory. However, it is interesting to note that Jackson (1996) found that working memory capacity did not correlate with gap filling. At the least, the CC model needs to be more precisely defined to account for these findings. It may be that limited rather than normal working memory abilities are related to perturbation and adaptation in older subjects or persons with aphasia. Future studies are needed to explore this possibility.

Experiment 2

Summary of Main Findings

Four behavioral findings are noteworthy for initiating the discussion of the imaging data. First, accuracy did not drop significantly for any subject while in the scanner. This finding provides evidence that results while brain activity was being measured were not contaminated by scanner noise. Second, group data showed significant perturbation only for the Compressed Complex Condition (though subjects 4, 5, 6, 7, 16, and 20 were perturbed in the Complex Condition). Third, subjects adapted to being perturbed in the Compressed Complex Condition by Adaptation Index 2, even though in Experiment 1, adaptation did not occur until item 3. Lastly, though the subjects as a group were not perturbed in the Complex Condition, an adaptive response was evident from measures of the Adaptation Indices in that condition. Thus, as indicated by the individual subject data in Chapter 5, there was significant individual variability in Experiment 2.

Perturbation and Adaptation in the Brain

Increases in complexity have been investigated in several neuroimaging studies. However, most of these studies have explored the mean differences in brain activity associated with complex task versus a simple task. In more traditional studies, certain regions have been shown to increase in activation monotonically as task demand increases. In particular, the dorsolateral prefrontal cortex (or the middle frontal gyri as described in this study) has been found in several studies to be essential for the processing of increasingly complex or demanding tasks (e.g., Braver et al., 1997; D'Esposito et al., 1995; Smith et al., 1998). Several other regions also have been shown to demonstrate increases in activation as a linguistic task becomes more complex. Particularly, the left inferior frontal gyri (e.g., Caplan et al., 1998; Carpenter et al., 1999; Rypma et al., 1999) and superior temporal gyri (Carpenter et al., 1999; Michael et al., 2001) have been shown to increase when syntactically complex structures are presented. However, no previous investigations explored whether or not subjects have adapted to the changes in complexity or whether brain patterns change as adaptation occurs.

In the present study, brain activation was investigated as task complexity increased and at a intervals following perturbation, where subjects were predicted to have adapted based on the behavioral findings of Experiment 1. The dependent measures made it possible to determine if the increases in activation: 1) were attributed to increases in the amount of brain volume involved during the task, or 2) were attributed to increases in the strength of the intensity change associated with the task, or 3) both. The following discussion will be presented by brain region, highlighting only those regions hypothesized in Chapter 4.

Superior Temporal Gyri

The superior temporal gyri have long been associated with the processing of linguistic information and have recently also been shown to increase in activity as syntactic complexity increases (e.g., Carpenter et al., 1999) and specifically for object relative versus active sentences (Michael et al., 2001). In research reported here, activation in this region was significantly above Baseline levels for the Compressed Simple, Complex, and Compressed Complex Conditions during perturbation blocks. This increased activation was not a result of a larger amount of area active (number of voxels); rather it reflected an increase in strength of activation. During adaptation, no change in activation was observed for the compressed condition, but intensity of activation in the Complex Condition no longer differed from Baseline levels. This region appears to be involved in processing more complex linguistic material, regardless of whether the complexity results from perceptual or syntactic factors. However, once adaptation occurs it is no longer needed for the processing of syntactically complex sentences. If a less stringent criterion for significance is used (see discussion for left inferior frontal gyrus above), then this region remained active during adaptation (see Table 14). This result suggests that the superior temporal gyrus is essential for carrying out the task, regardless of the level of complexity or the amount of exposure to the task.

Inferior Frontal Gyri

The inferior frontal gyri have most commonly been associated with syntactic processing (Caplan et al., 1998) or in processing only more complex syntax (Carpenter et al., 1999). In most cases, left sided dominance was found for this region, but homologous right-sided activation also was reported. In this research, the left inferior frontal gyrus was significantly active only during the Compressed Complex Condition during perturbation. This finding supports the notion that this region is responsible for processing complex syntax. However, in this case the activation of the region only differed from Baseline when the complexity was also increased by perceptual demand. During adaptation, the region was no longer significantly different from Baseline in the Compressed Complex Condition, but was significantly more active in the Compressed Simple and Complex Conditions.

Although the above interpretation is tentative, it is important to consider the following issues. First, it was the case that using the Bonferroni correction, a very conservative estimate of activation was established because many comparisons were made in the statistics. However, as discussed in Chapter 5, because the information presented here is novel with little previous research available for making hypotheses about the adaptive process in particular, the data for a less stringent alpha of .05 also were presented in Tables 12 and 13 in Chapter 5. Using that more lenient criterion of .05, the left inferior frontal gyrus would be considered active for the Compressed, Complex, and Compressed Complex. This was the case for perturbation (Table 12, p. 86) and adaptation (Table 14, p. 96). Thus, similar to previous reports this area is active during changes in linguistic demand related to either perturbation or adaptation. In summary, it appears as if the left inferior frontal region is active during processing of linguistic information.

Middle Frontal Gyri

As noted above, the middle frontal gyri were hypothesized to show strong activation patterns related to increases in complexity. During perturbation blocks, the middle frontal gyri did show significant increases in both dependent measures in the Compressed Simple, Complex, and Compressed Complex Conditions. These data indicate that this region is necessary for processing these linguistic stimuli regardless of their perceptual or syntactic complexity, at least as perturbation was initially encountered before adaptation could occur. Moreover, these data suggest that this brain region becomes active, even when behavioral performance did not show evidence of adaptation. Perhaps the activity in this region for the Compressed Simple and Complex conditions was needed to maintain performance levels. When demand is greatest, even with activation of this area, performance suffers.

In the adaptation blocks, the right middle frontal gyrus was no longer active in the complex conditions, but did still show increases in intensity for the Compressed Simple Condition. In contrast, the left middle frontal gyrus only showed increases in the complex conditions. Thus, it is possible that increased activity in these regions is needed to handle situations of increased demand. Further, as demands decreases, activity lessens as well.

These patterns in the middle frontal gyri suggest that they are involved bilaterally during perturbation. Increased activation may be needed to deal with the increased demand on a global level (not specific to the type of increased demand verbal or perceptual). Once adaptation occurs, it may be that the middle frontal gyri shift to more task-specific processing modes. This shift from global to specific suggests that adaptation to speech rate demands in this study occurs on the right and to syntactic demand on the left. These data are in line with classical models of the left hemisphere serving dominance for linguistic stimuli and the right hemisphere dominance for nonverbal stimuli (Smith & Jonides, 1999), particularly with stimuli of the sort used here. It is well know that the left hemisphere has strong associations with temporal processing (e.g., Robin, Tranel, & Damasio, 1990), but this lateralization occurs only at very fast rates, unlike the relatively slow rates of speech under compression used in the current study.

Superior Parietal Lobule

The superior parietal lobule has recently received interest as its role in general cognitive processing has been explored. This area is traditionally associated with attentional processes, particularly orienting attention (Corbetta, 1998; Rizzolatti & Craighero, 1998), and is usually thought of as a center for visuo-spatial processing in coordination with frontal regions (e.g., Diwadkar et al., 2000). In the present study, activation of the left superior parietal lobule was significantly above Baseline levels for the compressed conditions only during perturbation. During adaptation it only remained active for the Compressed Simple Condition. Superficially, these data suggest that the superior parietal lobule participates in the processing compressed speech regardless of the changes in complexity due to increased syntactic complexity. However, the work of Diwadkar and colleagues highlights the rich connections between this region and other regions of the brain, particularly frontal regions. Thus, this region may play a dynamic role in processing of demanding information, possibly via coordination with other brain regions. Given the strong link of this region with visual processing, it may be that this region, along with the angular and supramarginal gyri also shown to be active in this experiment, served to integrate information. The level of processing required to integrate across modalities may have been more demanding during the compressed conditions. The analyses used in the present study do not allow for exploration of interconnections or co-modulation of brain regions. Further work is needed to explore this possibility for all of the regions discussed.

Summary

This study provides evidence that perceptual and syntactic manipulations can serve to perturb language processing in young, normal individuals. Further, the subjects studied here were able to adapt under both syntactic and syntactic + perceptual demands. As is evident from the individual data, the level of complexity resulting in perturbation and the presence of adaptation to perturbation showed considerable individual variation. In all, these data suggest that the dynamic system framework has utility in understanding language processing.

This study also explored brain activation associated with perturbation and adaptation. Though preliminary, it appears as if some regions are more involved during perturbation, and other more involved during the period of adaptation. These findings support those of previous investigators exploring the effects of increased complexity on brain activity. They also provided evidence of the dynamic change of this brain activity over time when subjects became able to adapt to complexity in that some regions were active only during perturbation and others only during adaptation.

Limitations of the Current Study and Future Directions

Only young normal subjects were used in the present study. This was done in order to establish the parameters that serve to perturb language processing and then explore adaptation. An important next step will be to study how aging or brain pathology (developmental or acquired) may affect language processing within the framework of dynamic systems.

Whereas the use of the derived indices allowed for exploration of the dynamics of language processing in the current study, all measures were off-line and did not allow for measurement of processing as it unfolds in real time. For example, it may be the case that subjects were in fact perturbed when they encountered a change in complexity such as in the Compressed Simple Condition, but adapted too quickly to be detected with the measures used. Thus, future studies examining perturbation and adaptation in real time should provide a greater degree of specificity relative to the dynamic evolution of language processing.

The fMRI technology used in the second experiment was, in a sense, an on-line measure. However in order to use the blocked presentation of stimuli as discussed above, the ability to measure activity as subjects were perturbed was limited. That is, though it was assumed that subjects would be perturbed during the first two items of a block and then adapt during the last few items, the behavioral data revealed that several subjects had not yet adapted by the fourth item in a block (see Individual Performance in Chapter 5). As such, the data may not purely reflect perturbation and adaptation in that some subjects were still perturbed during the adaptation blocks. Development of innovative designs may help to determine whether or not the same patterns of performance and brain activity hold true with more discretely timed experiments as might be possible with an event-related design.

It also is the case that the fMRI technology does not allow for precise temporal resolution. Thus, the main questions that were answered in the current study were spatial in nature. Perturbation and adaptation are time related events and studies of these processes using such techniques as event related potential that allow for precise temporal measurement are needed.

Other analyses using the data collected here also are warranted. For example, exploring the variability of the intensity changes for each voxel across the time series in the fMRI data may allow more detailed characterization of instability associated with perturbation. Of course, with the current technology, each measurement of a region occurs every three seconds (repetition time for the scanner) perhaps not allowing enough discrete observations of fluctuation in intensity.

Finally, this study was not designed to test a model of dynamic systems. Rather, it was conceived around the general framework of dynamic systems theory and the theory was used as a guide in designing the study. Dynamic systems is a mathematical model through which the findings of the study reported here might be further elucidated in terms of, for example, whether or not the availability of the representations for parsing complex syntax is essential for adaptation. Future studies that use mathematical modeling of language as a dynamic system will be fruitful in furthering our understanding of how language is processed and what factors lead to inefficiencies in language processing in persons with brain injury.

APPENDIX A

Validation study of stimuli.

Data were collected for six pilot subjects performing the task for all stimuli. Subjects were three females and three males ranging in age from 24 to 33 years and in education from 16 to 22 years.

328 stimuli were presented using E-prime software with auditory stimuli presented over speakers and visual stimuli presented at the center of the screen on a laptop computer. Subjects were asked to listen to the sentences and then determine if the phrase presented on the screen was true or false relative to the sentence heard. The simple and complex sentences were presented in random order.

Accuracy and reaction time data for all subjects were entered into SPSS 10.0 for analyses. Repeated measures Analyses of Variance were significant for accuracy ($F(2, 10) = 6.75, p<.001$) and reaction time ($F(2, 10) = 75.04, p<.001$). Results were as follows:

Table 2. Validation Study Results

	Accuracy	Reaction Time
Simple	.99	1601 (539)
Object Cleft	.90	1833 (718)
Object Relative	.93	2012 (724)

Any items that were missed or were outliers for two or more subjects were removed from the study.

APPENDIX B

Experimental Stimuli.

Simple Sentences

The carpenter bought the stain for the cabinets.
The queen enjoyed her visit in Tucson, AZ.
The snowplow cleared the driveway for the family.
The marine recruits trained for the obstacle course.
The singer publicly addressed the right wing community.
The amateur cameraman fainted at the accident scene.
The troop leader ordered the new combat boots.
The burglar stole the diamonds and heirloom pearls.
The magician entertained the screaming crowd of preschoolers.
The weightlifter swiftly rescued the woman in danger.
The salon's manicurist filed the famous actor's toenails.
The polo star fell off the stallion's back.
The cheerleader combed her long, curly brown hair.
The rooster woke the entire farmhouse at dawn.
The creative landscaper planted a beautiful apple grove.
The blonde lifeguard saved the adolescent from drowning.
The nervous skater prepared for her debut performance.
The bouncy aerobics instructor led the gym class.
The angry construction worker yelled at the pedestrian.
The physical fitness trainer scheduled too many clients.
The homeowner replaced the carpet in the hallway.
The pilot launched the rocket over the trees.
The samurai master laughed heartily during the lesson.
The lumberjack cut down the old pine trees.
The hanglider landed in the Great Smokey Mountains.
The boxer won the highly publicized exhibition match.
The dealership sold the couple a new station wagon.
The zookeeper kept the big, beautiful peacock.
Yesterday, the carpool forgot to pick up Johnny.
The wood worker made a toy with scraps.
The butler escorted the visitors to the foyer.
The teacher published an essay on cultural differences.
The officer called the station for a message.
The bookstore carried only children's books by children.
The alcoholic slept on the bench Friday night.
The attorney borrowed the book from the library.

The landlady pulled the weed near the patio.
The robber saw the policeman at the payphone.
The preschool enjoyed a picnic by the swings.
The woman watched the artist in the park.
The grandchildren broke the vase in the hall.
The eccentric man wore a turban in Turkey.
The sheriff guarded the judge in the courtroom.
Sally took her tennis racket from the garage.
The toddler played with the dog at home.
The airline promoted the pilot having strict morals.
The photographer chased the runner in the race.
The electrician fixed the generator at the plant.
The director admired the stage at the playhouse.
The news praised the comedian in Sunday's newspaper.
The crowd liked the storyteller at the exhibition.
The maid hand washed the silverware after dinner.
The photographer saw the pictures on modern design.
The detailer washed the Mercedes at the dealership.
The salesman conned Doug into buying a car.
The accomplice disguised the inmate as an engineer.
The lawyer leased the office on Monday morning.
The youngster wrote the report about the scandal.
The librarian saved books on ancient art history.
The father resisted learning about high school trends.
The police helicopter lost control during the rescue.
The cat climbed the pecan tree on Broadway.
The daughter read a letter to her father.
The mattress store allows customers to lay down.
The commercial advertised the new and improved glue.
The doctor hired the maid twenty years ago.
The baseball player struck out on first base.
Children usually enjoy going to school on Mondays.
Cellular phones changed the long distance companies forever.
The paper bag blew swiftly across the park.
The sunflowers grew tall in the open field.
The laughing clown jumped around at the circus.
The tap dancer tutored the Spaniard in chemistry.
The divorcee adopted six orphaned and homeless children.
The student found a new career in bartending.
The novice hiker discovered the poisonous rattlesnake.
John ate the ice cream cone with sprinkles.
Susie hugged the teddy bear after scary stories.

Laura developed into a strong and beautiful dancer.
The newscaster always wore the ugly brown tie.
Dinosaurs roamed the earth for millions of years.
Everyone loved the planted gardenias bordering the park.
The woman thanked the academy for the award.
Hundreds of normal people like liver and onions.
The southern states flooded during the rainy season.
Fido usually buried his bone under the fence.
Joanne lounged in the comfortable chair after work.
The girl kept a journal of her adventures.
The clock struck at a quarter after the hour.
The palm trees softly swayed in the wind.
The horses galloped quickly through the open field.
The old friends visit the pool hall weekly.
The picture frame broke during the small earthquake
The secretary bought four boxes of typing paper.
The fisherman carried his tackle box with him.
The caller hung up after waiting 30 minutes.
Volleyball players need kneepads to avoid knee injuries.
The sailor disliked Bobby for his unorthodox beliefs.
Making brownies for friends pleases even strict dieters
Scientists recommend washing your hands throughout the day.
Temperatures in Tucson often reach stifling triple digits.
Seafood restaurants serve the freshest fish and shrimp.
Local artists sell their pieces at national galleries.
Sarah confronted the man at the butcher shop.
Boxes of presents arrived for the new baby.
Pine trees always drop pine needles and cones.
My mother said to pick up my room.
The rabbit lost the race to the turtle.
The coffee table belonged to the owner's grandfather.
Some people like household jobs on boring weekends.
The people ordered 5 hamburgers with French fries.
The athlete proudly boarded a plane to Sydney.
Janice likes to watch football on Sunday afternoons.
The detective accused the captain of the murder.
The chocolate addict thanked the candy storeowner.
The clothesline flapped during the stormy evening weather.
Bill admired the violinist in the Boston symphony.
The teacher persuaded the principal to promote her.
Don rides his bicycle to the dentist's office.
The infant sleeps on the old yellow crib.

Every morning the lady reads trendy fashion magazines.
The policeman chased the burglar on the roof.
The rookie player hit a grand slam homerun.
The truck driver retired after driving many miles.
The candidates debated the issues on network tv.
The cross hung above the door at the church.
The coach called the play in the game.
Hillary argued the case to the chief executives.
The capital building sits on north Pennsylvania Avenue.
Traditional Irish pubs appeal to most foreign travelers.
Hockey players wear lots of heavy protective gear.
The car salesman guaranteed the car's windshield wipers.
Basketball players gather at the gym for practice.
The sale tag claimed fifty percent off everything.
The bookshelf held four boxes of books.
The priest dedicated the new building in France.
The fresh popcorn smelled of butter and salt.
Team USA won the first Olympic soccer game.
Late night television lacks deep, academic subject matter.
Fast food restaurants serve lots of fried foods.
Magazines advertise many popular items for the readers.
Tile floors require hours of care and maintenance.
The dove ate seed from the bird feeder.
The train pulled into the station at four.
According to myth, broken mirrors bring bad luck.
The flowerpot held many beautiful small flowers.
The water in the ocean glistens in moonlight.
The loyal dog happily wagged his furry tail.
The shy child smiled at the funny clown.
Angry travelers blame the airlines for frequent delays.
Only Marsha knew the man at the hotel.
The little boy carefully jumped on the trampoline.
The gentleman insisted on paying for the dinner.
The nurse baked cupcakes for the children's ward.
The car company hid information about the tires.
Beach volleyball joined the Olympics in Atlanta.
Very tall people avoid hitting their heads.
The stock market depends on other people's money.
Dedicated athletes work so hard for their achievements.
Beach goers fly colorful kites on windy days.
The landscaper trimmed the trees along the house.
The family displayed the portrait in the foyer.

Yoga relaxes even the most uptight tense people.
Coffee lovers brew tons of beans every day.
The liberal physician saved the injured man's legs.
The maid swept the patio in the backyard.
The cyclist found the lost bicycle in town.
The carpenter built the doghouse for Bowser.
The prom queen proudly marched in the parade.

Object Clefts

It was the journalist whom the accomplished surgeon kissed after the successful heart transplant surgery.
It was the pretty actress whom the sitcom producer discovered during the annual talent search.
It was the sincere toddler whom the preschool teacher believed with absolute certainty and faith.
It was the chef whom the housewife coerced into baking the four-tier wedding cake.
It was the chocolate milkshake that the cheerleader recommended to the varsity squad of twenty.
It was the physician's orders that the author ignored after the malpractice suit last month.
It was the photograph of her father that the girl treasured most in her scrapbook.
It was the bank teller whom the caterer reported to the police for stealing pastries.
It was the prison inmate whom the producer cast in the film about dysfunctional families.
It was the photographer whom the tenant noticed near the garbage of the actress.
It was the volunteer whom the yearbook student photographed at the seventy-fifth crafts fair.
It was the scary monster that the youngster imagined in the dark closet last night.
It was the guitar player whom the disc jockey remembered from chilhood days in Montana.
It was the grimacing woman whom the naughty boy kicked during the competitive soccer game.
It was the lottery prizewinner whom the manager announced in front of the crowd
It was the reporter whom the lawyer pushed down the stairs for writing the article.
It was the music-loving teenager whom the tenant asked to turn off the music.
It was the bakery worker whom the food critic chastised on her weekly talk show.
It was the computer that the clerk hit for incorrectly tallying the days total sales.
It was the graduate student whom the national philanthropy awarded a scholarship last year.

It was the graduate student from Psychology class that the coach drafted on the team.
It was the millionaire whom the young sailor envied after losing money in the Bahamas.
It was the professor whom the dentist lectured on good oral hygiene after the visit.
It was the aspiring architect's cake that the well-known baker judged in the contest.
It was the restless father whom the physician admitted for further examination late one night.
It was the Indians whom the cowboy tricked by hiding in the valley over night.
It was the columnist whom the pupil praised for honesty and outstanding service to the community.
It was Dan whom the wealthy man rented a room in the mansion on Broadway.
It was the friendly operator whom the cheap customer called to complain about his bill.
It was the fireman whom the little girl tripped on his way to the building.
It was the gymnast whom the professor considered for a role in the Italian documentary.
It was the silly spokeswoman whom the Russian people despised following the last British summit.
It was the interpreter whom John recruited after the mishap in the library that afternoon.
It was the fisherman whom the bishop blamed for the destruction of the ocean ecology.
It was the fiancé whom the family minister interviewed for two hours before the wedding.
It was the five-dollar parakeet at the pet store that the boy wanted incessantly.
It was the trendy fashion designer that the magazine writer profiled in the March issue.
It was the local grocer that the thief telephoned early in the afternoon last week.
It was the warden whom the inmate suspected in the escape of the convicted molester.
It was the shoe by the door that the postman accidentally kicked into the bushes.
It was the parrot from Africa that the maid hated for its loud, obnoxious cackling.
It was the former political activist whom the reporter covered in the special Sunday column.
It was the impoverished gardener whom the landowner willed all of his worldly possessions.
It was the director of transportation whom the cab driver heard over the shop intercom.
It was the colonel whom the orphan followed back to the very secure army base.
It was the hyperactive monkey that the lazy elephant watched from its pen most days.

It was the traveling medical doctors that the villagers trusted for good products and potions.
It was the postman whom the unleashed dog chased down the street four times weekly.
It was the cheerleader Natasha whom Colin favored at the high school dance on Friday.
It was the fifth chair violin that the principal asked to play a solo tonight.
It was the sculptor at the museum whom the child chose as a role model.
It was the patient with lung cancer whom the transplant counselor remembered during the ceremony.
It was the debut album that the new heavy metal band advertised on the Internet.
It was a terrible tornado that the town blamed for the extinction of the beaver.
It was the painting from the gallery that the woman hung in the dining room
It was the childproof knife that the man used to cut the Halloween pumpkin.
It was the Bach sonata that the renowned soprano performed after the annual celebrity dinner.
It was the mechanic at the dealership whom the van owner thanked for his honesty.
It was the raskly rabbit that Elmer Fudd hunted after years of frustration at home.
It was the nurse from the healthcare agency that the family thanked for Joan's care.
It was the poker player that the sheriff found counting his money behind the bar.
It was the defendant whom the jurors feared throughout the trial for the double murder.
It was the institute for tribal history that the public relations expert approached for donations.
It was the stunt motorcyclist whom the commentator followed during the tv special on daredevils.
It was the blue paddleboat that the people rode around the lake in Boston.
It was a herd of camels that the caravan used to travel across the desert.
It was the new editor that the author despised for the rejection of the dissertation.
It was the videotape that the store manager reviewed after the break-in last evening.
It was the bargain shopper whom the salesman convinced to buy the broken alarm clock.
It was the feminist that the retirees feared for supporting laws against medical prescription coverage.
It was the old sedan that the owner restored to enter the antique car show.
It was the heart surgeon whom the patient sued for accidentally removing the wrong organ.
It was the rowing crew that the chancellor honored at the graduation dinner on Tuesday.
It was the ski instructor from Utah whom the beginning skier requested at the lodge.
It was the comic whom the director cast for the hunchback role in the story.

It was the housewife whom the butler thanked for allowing double the vacation time.
It was the well-known laundry service that the maid recommended to the new parents.
It was the bride whom the best man knew from class at the preparatory school.
It was the painter from Spain whom the art historians studied at the local museum.
It was the ceiling at the famous cathedral that the construction crew restored last month.

Object Relatives

The busboy pocketed the rare coins that the secretary had left on the small plate.
The editor proofread the conditions that Mary stipulated in a meeting with the executive branch.
The reporter interviewed the friendly talk show host who the public watched for many years.
The crazed fan adored the lead singer who the bodyguards protected before and after concerts.
The small town enjoyed the light snowstorm that the weatherman predicted using fancy new equipment.
The blue jay saw the nest that the woman saved from the wild fire in Wyoming.
The witch saw the map that the wizard buried near town before sunrise that morning.
The lawyer represented the defendant who the witness said was walking at the crime scene.
The pit bull bit the therapist whom the journalist accused of malpractice near the medical complex.
The gentleman bought the crib that the craftsman made in the spacious and expensive workshop.
The principal hired the teacher whom the students admired for her community work with children.
The gypsy feared the hurricane that the fortuneteller predicted near the coast of the Carolinas
The pilot crashed in the terrible blizzard that the weather center warned the town about.
The truck driver delivered the eggs that the farmer collected from the hen house this morning.
The homeless man slept on the couch that the landlord threw into the street.
The forester punished the gang of kids that the camper blamed for the devastating fire.

The nice gentleman bought the guest book that the attendants signed before the wedding ceremony.
The neighbor thanked the gardener whom the lady employed after hard work in the yard.
The fireman investigated the corner house that the earthquake destroyed after the long hard winter.
The gallery showcased the artist who the foreigner knew from the pictures of war victims.
The rich shopper insulted the salesperson that the department store later fired for extreme tardiness.
Many women tried the low fat diets of the 80s that scientists proved didn't work.
The president granted the freedom that the people demanded at the rally in Washington DC.
The woman bought furniture at the estate sale that the family held after the funeral.
The farmer exclusively grew the corn that the farm stand sold in less than an hour.
The mayor honored the fire department volunteers who the homeowners valued for dedication and courage.
The rude Eskimo bothered the conservationist whom the kind doctor praised at the charity event.
The family saw the Tony award winning comedy that the New York Times recommended highly.
The queen hired the interior designer that the prince later married at the grand palace.
The visitor feared the ghosts that the psychic sensed around the house in the forest.
The clerk skillfully transcribed the name of the intruder that Henry stated to the jury.
The fan saw the guitar pick that the absent-minded drummer lost before the rehearsal.
The reporter interviewed the thief that the dancer accused of burglary in the town square.
The famous equestrian rode the prize-winning thoroughbred that the housekeeper brushed in the garage.
The squirrel chased the butterfly that the energetic beagle barked at as he trotted along.
The ranger found the hunter that the huge blizzard buried in the national park yesterday.
The coach dismissed the young soccer player who his assistant reported for missing several practices.
The couple adopted the healthy Russian newborn that John found in an orphanage in Moscow.
The responsible babysitter hugged the crying toddler whom the boy pushed on the playground.

The children hated the brat that the principal frequently called to his office at school.
The police arrested the man that the neighbor saw sneaking out of the house yesterday.
The careless employee knocked over the hot chocolate that the crafty secretary made from scratch.
The scientists watched the comet that the research institute named after the famous Russian astronomer.
The couple liked the elegant room that the contractor finished in the newly renovated apartment.
The assistant hid the package that John noticed in the conference area earlier this morning.
The passengers adored the giddy stewardess who the head manager promoted after the transport crisis.
The bartender cleaned the tavern where the college students held the homecoming party last night.
The professor found the mall that the author visited while in town for the conference.
The lit candle sat on the table that the piano vibrated during Beethoven's fifth concerto.
The campus cheered for the soccer team that the announcer named at the national tournament.
The speech therapist retired from the high school that the stutterer attended for four years.
The visitor asked for the Spanish-speaking waitress that the oriental chef used for interpreting.
The students liked the professor that the university fired after the scandal in the math department.
The guitarists envied the famous songwriter that the academy awarded a Grammy for Best Song.
The mechanic removed the part that the manufacturer sold as brand new later that day.
The woman set the table that the devoted husband bought in preparation for the guests.
The Olympic committee suspected the swimmer whom the Chinese accused of cheating during the race.
Benedict Arnold was the traitor whom the New England colonists accused of blasphemous crimes.
The tennis player lost the match that the media advertised repeatedly on prime time tv.
The judge sentenced the criminal whom the public recognized from the wanted posters in town.

The cheerleader dated the basketball player whom Chicago signed for a multi-million dollar contract.
The commander relied on the anxious military officer whom the general blamed for the war.
The actor wore the leopard pants that the fashion designer made for the awards ceremony.
Suzanne owned the canary diamond that the auctioneer appraised at three times the original price.
Michael adored the puppy that the pet storeowner found at the certified breeder's dog show.
The small porcelain figure fell from the shelf that the movers lifted into the truck.
The technician washed the tweezers that Jacob left on the counter in the casting department.
The music teacher loved the children whom the parents brought to the institute after school.
The actor whom the modeling agency had fired two years ago played superman.
The bandleader stepped on the sprinkler that the city installed on the football field.
The gentleman phoned the ticket master that the paper listed in the entertainment section on Saturday.
The patient stayed at the hospital that the soap opera used for its dramatic scenes.
The retirement home resident spoke about the movies that Charlie Chaplin created in the silent era.
The giraffe ran from the orangutan that the zookeeper accidentally freed from the cage.
The neighbor heard the Scottish terrier that the elderly woman walked every morning at 5.
The magician saw the rabbit that his assistant chased after the hat trick failed miserably.
The toy store donated the new toys that the marines gave to children at Christmas.
The teacher found the child's homework that the dog reportedly ate at home last night.

APPENDIX C

Percent correct and Reaction Time data for in Experiment 1.

	Simple		Compressed Simple		Complex		Compressed Complex	
Subject	% correct	RT (SD)	% correct	RT (SD)	% correct	RT (SD)	% correct	RT (SD)
1	100	1029 (236)	100	1002 (197)	93	1207 (303)	96	1237 (341)
2	99	1390 (436)	95	1342 (380)	96	1510 (567)	95	1560 (519)
3	100	2092 (699)	100	2403 (896)	91	2554 (742)	82	2598 (892)
4*	98	1682 (443)	97	1435 (306)	87	2147 (604)	93	2024 (667)
5*	99	1534 (508)	98	1466 (332)	92	1816 (607)	90	1831 (544)
6*	99	1572 (296)	97	1452 (278)	93	2086 (514)	81	1957 (518)
7*	94	1144 (176)	100	1105 (202)	89	1429 (270)	91	1481 (315)
8	92	1622 (306)	93	1524 (231)	82	1832 (379)	62	1659 (406)
9*	99	1505 (351)	100	1613 (402)	91	1768 (480)	89	1811 (555)
10	98	1486 (364)	95	1344 (352)	72	1761 (584)	71	1538 (353)
11*	99	1527 (288)	100	1492 (264)	89	1875 (539)	96	1999 (533)
12	88	969 (243)	77	907 (241)	62	1173 (383)	56	1111 (282)
13	98	1487 (400)	98	1320 (290)	93	2005 (553)	80	1872 (514)
14	99	1727 (385)	87	1562 (367)	74	1945 (529)	69	2153 (448)
15*	98	1689 (472)	98	1568 (362)	93	1751 (518)	88	1711 (455)
16*	100	1315 (279)	95	1273 (271)	84	1384 (329)	87	1455 (268)
17	97	1546 (412)	100	1462 (436)	90	2088 (563)	74	2160 (743)
18	97	1595 (475)	100	1566 (417)	96	1762 (532)	88	1652 (385)
19	96	1367 (288)	95	1316 (222)	81	1604 (343)	91	1524 (351)
20*	97	1295 (243)	98	1304 (226)	95	1612 (346)	87	1712 (394)
Mean	97		95		86		82	

* Subjects participating in Experiment 2

APPENDIX D

Performance on the Test Of Nonverbal Intelligence-3 and Listening Span Test.

Subject	TONI-3 Raw Score	TONI-3 Quotient *	TONI-3 Percentile Rank	Listening Span – Total Words	Listening Span - Questions	Listening Span Test**
1	41	125	95	87	67	4.5
2	38	113	81	79	58	4.5
3	41	125	95	68	100	4
4	39	115	84	85	N/a	5
5	41	125	95	80	78	5
6	40	119	90	81	89	4.5
7	26	93	32	79	75	4.5
8	36	110	74	57	100	3.5
9	39	115	84	76	67	5
10	21	84	14	61	78	3.5
11	23	88	14	75	67	3.5
12	39	115	84	66	78	4
13	41	125	95	78	75	5
14	42	130	98	79	67	4.5
15	42	130	98	67	89	4
16	42	130	98	84	83	5
17	26	93	32	72	67	4.5
18	44	140	99	62	89	3.5
19	35	108	70	86	100	5
20	40	119	90	88	83	5

*Normal performance is a Quotient of 100 ± 15 (SD) = 85-115.

**Average performance for normal subjects on the Reading Span Test is 3.5 (Just & Carpenter, 1992).

APPENDIX E

Correlation coefficients (significance) for the relations between the TONI-3 and LST and experimental variables.

Variable	TONI-3 Quotient	LST Total Words	LST Questions	LST Score
PI Compressed Simple	-.127 (.594)	-.134 (.573)	.381 (.108)	-.167 (.482)
PI Complex	-.021 (.931)	-.208 (.378)	-.146 (.552)	-.119 (.618)
PI Compressed Complex	-.204 (.389)	.103 (.665)	-.142 (.562)	.153 (.518)
AI2 Complex	.016 (.947)	.438 (.053)	.064 (.794)	.436 (.055)
AI2 Compressed Complex	-.114 (.633)	.190 (.422)	-.319 (.183)	.392 (.087)
AI3 Complex	-.048 (.840)	.102 (.668)	-.381 (.107)	.049 (.838)
AI3 Compressed Complex	.075 (.752)	.406 (.075)	-.211 (.387)	.340 (.143)

APPENDIX F

Percent correct performance and Reaction Time data for each subject by condition in Experiment 2.

	Simple		Compressed Simple		Complex		Compressed Complex	
Subject	% correct	RT (SD)	% correct	RT (SD)	% correct	RT (SD)	% correct	RT (SD)
4	95	1863 (493)	93	1917 (471)	85	2208 (610)	82	2441 (628)
5	95	1893 (533)	100	2016 (573)	90	2212 (658)	78	2407 (553)
6	96	1964 (414)	100	1946 (493)	89	2201 (490)	80	2441 (540)
7	95	1696 (363)	100	1812 (467)	79	2019 (510)	82	2180 (502)
9	98	1754 (518)	100	1965 (498)	97	1989 (559)	81	2206 (700)
11	96	1468 (306)	89	1523 (373)	76	1725 (602)	76	1790 (463)
15	88	1655 (561)	98	1655 (506)	98	1532 (356)	78	1784 (473)
16	96	1337 (281)	95	1489 (224)	91	1474 (314)	80	1642 (310)
20	94	1479 (390)	100	1458 (304)	89	1792 (487)	79	1757 (412)
Mean	95		97		88		80	

APPENDIX I

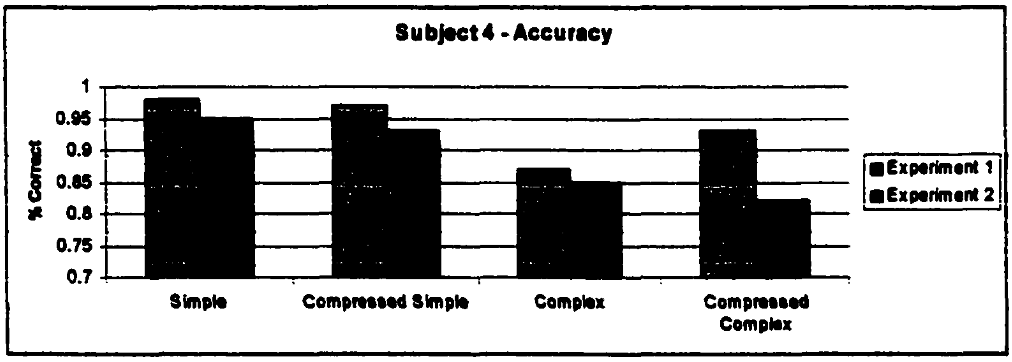
Detailed descriptions of each subject's performance in Experiment 2.

Subject 4 (male, 35 years old)

Accuracy

Accuracy for Subject 4 was slightly lower in Experiment 2 than in 1, particularly for the Compressed Complex Condition (Figure 7). In Experiment 1, he was more accurate for the Compressed Complex than in the Complex Condition, but this was not true in Experiment 2, where a gradual decline in accuracy with increasing complexity was observed.

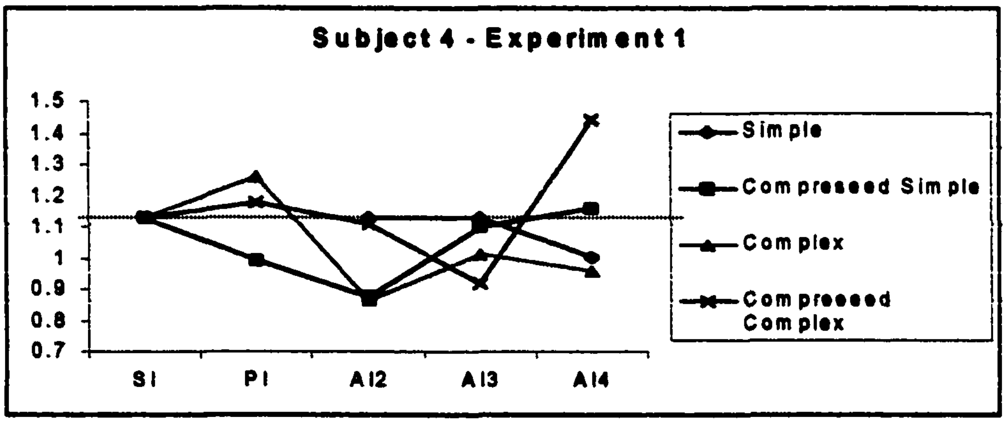
Figure 10. Accuracy for Subject 4 across experiments.



Reaction Time (RT)

For the RT indices, Subject 4 was highly variable in Experiment 1 and showed little stability in the Simple Condition (SI = 1.13; recall SI = 1.0 reflects perfect stability). This subject was perturbed in the Complex Condition (PI = 1.26) and adapted in a pattern similar to mean data reported above. However, in the Compressed Complex Condition, Subject 4 was only slightly perturbed (as indicated by the PI relative to the SI; PI = 1.18), and then adapted across items two and three. Interestingly, he then appeared perturbed for item four, suggesting he was never able to maintain a stable state. Increases in the AI also were observed for items three and four in the Compressed Simple Condition, though these values hovered around the SI (see Figure 8).

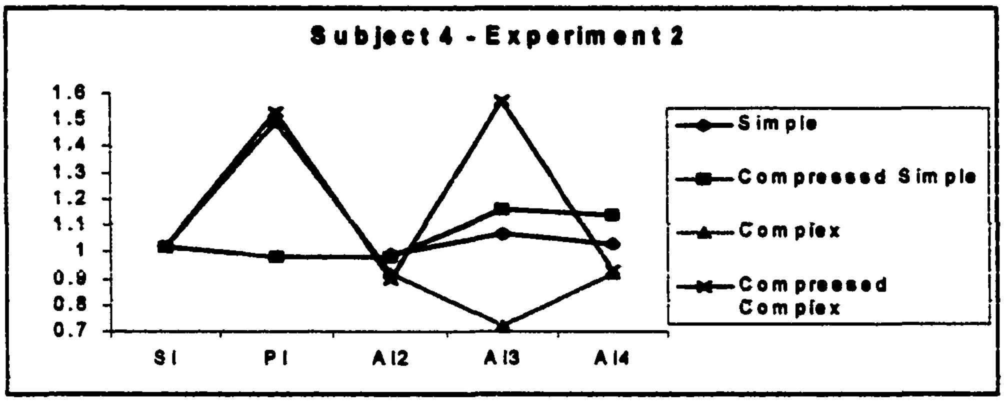
Figure 11. Stability, Perturbation, and Adaptation Indices for Subject 4 in Experiment 1.



---------------- Indicates level of stability.

In Experiment 2, Subject 4 was more stable in the Simple Condition (SI = 1.02), than in Experiment 1. Performance for the Compressed Simple Condition also appeared relatively stable (AIs ranged from .99 to 1.07). He demonstrated clear perturbation during both the Complex (PI = 1.49) and Compressed Complex (PI = 1.53) Conditions. In the Complex Condition Subject 4 adapted to perturbation. An interesting performance pattern was seen in the Compressed Complex. Specifically, the AI for the third items in the Compressed Complex blocks were at the level of that observed for the PI (Figure 9). These data suggest that Subject 4 never fully adapted to perturbation in the Compressed Complex condition in either Experiment.

Figure 12. Stability, Perturbation, and Adaptation Indices for Subject 4 in Experiment 2.



Imaging Data

Subject 4 had fewer regions showing activation than all other subjects (see Table 16). Of the regions hypothesized to be active, only the middle and superior temporal, middle frontal, and superior frontal regions showed activation for this subject.

In the Compressed Simple Condition, increases in intensity greater than 30% above Baseline in both perturbation and adaptation blocks in the right middle frontal gyrus, and the left and right superior temporal gyri were observed (i.e., the region was active during the condition regardless of block type). Increases of this magnitude were not seen in any region only for the perturbation blocks. For the adaptation blocks only, increases in intensity were observed in the right middle temporal gyrus and the left occipital lobe. No large differences between intensities of perturbation versus adaptation blocks (indicating that a region may be solely involved in one or the other process) were observed in this condition.

For the Complex Condition, a large increase in intensities for both the perturbation and adaptation blocks was observed for the left superior temporal gyrus. The only region showing a greater than 30% increase only in the perturbation blocks was the right lateral superior frontal gyrus (mean change = 36%). The only one showing an increase only in the adaptation blocks was the left fusiform gyrus (mean change = 63%). Large differences in intensities between perturbation and adaptation blocks were observed for a few regions in the Complex Condition. The only region showing much larger intensity changes in the perturbation blocks than in the adaptation blocks was the right lateral superior frontal gyrus (mean change for perturbation blocks = 36%; mean change for adaptation blocks = 1%; difference = 34%). Regions with much higher intensities during the adaptation blocks than the perturbation blocks in this condition were: the left superior temporal gyrus (perturbation = 33%; adaptation = 65%; difference = 32%), the right middle frontal gyrus (mean change for perturbation blocks = -

76%; mean change for adaptation blocks = 28%; difference = 104%), and the left fusiform gyrus (mean change for perturbation blocks = 9%; mean change for adaptation blocks = 63%; difference = 54%).

In the Compressed Complex Condition, the only regions for which an increase in intensity was greater than 30% above Baseline were the left and right superior temporal gyri. On the left, this increase was only in the adaptation blocks. On the right, the increase was evident in both block types. Regions in which a large difference existed between the perturbation and adaptation blocks included:

1. with the perturbation blocks being more intense than the adaptation blocks: the left fusiform gyrus (mean change for perturbation blocks = 27%; mean change for adaptation blocks = -33%; difference = 60%)
2. with the adaptation blocks being more intense than the perturbation blocks: the left middle temporal gyrus (mean change for perturbation blocks = -19%; mean change for adaptation blocks = 15%; difference = 34%) and the left superior temporal gyrus (mean change for perturbation blocks = 17%; mean change for adaptation blocks = 59%; difference = 42%).

Table 17. Regions showing greater than 30% intensity change for each condition for Subject 4.

Region	Compressed Simple		Complex		Compressed Complex	
	Left	Right	Left	Right	Left	Right
Middle Temporal Gyrus (P)						
Middle Temporal Gyrus (A)		*				
Superior Temporal Gyrus (P)	*	*	*			*
Superior Temporal Gyrus (A)	*	*	*		*	*
Middle Frontal Gyrus (P)		*				
Middle Frontal Gyrus (A)		*				
Superior Frontal Gyrus, Lateral (P)				*		*
Superior Frontal Gyrus, Lateral (A)						
Fusiform Gyrus (P)						
Fusiform Gyrus (A)			*			
Occipital Lobe (P)						
Occipital Lobe (A)	*					

Summary

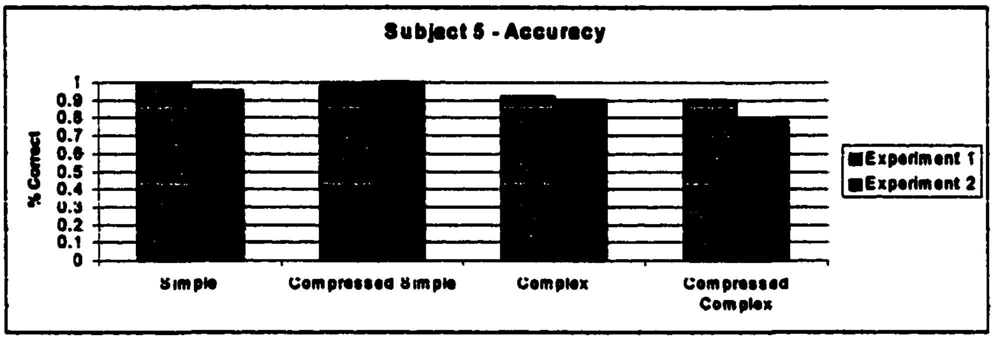
Because the only clear pattern of behavioral performance in Experiment 2 for Subject 4 was perturbation and adaptation in the Complex Condition, it would be hypothesized that regions involved in this condition would show increases in activation during perturbation and reductions with adaptation. The only region showing this pattern was the lateral aspect of the right superior frontal gyrus. Conversely, because Subject 4 adapted to being perturbed in this condition, some regions may be involved exclusively for the adaptive process and therefore would show increases in activation only in the adaptation blocks. This pattern was found for the left superior temporal gyrus, the right middle frontal gyrus, and the left fusiform gyrus.

Subject 5 (female, 20 years old)

Accuracy

Similar accuracy data were observed for Subject 5 in both experiments (Figure 10).

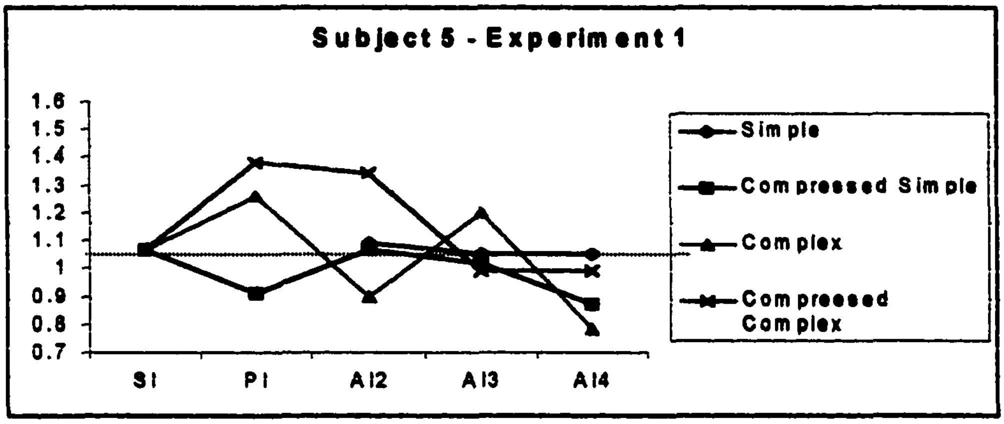
Figure 13. Accuracy for Subject 5 across experiments.



Reaction Time Indices

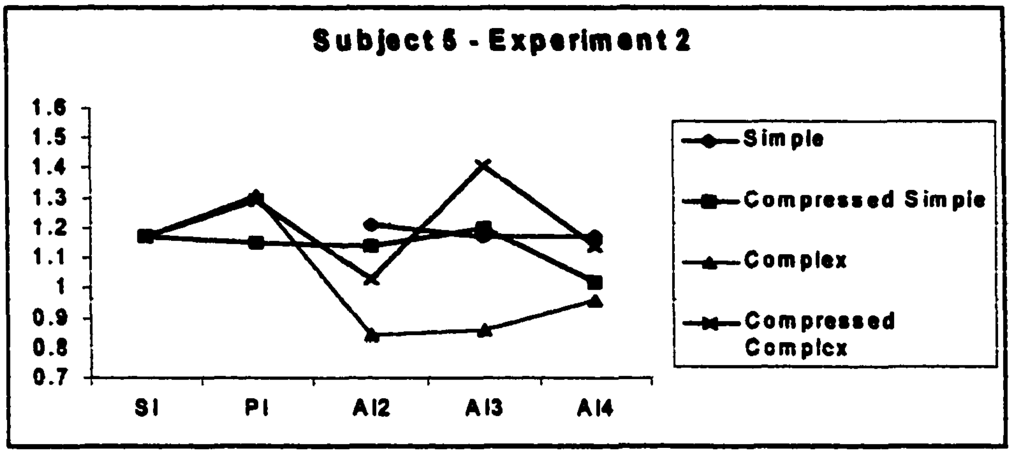
Subject 5 was relatively stable in Experiment 1, as evidenced by the SI (1.07) and the little variation in the AIs for this condition (see Figure 11). Stable performance also was seen in the Compressed Simple Condition. This subject was perturbed in the Complex (PI = 1.26) and Compressed Complex (PI = 1.38) Conditions. In the Complex Condition, she did not adapt as the AI increased back to the level of the PI for item three. In the Compressed Complex condition, she adapted by item three.

Figure 14. Stability, Perturbation, and Adaptation Indices for Subject 5 in Experiment 1.



In Experiment 2, Subject 5 was less stable than in Experiment 1 (SI = 1.17). However the AIs in Experiment 2 for the Simple Conditions did not greatly differ between experiments (Figure 12). Performance in the Compressed Simple Condition was stable, but AI4 dropped. She was perturbed in the Complex (PI = 1.31) and Compressed Complex (PI = 1.29) Conditions, but only adapted in the Complex Condition. In the Compressed Complex, AIs remained high for item three and no adaptive pattern was evident.

Figure 15. Stability, Perturbation, and Adaptation Indices for Subject 5 in Experiment 2.



Imaging Data

Subject 5 showed activation (often bilateral) in several brain regions. These regions included the hypothesized temporal, frontal, and parietal regions with the addition of the thalamus (Table 17). For the Compressed Simple Condition, only the left medial superior frontal gyrus showed increases in intensity of greater than 30% for both the perturbation and adaptation blocks. All other regions that showed large increases in intensity did so only in the adaptation blocks. These regions included: the right superior temporal gyrus, the left and right angular gyri, the right supramarginal gyrus, the left and right fusiform gyri, the left and right occipital lobes, and the left thalamus. Regions in which a large difference was observed between the perturbation and adaptation blocks also showed this difference with the adaptation blocks showing much higher intensities than the perturbation blocks. These regions included:

1. the right superior temporal gyrus (mean change for perturbation blocks = -5%; mean change for adaptation blocks = 34%; difference = 39%)
2. the right supramarginal gyrus (mean change for perturbation blocks = -25%; mean change for adaptation blocks = 34%; difference = 60%)
3. the left fusiform gyrus (mean change for perturbation blocks = -31%; mean change for adaptation blocks = 34%; difference = 65%)
4. the left thalamus (mean change for perturbation blocks = -10%; mean change for adaptation blocks = 37%; difference = 47%).

For the Complex Condition, a few regions increased in intensity across block types indicating that they were globally involved for this condition. Those included: the left middle temporal gyrus, the right superior temporal gyrus, the right middle frontal gyrus, the left medial superior frontal gyrus, and the left thalamus. No regions showed increased intensities solely in the perturbation blocks. Several regions had substantial increases in intensity only in the adaptation blocks. They were: the left superior temporal gyrus, the left middle frontal gyrus, the left and right lateral superior frontal gyri, the right medial superior frontal gyrus, the left supramarginal gyrus, the left superior parietal lobule, the left and right cerebellum, the left and right fusiform gyri, and the right occipital lobe. Large differences were measured between in the intensities of the perturbation and adaptation blocks in a few regions and in all the intensities were higher in the adaptation blocks. They were:

1. the right middle temporal gyrus (mean change for perturbation blocks = -36%; mean change for adaptation blocks = 21%; difference = 57%)
2. the left lateral superior frontal gyrus (mean change for perturbation blocks = -4%; mean change for adaptation blocks = 36%; difference = 40%)
3. the right lateral superior frontal gyrus (mean change for perturbation blocks = 3%; mean change for adaptation blocks = 51%; difference = 48%)
4. the right medial superior frontal gyrus (mean change for perturbation blocks = 2%; mean change for adaptation blocks = 33%; difference = 31%)
5. the right cerebellum (mean change for perturbation blocks = -4%; mean change for adaptation blocks = 42%; difference = 46%)
6. the right fusiform gyrus (mean change for perturbation blocks = -14%; mean change for adaptation blocks = 44%; difference = 58%)
7. the right occipital lobe (mean change for perturbation blocks = 10%; mean change for adaptation blocks = 41%; difference = 31%)

In the Compressed Complex Condition, all regions that were active had increased intensities in both the perturbation and adaptation blocks with little difference between the two (see Table 17). The only exception was the left

Table 18. Regions showing greater than 30% percent intensity change for each condition for Subject 5.

Region	Compressed Simple		Complex		Compressed Complex	
	Left	Right	Left	Right	Left	Right
Middle Temporal Gyrus (P)			*		*	
Middle Temporal Gyrus (A)			*		*	
Superior Temporal Gyrus (P)				*	*	*
Superior Temporal Gyrus (A)		*	*	*	*	*
Middle Frontal Gyrus (P)				*	*	*
Middle Frontal Gyrus (A)			*	*	*	*
Superior Frontal Gyrus, Lateral (P)					*	*
Superior Frontal Gyrus, Lateral (A)			*	*	*	*
Superior Frontal Gyrus, Medial (P)	*		*		*	
Superior Frontal Gyrus, Medial (A)	*		*	*	*	
Angular Gyrus (P)						
Angular Gyrus (A)	*	*				
Supramarginal Gyrus (P)					*	*
Supramarginal Gyrus (A)		*	*		*	*
Superior Parietal Lobule (P)						
Superior Parietal Lobule (A)			*			
Cerebellum (P)					*	*
Cerebellum (A)			*	*	*	*
Fusiform Gyrus (P)					*	*
Fusiform Gyrus (A)	*	*	*	*	*	*
Occipital Lobe (P)						
Occipital Lobe (A)	*	*		*		*
Thalamus (P)			*			
Thalamus (A)	*		*		*	

Note: P = Perturbation Blocks; A = Adaptation Blocks

thalamus in which the only substantial (greater than 30%) increase in intensity was in the adaptation blocks. These data suggest that all of these regions were needed for Subject 5 to perform the task at this high level of complexity and that, like her behavioral data suggested, no regions appeared to be involved solely in perturbation or adaptation.

Summary

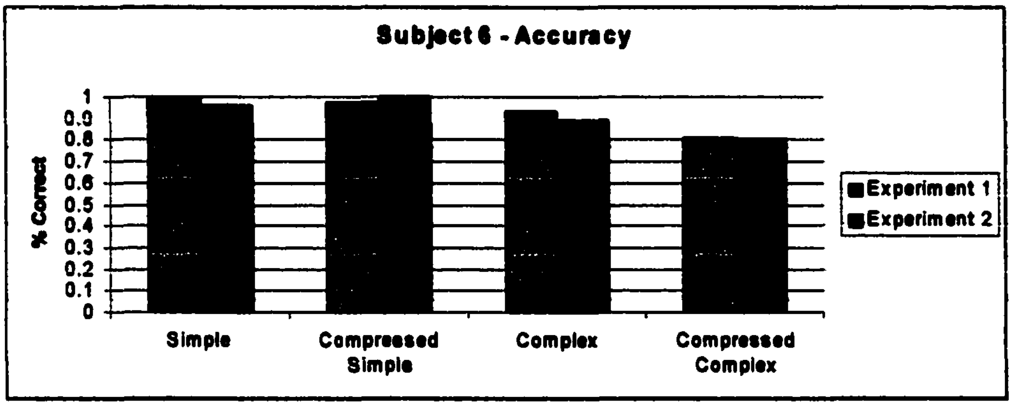
Subject 5 was perturbed in the Complex and Compressed Complex Conditions in Experiments 1 and 2. She adapted to being perturbed in the Complex Condition, but did not do so in the Compressed Complex Condition. The expected brain-behavior relation would be for areas associated with the Complex Condition to show increases in the perturbation blocks with subsequent decreases in the adaptation blocks. Or, some regions associated with adaptation would be more active during adaptation than the perturbation blocks. The latter trend held true for Subject 5. Regions that appeared more active during adaptation included the hypothesized temporal and frontal regions as well as the cerebellum, fusiform gyri, and the occipital lobe. For the Compressed Complex Condition, increases in intensity were hypothesized during the perturbation blocks. However, no regions showed increased intensities specific to perturbation or adaptation (see Table 17). Rather, regions involved in the task were equally intense in both block types.

Subject 6 (female, 35 years old)

Accuracy

Subject 6's accuracy between Experiments was similar (Figure 13). A decline in accuracy as the task became more complex was observed.

Figure 16. Accuracy for Subject 6 across experiments.



Reaction Time

Subject 6 was stable in Experiment 1 (SI = 1.03), but showed higher RT indices to the second items in those blocks than for the other items (AI2 = 1.09; see Figure 14). She was perturbed in the Complex (PI = 1.25) and Compressed Complex (PI = 1.22) Conditions. In the Complex Condition, she did not adapt until AI4. In the Compressed Complex Condition, it was not clear that she ever truly adapted, though AI3 (mean = .93) did drop to the level of stability.

In Experiment 2, Subject 6 was stable (SI = 1.01) and the AIs remained consistent in the Simple Condition (AIs ranged from .98 to 1.04; see Figure 15). Performance in the Compressed Simple Condition was interesting in that she was not perturbed, but showed a substantive increase in reaction time indices for items three and four. She was perturbed in the Complex (PI = 1.22) and Compressed

Complex (PI = 1.38) Conditions. However, in this experiment, she adapted in both cases. For the Complex Condition, she did not adapt until AI3. In the Compressed Complex Condition, she adapted by item 2.

Figure 17. Stability, Perturbation, and Adaptation Indices for Subject 6 in Experiment 1.

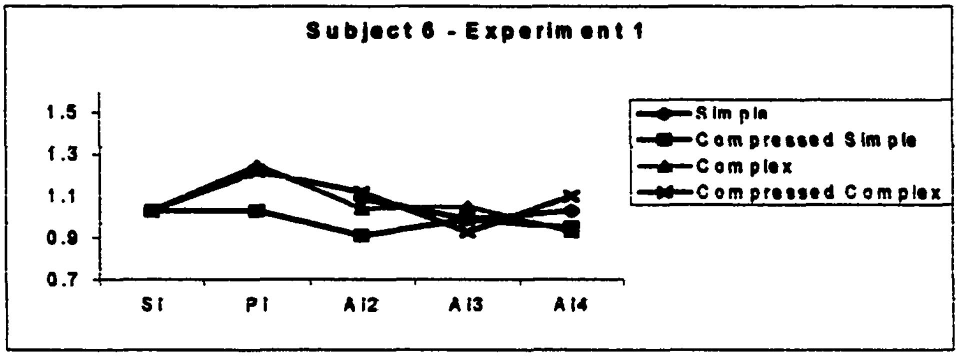
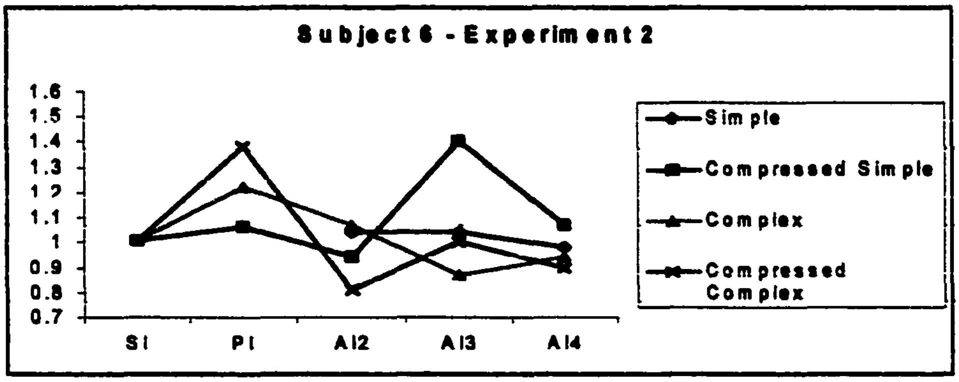


Figure 18. Stability, Perturbation, and Adaptation Indices for Subject 6 in Experiment 2.



Imaging Data

Subject 6 showed increased intensities in all of the hypothesized regions except the superior temporal gyrus (Table 18). In the Compressed Simple Condition, the only regions for which large changes in intensity were observed for both perturbation and adaptation blocks were the left lateral superior frontal gyrus and the left supramarginal gyrus. The only region showing increased intensity only during the perturbation blocks in this condition was the right inferior frontal gyrus. Regions with large increases in intensity during only the adaptation blocks were: the left middle frontal gyrus, the right angular gyrus, the left superior parietal lobule, and the left occipital lobe. The only region for which a large difference existed between perturbation and adaptation blocks was the right angular gyrus (mean change for perturbation blocks = 8%; mean change for adaptation blocks = 49%; difference = 41%).

In the Complex Condition, most regions that were active had increased intensities in both block types (Table 18). The only region with increased intensity only during perturbation blocks was the right middle frontal gyrus. The only region with increased intensity during the adaptation blocks was the right inferior frontal gyrus. No substantial differences between perturbation and adaptation blocks existed in the Complex Condition.

For the Compressed Complex Condition, again active regions had intensities greater than 30% above Baseline during both block types. The fusiform gyri were the only regions showing an increase only during perturbation blocks. During adaptation blocks, the left middle temporal gyrus and the left inferior frontal gyrus showed increased intensities. The fusiform gyri were more intense in the perturbation than the adaptation blocks (left: mean change for perturbation blocks = 48%; mean change for adaptation blocks = -42%; difference = 90%; right: mean change for perturbation blocks = 58%; mean change for adaptation blocks = 26%; difference = 32%). The only region for which higher intensities were found during adaptation than perturbation blocks was the left middle temporal gyrus (mean change for perturbation blocks = 17%; mean change for adaptation blocks = 59%; difference = 42%).

Summary

Subject 6 was perturbed and then adapted in the Complex and Compressed Complex Conditions in both experiments. She was relatively stable in both experiments (SI for Experiment 1 = 1.03; for Experiment 2 = 1.01). However, she showed variable performance as evidenced by increases in RT indicies for both the Simple (particularly in Experiment 1 with an increase in AI2 = 1.09) and the Compressed Simple (particularly in Experiment 2 with an increase in AI2 = 1.40) Conditions. The hypotheses for this subject's brain-behavior relations were as in the other subject, that is, with certain regions showing increased intensity during perturbation blocks, particularly if they are involved with processing more complex information. Other regions may show increased intensities specific to the process

Table 19. Regions showing greater than 30% percent intensity change for each condition for Subject 6.

Region	Compressed Simple		Complex		Compressed Complex	
	Left	Right	Left	Right	Left	Right
Middle Temporal Gyrus (P)			*			
Middle Temporal Gyrus (A)			*		*	
Middle Frontal Gyrus (P)			*	*	*	*
Middle Frontal Gyrus (A)	*		*		*	*
Superior Frontal Gyrus, Lateral (P)	*		*		*	
Superior Frontal Gyrus, Lateral (A)	*		*		*	
Superior Frontal Gyrus, Medial (P)						
Superior Frontal Gyrus, Medial (A)					*	
Angular Gyrus (P)				*		*
Angular Gyrus (A)		*		*		*
Supramarginal Gyrus (P)	*		*		*	
Supramarginal Gyrus (A)	*		*		*	
Superior Parietal Lobule (P)					*	*
Superior Parietal Lobule (A)	*				*	*
Cerebellum (P)						*
Cerebellum (A)						*
Fusiform Gyrus (P)					*	*
Fusiform Gyrus (A)						
Occipital Lobe (P)						*
Occipital Lobe (A)	*					*

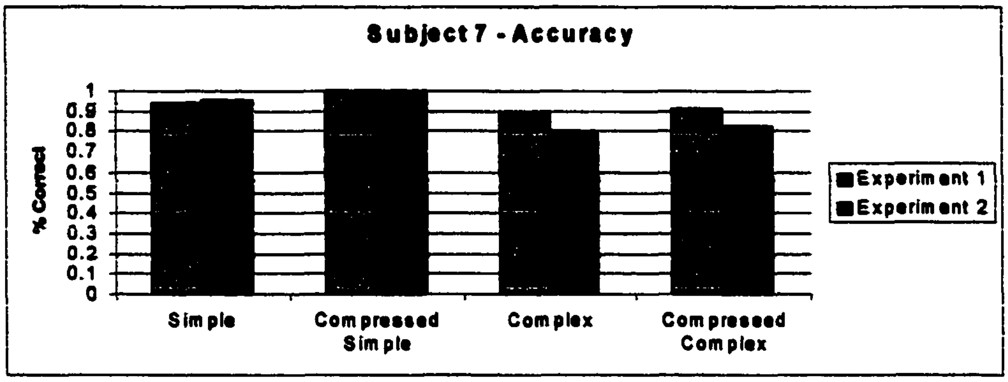
of adaptation and these regions should be observed more so in the adaptation blocks. Most regions, if active during any condition, were active during both block types (Table 18). The regions showing activation only during perturbation blocks in the conditions in which Subject 6 was perturbed were the right middle frontal gyrus and the fusiform gyri. Adaptation blocks for these conditions showed increase the left middle temporal gyrus and the inferior frontal gyri.

Subject 7 (male, 19 years old)

Accuracy

Subject 7 showed a slight decrement in accuracy during Experiment 2 as compared to 1, but only in the more complex conditions (Figure 16). In both conditions, the decrement was less than 15%.

Figure 19. Accuracy for Subject 7 across experiments.

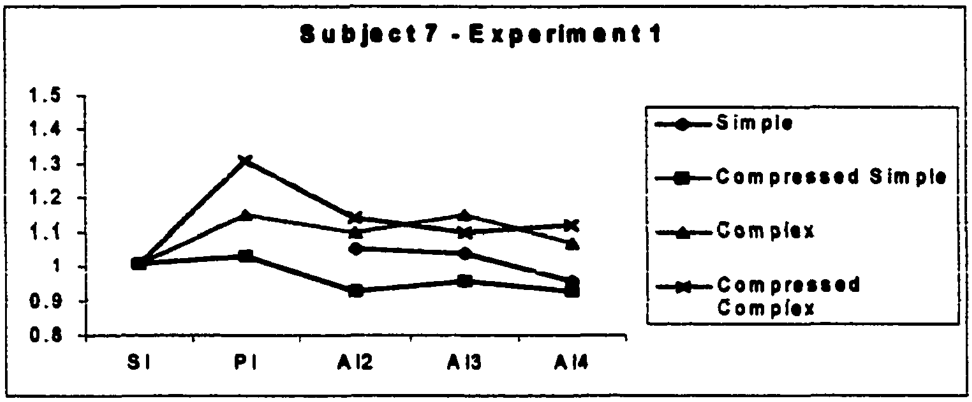


Reaction Time

In Experiment 1, Subject 7 was relatively stable (SI = 1.01), though a slight increase in RTs was observed for AI2 (1.05) and AI3 (1.04) in the Simple Condition (Figure 17). He was not perturbed in the Compressed Simple Condition and remained stable in that condition. He was perturbed in the Complex (PI =

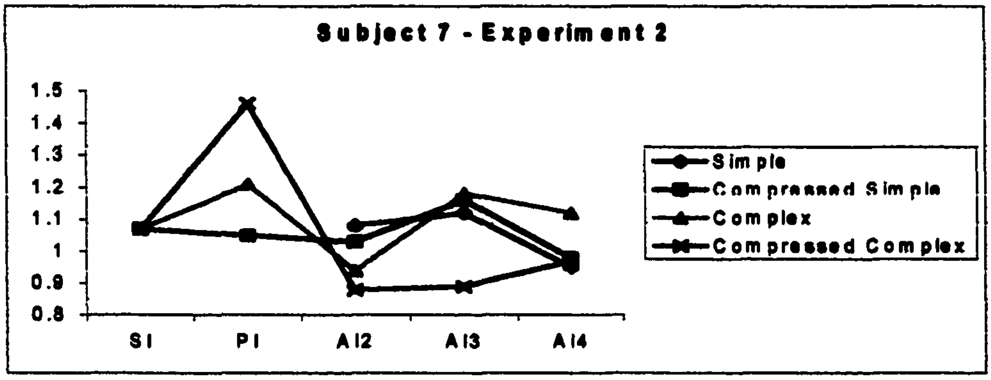
1.15) and Compressed Complex (PI = 1.31) conditions and though he showed adaptation, he never returned to the level of stability in either condition.

Figure 20. Stability, Perturbation, and Adaptation indices for Subject 7 in Experiment 1.



In Experiment 2, Subject 7 was not quite as stable as he had been in Experiment 1 (SI = 1.07), and showed increased RT indicies in both the Simple and Compressed Simple Conditions for item 3 (AI3 Simple = 1.12; AI3 Compressed Simple = 1.16). He was perturbed in the Complex Condition (PI = 1.21), and more so in the Compressed Complex Condition (PI = 1.46; Figure 18). He showed a decrease in the index for item 2 in the Complex Condition, but then an increase for items 3 and 4. For the Compressed Complex Condition, Subject 7 adapted for item 2 and remained stable for items 3 and 4.

Figure 21. Stability, Perturbation, and Adaptation indices for Subject 7 in Experiment 2.



Imaging Data

Subject 7 showed activation in all of the hypothesized regions (Table 19). In the Compressed Simple Condition, regions showing increases of intensity greater than 30% above Baseline in both the perturbation and adaptation blocks were the left middle temporal gyrus, the left superior temporal gyrus, the left inferior frontal gyrus, the left middle frontal gyrus, the left lateral superior frontal gyrus, the left supramarginal gyrus, the left superior parietal lobule, and the right cerebellum. Three regions showed increases only in the perturbation blocks: the right middle frontal gyrus, the left medial superior frontal gyrus, and the right parahippocampus. Regions in which increases were observed only for the adaptation blocks were: the left angular gyrus, the right superior parietal lobule, and the left and right fusiform gyri. Large differences between block types were not found in the Compressed Simple Condition for any region.

For the Complex Condition, the following regions showed substantive increases in intensity across block types: the left and right middle temporal gyri, the right superior temporal gyrus, the left and right middle frontal gyri, the left and right lateral superior frontal gyri, the left medial superior frontal gyrus, and the left supramarginal gyrus. Regions with increased intensities only during the perturbation blocks were: the left superior temporal gyrus, the left middle frontal gyrus, the right hippocampus, and the right parahippocampus. The only region for which an increase above 30% was observed only in the adaptation blocks was the right fusiform gyrus. The perturbation blocks (mean change = 56%) were considerably more intense in the left superior parietal lobule than the adaptation blocks (mean change = -28%; difference = 85%). The adaptation blocks (mean change = 2%) were more intense than the perturbation blocks (mean change = 32%) in the right fusiform gyrus (difference = 30%).

For the Compressed Complex Condition, regions intense during both the perturbation and adaptation blocks were: the right middle temporal gyrus, the left superior temporal gyrus, the left inferior frontal gyrus, the left lateral superior frontal gyrus, the left angular gyrus, and the left supramarginal gyrus. Regions showing increased intensities only during perturbation blocks were the left middle temporal gyrus, the left middle frontal gyrus, the left medial superior frontal gyrus, the left superior parietal lobule, and the right hippocampus. The only regions showing increased intensities during the adaptation blocks were the right cerebellum and the right fusiform gyrus. Regions for which a large difference existed between block types where higher intensities were present in the perturbation blocks were the left superior parietal lobule (mean change for perturbation blocks = 67%; mean change for adaptation blocks = .4%; difference = 68%) and the right hippocampus (mean change for perturbation blocks = -33%; mean change for adaptation blocks = -17%; difference = 50%). The only region showing considerably more intensity in the adaptation blocks than the perturbation blocks was the right superior temporal gyrus (mean change for perturbation blocks = -62%; mean change for adaptation blocks = 25%; difference = 87%).

Summary

Subject 7 was perturbed in the Complex and Compressed Complex Conditions. He did not adapt in the Complex Condition in either experiment, but did adapt in the Compressed Complex Condition in Experiment 2. The hypotheses for this subject are the same as those of Subject 5 and 6. Like the other subjects, most regions that were active in any condition were active during both the perturbation and adaptation blocks (Table 19). Regions common across these two conditions during perturbation blocks only were the left middle frontal gyrus and the right hippocampus. The only region active only during adaptation blocks in both conditions was the right fusiform gyrus. The left superior parietal lobule was uniquely involved in perturbation for both conditions with a substantial drop during the adaptation blocks for the Complex and the Compressed Complex Conditions.

Table 20. Regions showing greater than 30% percent intensity change for each condition for Subject 7.

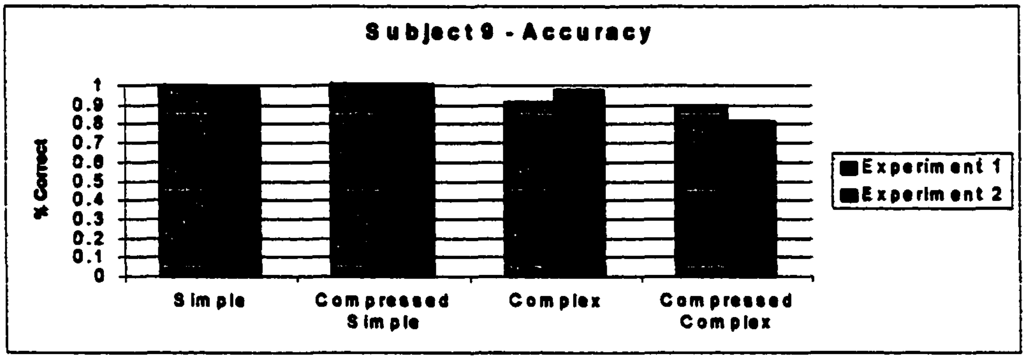
Region	Compressed Simple		Complex		Compressed Complex	
	Left	Right	Left	Right	Left	Right
Middle Temporal Gyrus (P)	*		*	*	*	*
Middle Temporal Gyrus (A)	*		*	*		*
Superior Temporal Gyrus (P)	*		*	*	*	
Superior Temporal Gyrus (A)	*			*	*	
Inferior Frontal Gyrus (P)	*		*	*	*	
Inferior Frontal Gyrus (A)	*		*	*	*	
Middle Frontal Gyrus (P)	*	*	*	*	*	
Middle Frontal Gyrus (A)	*			*		
Superior Frontal Gyrus, Lateral (P)	*		*	*	*	
Superior Frontal Gyrus, Lateral (A)	*		*	*	*	
Superior Frontal Gyrus, Medial (P)	*		*		*	
Superior Frontal Gyrus, Medial (A)			*			
Angular Gyrus (P)					*	
Angular Gyrus (A)	*				*	
Supramarginal Gyrus (P)	*		*		*	
Supramarginal Gyrus (A)	*		*		*	
Superior Parietal Lobule (P)	*		*		*	
Superior Parietal Lobule (A)	*	*				
Cerebellum (P)		*				
Cerebellum (A)		*			*	
Fusiform Gyrus (P)						
Fusiform Gyrus (A)	*	*		*		*
Occipital Lobe (P)						
Occipital Lobe (A)		*				
Hippocampus (P)				*		*
Hippocampus (A)						
Parahippocampus (P)		*		*		
Parahippocampus (A)						

Subject 9 (female, 20 years old)

Accuracy

Subject 9 had little difference in accuracy from Experiment 1 to 2. Accuracy was slightly higher for the Complex Condition and slightly lower for the Compressed Complex Condition in Experiment 2 (Figure 19).

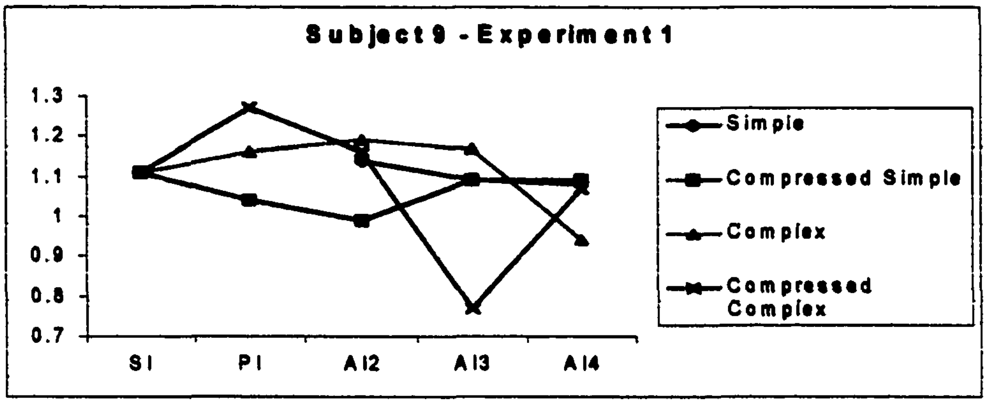
Figure 22. Accuracy for Subject 9 across experiments.



Reaction Time

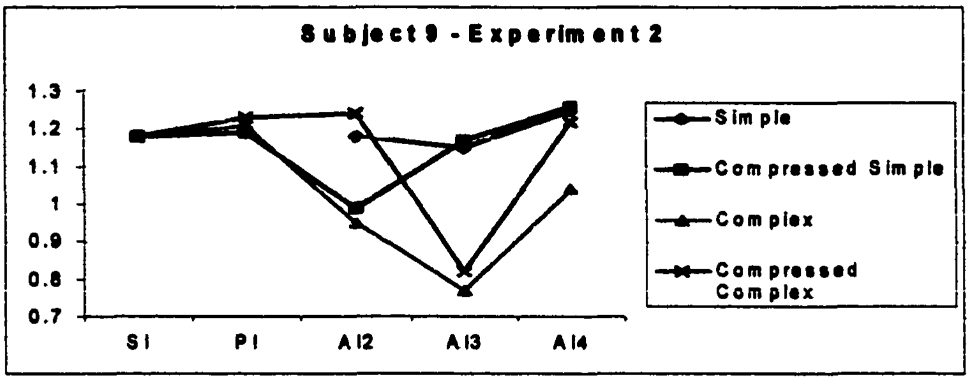
In Experiment 1, Subject 9 was not very stable (SI = 1.11) with AIs in the Simple Condition ranging from 1.08 to 1.14. She was perturbed in the Complex (PI = 1.16) and Compressed Complex (PI = 1.27) Conditions (Figure 20). In the Complex Condition, there was not a peak perturbation for the first item. Rather, the indicies increased for items one through three and then dropped dramatically for item four. These data may suggest that the subject did not adapt until the fourth item. In the Compressed Complex Condition, Subject 9 had not yet adapted at AI2, but then increased again for AI4. Again, the pattern indicates little adaptation.

Figure 23. Stability, Perturbation, and Adaptation indices for Subject 9 in Experiment 1.



In Experiment 2, Subject 9 was less stable than she had been in Experiment 1 (SI = 1.18; AIs ranged from 1.15 to 1.25). As was the case for the Complex Condition in Experiment 1, no clear patterns of perturbation or adaptation were evident for any condition in Experiment 2 (Figure 21). For the Compressed Simple Condition, indices were faster for AI2, but then returned to at or above the SI. For the Complex and Compressed Complex Conditions, the same was true but it was AI3 for which the indices were lower. Overall, Subject 9 was not stable to begin with and therefore had no stable state to which to return.

Figure 24. Stability, Perturbation, and Adaptation indices for Subject 9 in Experiment 2.



Imaging Data

Unlike the other subjects, Subject 9 showed no activation in the temporal lobes. Also unlike the other subjects, Subject 9 had several regions showing increased intensities only during either perturbation or adaptation blocks (Table 20). In the Compressed Simple Condition, large intensity changes were found in the perturbation and adaptation blocks in the left and right inferior frontal gyri, the left and right middle

frontal gyri, and the right occipital lobe. No region showed increased intensities only in the perturbation blocks. In the adaptation blocks, large increases in intensity were observed for the right medial superior frontal gyrus, the right supramarginal gyrus, and the right parahippocampus. No regions showed substantial differences between perturbation and adaptation blocks in this condition.

In the Complex Condition, only the left medial superior frontal gyrus, the right supramarginal gyrus, and the left occipital lobe had increases in intensity above 30% for both block types. Regions showing large changes in intensity above Baseline levels for perturbation blocks only included: the right inferior frontal gyrus, the right middle frontal gyrus, the left and right angular gyri, the right cerebellum, and the right fusiform gyrus. Regions showing increased intensities only during adaptation blocks included: the left middle frontal gyrus, the right lateral superior frontal gyrus, the right medial superior frontal gyrus during the Compressed Simple Condition, and the right fusiform gyrus. Some regions showed considerable difference in intensity between the perturbation and adaptation blocks. In the Complex Condition, only the right angular gyrus showed such a change with greater intensities in the perturbation blocks (mean change for perturbation blocks = 33%; mean change for adaptation blocks = -3%; difference = 36%).

In the Compressed Complex Condition, Subject 9 showed the greatest changes between block types. No regions in this condition showed substantial increases in intensity in both block types. Only the right middle frontal gyrus increases in intensity only for the perturbation blocks. For adaptation blocks, considerable increases in intensity were observed for the left and right cerebellum and the left fusiform gyrus. Regions showing considerably higher intensities during perturbation than adaptation blocks were in the Compressed Complex Condition and included:

1. **The left inferior frontal gyrus (mean change for perturbation blocks = 27%; mean change for adaptation blocks = –27%, difference = 54%).**
2. **The left middle frontal gyrus (mean change for perturbation blocks = 21%; mean change for adaptation blocks = -23%, difference = 44%).**
3. **The right middle frontal gyrus (mean change for perturbation blocks = 87%; mean change for adaptation blocks = -77%, difference = 166%).**

Regions showing considerably higher intensities during the adaptation than the perturbation blocks in the Compressed Complex Condition were:

1. **The right inferior frontal gyrus (mean change for perturbation blocks = -28%; mean change for adaptation blocks = 16%, difference = 44%).**
2. **The right angular gyrus (mean change for perturbation blocks = -15%; mean change for adaptation blocks = 24%; difference = 39%).**
3. **The left cerebellum (mean change for perturbation blocks = -27%; mean change for adaptation blocks = 50%, difference = 78%).**
4. **The right cerebellum (mean change for perturbation blocks = -14%; mean change for adaptation blocks = 42%, difference = 57%).**
5. **The left fusiform gyrus (mean change for the perturbation blocks = -3%; mean change for the adaptation blocks = 36%; difference = 39%).**
6. **The right fusiform gyrus (mean change for perturbation blocks = -14%; mean change for adaptation blocks = 28%; difference = 42%.**

7. The right occipital lobe (mean change = -14%; mean change for adaptation blocks = 23%; difference = 37%).

Table 21. Regions showing greater than 30% percent intensity change for each condition for Subject 9.

Region	Compressed Simple		Complex		Compressed Complex	
	Left	Right	Left	Right	Left	Right
Inferior Frontal Gyrus (P)	*	*		*		
Inferior Frontal Gyrus (A)	*	*				
Middle Frontal Gyrus (P)	*	*		*		*
Middle Frontal Gyrus (A)	*	*	*			
Superior Frontal Gyrus, Lateral (P)						
Superior Frontal Gyrus, Lateral (A)				*		
Superior Frontal Gyrus, Medial (P)	*		*			
Superior Frontal Gyrus, Medial (A)	*	*	*			
Angular Gyrus (P)		*	*	*		
Angular Gyrus (A)		*			*	
Supramarginal Gyrus (P)				*		
Supramarginal Gyrus (A)		*		*		*
Cerebellum (P)	*			*		
Cerebellum (A)	*				*	*
Fusiform Gyrus (P)	*			*		
Fusiform Gyrus (A)	*				*	
Occipital Lobe (P)		*	*			
Occipital Lobe (A)		*	*			
Parahippocampus (P)						
Parahippocampus (A)	*					

Summary

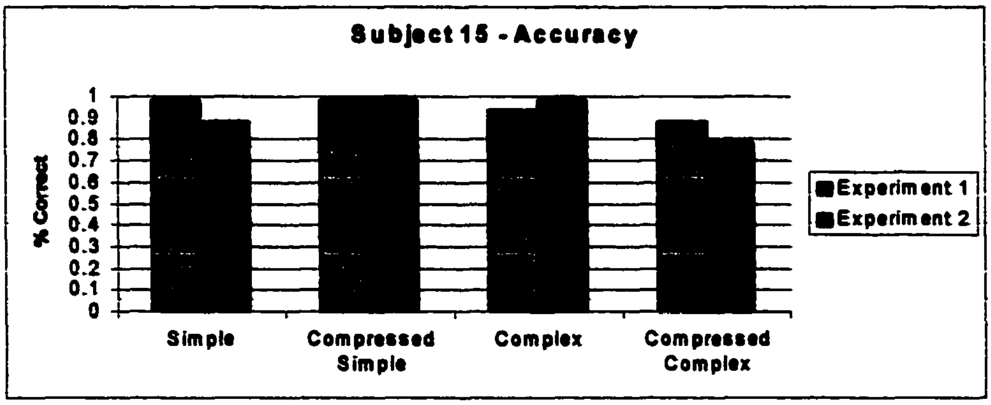
Subject 9's behavioral data in Experiments 1 and 2 revealed that she was not very stable in the Simple Condition and her performance was variable across conditions. Thus, the hypotheses for brain-behavior relations are unclear. The data were most telling in the Compressed Complex Condition in which several regions were involved solely in the adaptive process. On finding that differed from the other subjects was that only a few regions were active in both the perturbation and adaptation blocks across conditions suggesting that the core few regions that appeared globally involved in the task (including the temporal lobes) were not found for Subject 9.

Subject 15 (male, 23 years old)

Accuracy

Subject 15 had lower accuracy for the Simple and the Compressed Complex Conditions in Experiment 2 than he had in Experiment 1 (Figure 22). The difference was 10% in both cases. Accuracy did not change at all for the Compressed Simple Condition and improved 5% in the Complex Condition.

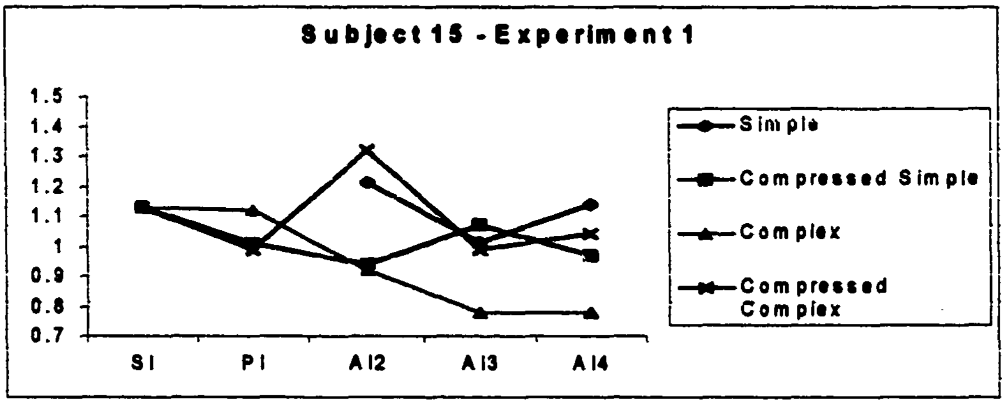
Figure 25. Accuracy for Subject 15 across experiments.



Reaction Time

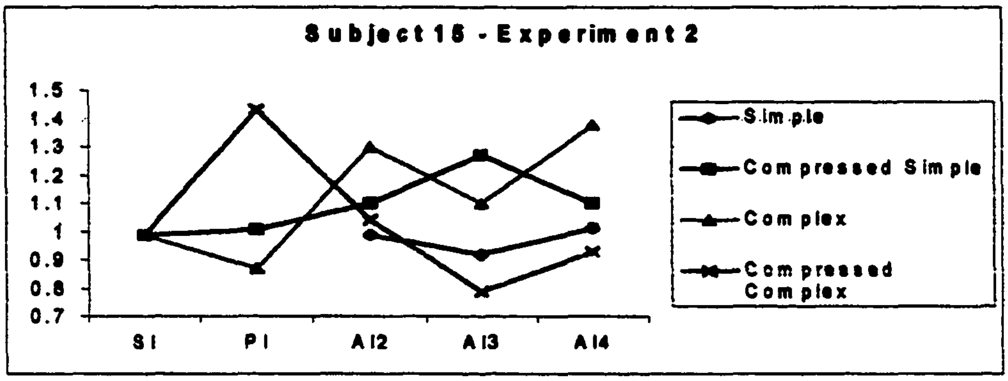
In Experiment 1, Subject 15 was not stable to begin with (SI = 1.13; AIs in the Simple Condition ranged from 1.01 to 1.21). The PIs did not differ for any of the conditions (Figure 23). However, the AIs in the Complex condition were less than 1, indicating that he had adapted in this condition. In the Compressed Complex Condition, much slower RTs were measured for item 2, and they then dropped back to the level of stability. Overall, Subject 15's performance in Experiment 1 was variable with no clear patterns.

Figure 26. Stability, Perturbation, and Adaptation indices for Subject 15 in Experiment 1.



In Experiment 2, Subject 15's performance also was variable. He appeared stable, as indicated by the SI (.99) and performance remained stable in the Simple Condition (AIs ranged from .92 to 1.01). The PIs for the Compressed Simple and Complex Conditions did not differ greatly from the SI, indicating no perturbation in these conditions (Figure 24). However, for both conditions the AIs drifted to levels well higher than stability. In the Compressed Simple Condition, Subject 15's performance was more similar to that of the other subjects. That is, he was perturbed and showed an adaptive response that was evident by AI2.

Figure 27. Stability, Perturbation, and Adaptation indices for Subject 15 in Experiment 2.



Imaging Data

Subject 15 showed activation in several areas with a higher proportion of them being in left hemisphere only (see Table 21). Many of these regions showed increased intensities specific to perturbation or adaptation blocks, but the more frequently this specificity was for the perturbation blocks in the complex conditions.

In the Compressed Simple Condition, the left middle temporal gyrus, the left medial superior frontal gyrus, and the right lateral superior frontal gyrus showed increases in intensity well above Baseline for both block types. Only the left fusiform gyrus showed a substantial increase in intensity only in the perturbation blocks. Regions showing greater than 30% increases in intensity during adaptation blocks only were: the left superior temporal gyrus, the right inferior frontal gyrus, the right medial superior frontal gyrus, the left and right angular gyri, and the left occipital lobe. Subject 15 had several regions where a large difference was observed in intensity levels between perturbation and adaptation blocks. For the Compressed Simple Condition, these difference were observed only in the direction of higher intensities in the adaptation blocks and were found in the following regions:

1. the right middle frontal gyrus (mean change for perturbation blocks = 27%; mean change for adaptation blocks = 59%; difference = 32%)
2. the left angular gyrus (mean change for perturbation blocks = 3%; mean change for adaptation blocks = 50%; difference = 47%)
3. the right angular gyrus (mean change for perturbation blocks = 13%; mean change for adaptation blocks = 46%; difference = 33%).

In the Complex Condition, regions involved during both the perturbation and adapation blocks were the left middle temporal gyrus and the right angular gyrus. Regions showing increases in intensity only during the perturbation blocks were the right inferior frontal gyrus and the left medial superior frontal gyrus. In the adaptation blocks, increases were observed in the left cerebellum and the right fusiform gyrus. Large differences were observed where higher intensities were observed in the perturbation blocks. Regions showing this pattern were:

1. the left inferior frontal gyrus (mean change for perturbation blocks = 39%; mean change for adaptation blocks = -4%; difference = 43%)
2. the right inferior frontal gyrus (mean change for perturbation blocks = 30%; mean change for adaptation blocks = -.5%; difference = 30%)
3. the right middle frontal gyrus (mean change for perturbation blocks = 18%; mean change for adaptation blocks = -16%; difference = 34%)
4. the medial aspect of the left superior frontal gyrus (mean change for perturbation blocks = 34%; mean change for adaptation = -34%; difference = 68%)
5. the medial aspect of the right superior frontal gyrus (mean change for perturbation blocks = 19%; mean change for adaptation blocks = -39%; difference = 59%)

Only the right fusiform gyrus showed higher intensities during the adaptation blocks than the perturbation blocks in the Complex Condition (mean change for perturbation blocks = -11%; mean change for adaptation blocks = 35%; difference = 46%).

In the Compressed Complex Condition, no regions showed considerable increases in intensity in both block types. Regions showing increases of greater than 30% during perturbation blocks only included: the left middle temporal gyrus, the left superior temporal gyrus, the left inferior frontal gyrus, the medial aspect of the right superior frontal gyrus, and the left and right cerebellum. The only region for which a large difference was observed between block types was the angular gyrus. On the left, this region was more intense during the perturbation block (mean change for perturbation blocks = 15%; mean change for adaptation blocks = -39%; difference = 53%). On the right, the region was more intense during the adaptation blocks (mean change for perturbation blocks = -24%; mean change for adaptation blocks = 11%; difference = 35%).

Summary

Subject 15 was quite variable across conditions, and in Experiment 2 only was clearly perturbed and adapted in the Compressed Complex Condition. Like the previous subject, hypotheses for this type of performance are not clear. Surprisingly, few regions were active in the condition in which he was perturbed and adapted. Like the other subjects, however, the regions appearing to be specific to performing the task included the hypothesized regions in the temporal and frontal lobes.

Table 22. Regions showing greater than 30% percent intensity change for each condition for Subject 15.

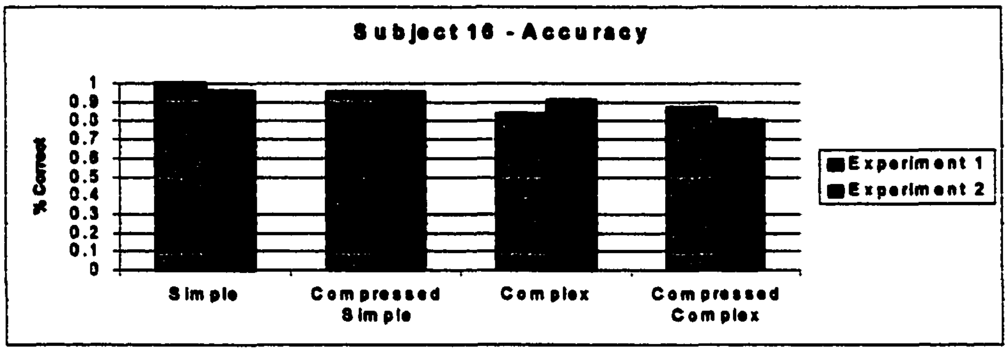
Region	Compressed Simple		Complex		Compressed Complex	
	Left	Right	Left	Right	Left	Right
Middle Temporal Gyrus (P)	*		*		*	
Middle Temporal Gyrus (A)	*		*			
Superior Temporal Gyrus (P)					*	
Superior Temporal Gyrus (A)	*					
Inferior Frontal Gyrus (P)			*	*	*	
Inferior Frontal Gyrus (A)		*				
Middle Frontal Gyrus (P)						
Middle Frontal Gyrus (A)		*				
Superior Frontal Gyrus, Lateral (P)		*				
Superior Frontal Gyrus, Lateral (A)		*				
Superior Frontal Gyrus, Medial (P)	*		*			*
Superior Frontal Gyrus, Medial (A)	*	*				
Angular Gyrus (P)				*		
Angular Gyrus (A)	*	*		*		
Supramarginal Gyrus (P)						
Supramarginal Gyrus (A)						
Cerebellum (P)	*	*			*	*
Cerebellum (A)	*	*	*			
Fusiform Gyrus (P)	*					
Fusiform Gyrus (A)				*		
Occipital Lobe (P)						
Occipital Lobe (A)	*					

Subject 16 (male, 21 years old)

Accuracy

Subject 16 showed a gradual decline in accuracy with increasing complexity in both experiments. Little difference existed between his performance in Experiments 1 and 2 (Figure 25).

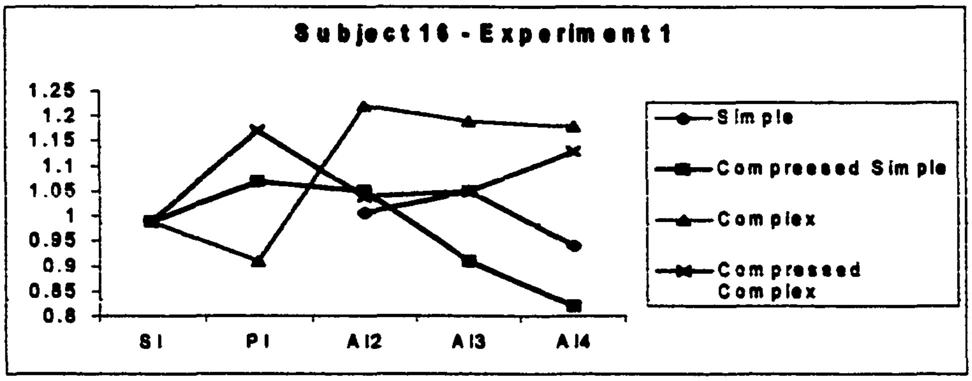
Figure 28. Accuracy for Subject 16 across experiments.



Reaction Time

In Experiment 1, Subject 16 showed variable performance (Figure 26). He was relatively stable in the Simple Condition (SI = .99; AIs ranged from .94 to 1.05). He was perturbed in the Compressed Simple Condition (PI = 1.07) and showed an adaptive response by AI3. In the Complex Condition, he was not perturbed (PI = .91), but showed a steep increase in RTs for AIs two through four, indicating he was perturbed in the Condition, but not for the first items of the blocks. In the Compressed Complex Condition, Subject 16 was perturbed (PI = 1.17), and though RTs dropped performance never returned to the level of stability.

Figure 29. Stability, Perturbation, and Adaptation indices for Subject 16 in Experiment 1.

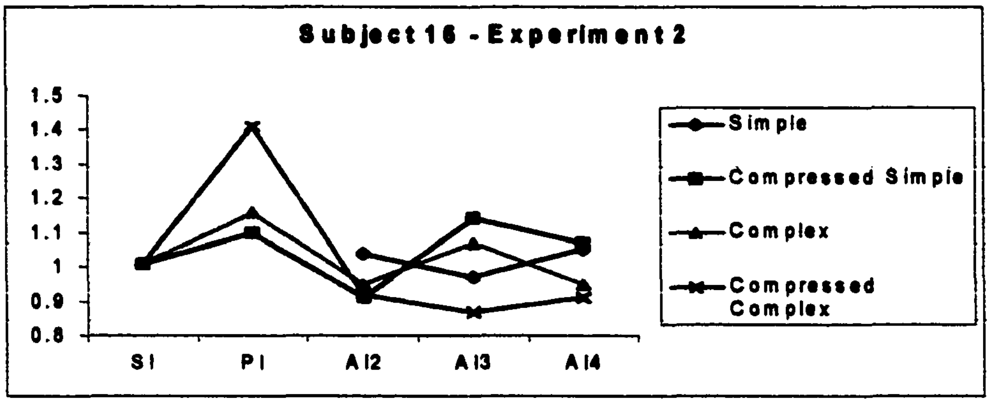


In Experiment 2, Subject 16 again was relatively stable in the Simple Condition (SI = 1.01, AIs ranged from .97 to 1.05). He was clearly perturbed in all conditions (Figure 27). For the Compressed Simple Condition, Subject 16 was perturbed to a small degree (PI = 1.10), but he did not evidence an adaptive response. In the Complex Condition, he again was perturbed (PI = 1.16) and then RTs dropped for AI2 (.91), increased again for AI3 (1.07), and then dropped again for AI4 (.95). In the Compressed Complex Condition, he showed a more clear perturbation (PI = 1.41) followed by adaptation.

Imaging Data

For Subject 16, most active regions showed intensity levels well above Baseline in perturbation and adaptation blocks (see Table 22). For the Compressed Simple Condition, regions substantially intense during both block types included: the right middle frontal gyrus, the left and right superior temporal gyrus, the left

Figure 30. Stability, Perturbation, and Adaptation indices for Subject 16 in Experiment 2.



and right inferior frontal gyri, the left and right middle frontal gyri, the left and right lateral superior frontal gyri, the left medial superior frontal gyrus, the right supramarginal gyrus, the right cerebellum, the left and right fusiform gyri, and the right occipital lobe. Regions showing increases in intensity only for perturbation blocks were the left middle temporal gyrus and the right superior parietal lobule. Regions showing increases in intensity only during the adaptation blocks were: the right medial superior frontal gyrus, the right angular gyrus, the left supramarginal gyrus, the left superior parietal lobule, the left cerebellum, and the left occipital lobe. For the Compressed Simple Condition, the only large difference between block types was in the left middle temporal gyrus (mean change for perturbation blocks = 42%; mean change for adaptation blocks = .5%; difference = 42%).

In the Complex Condition, regions that were highly intense during both block types were: the left superior temporal gyrus, the left inferior frontal gyrus, the left middle frontal gyrus, the lateral and medial aspects of the left superior frontal gyrus, the right supramarginal gyrus, and the left superior parietal lobule. Regions showing substantial increases in intensity above Baseline in the perturbation blocks were: the left middle temporal gyrus, the right superior temporal gyrus, the right middle frontal gyrus, the right medial superior frontal gyrus, the left angular gyrus, the left supramarginal gyrus, the left and right fusiform gyri, and the left occipital lobe. No regions were considerably intense only during the adaptation blocks. For the Complex Condition, larger intensities were seen in the perturbation than the adaptation blocks in:

1. the left middle temporal gyrus (mean change for perturbation blocks = 56%; mean change for adaptation blocks = 13%; difference = 42%).
2. the left fusiform gyrus (mean change for perturbation blocks = 32%; mean change for adaptation blocks = -.5%; difference = 33%)
3. the left occipital lobe (mean change for perturbation blocks = 33%; mean change for adaptation blocks = 1%; difference = 32%)

In the Compressed Complex Condition, regions highly intense during both block types were: the left middle temporal gyrus, the left and right superior temporal gyri, the left and right inferior frontal gyri, the left and right middle frontal gyri, the left medial and the right lateral superior frontal gyri, the left and right supramarginal gyri, and the left superior parietal lobule. No regions were

Table 23. Regions showing greater than 30% percent intensity change for each condition for Subject 16.

Region	Compressed Simple		Complex		Compressed Complex	
	Left	Right	Left	Right	Left	Right
Middle Temporal Gyrus (P)	*	*	*		*	
Middle Temporal Gyrus (A)		*			*	
Superior Temporal Gyrus (P)	*	*	*	*	*	*
Superior Temporal Gyrus (A)	*	*	*		*	*
Inferior Frontal Gyrus (P)	*	*	*		*	*
Inferior Frontal Gyrus (A)	*	*	*		*	*
Middle Frontal Gyrus (P)	*	*	*	*	*	*
Middle Frontal Gyrus (A)	*	*	*		*	*
Superior Frontal Gyrus, Lateral (P)	*	*	*			*
Superior Frontal Gyrus, Lateral (A)	*	*	*		*	*
Superior Frontal Gyrus, Medial (P)	*		*	*	*	
Superior Frontal Gyrus, Medial (A)	*	*	*		*	
Angular Gyrus (P)			*			
Angular Gyrus (A)		*			*	
Supramarginal Gyrus (P)			*		*	
Supramarginal Gyrus (A)	*				*	
Superior Parietal Lobule (P)		*	*		*	
Superior Parietal Lobule (A)	*		*		*	
Cerebellum (P)		*				
Cerebellum (A)	*	*			*	*
Fusiform Gyrus (P)	*	*	*	*		
Fusiform Gyrus (A)	*	*			*	
Occipital Lobe (P)		*	*			
Occipital Lobe (A)	*	*			*	

highly intense only during perturbation blocks. Regions showing increases in intensity only during the adaptation blocks were: the left lateral superior frontal gyrus, the left angular gyrus, the left cerebellum, the left fusiform gyrus, and the left occipital lobe. No such large differences existed between perturbation and adaptation blocks in the Compressed Complex Condition.

Summary

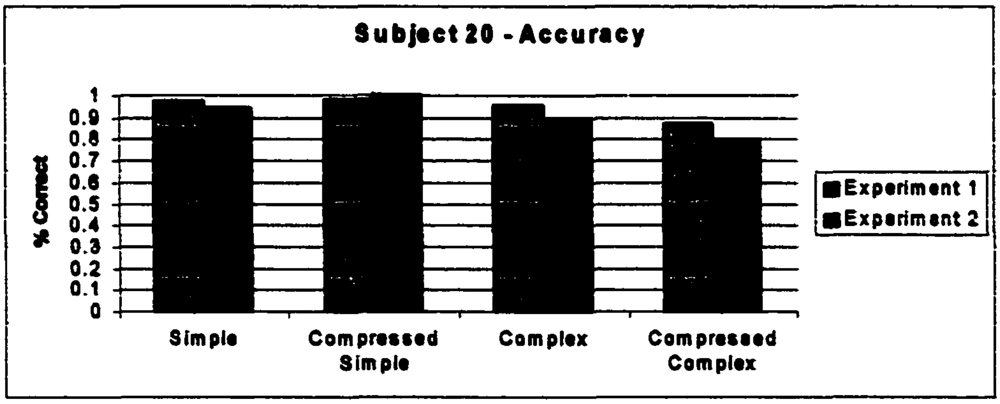
As with the last two subjects, Subject 16's was not perturbed and did not adapt, except for the Compressed Complex Condition in Experiment 2. This subject's imaging data showed several regions that were involved globally across conditions (the middle and superior temporal lobes, the inferior and middle frontal lobes, the superior parietal lobules).

Subject 20 (male, 29 years old)

Accuracy

Subject 20 showed a slight decrease in accuracy with increasing complexity in both experiments. Little difference was observed between experiments (Figure 28).

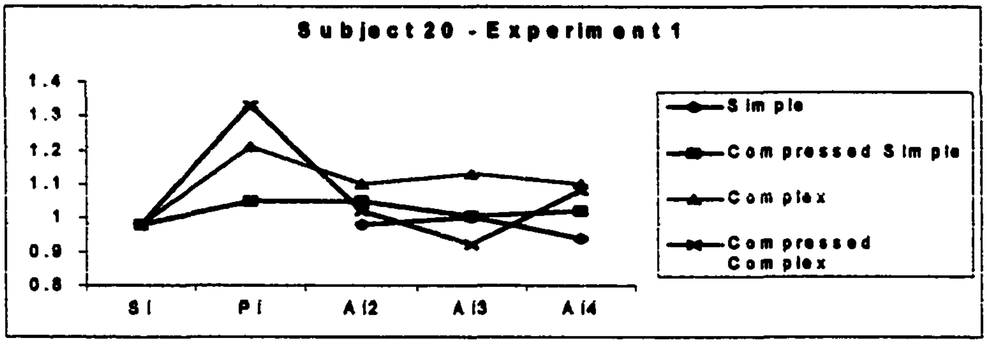
Figure 31. Accuracy for Subject 20 across experiments.



Reaction Time

In Experiment 1, Subject 20 was quite stable in the Simple Condition (SI = .98; AIs ranged from .94 to 1.002; see Figure 29). His indices also remained stable in the Compressed Simple Condition (PI = 1.05; AIs ranged from 1.005 to 1.05). He was perturbed in the Complex Condition (PI = 1.21) and though the AIs dropped from the level of the PI, they did not return to stability. In the Compressed Complex Condition, Subject 20 was perturbed (PI = 1.29) and he adapted by AI3.

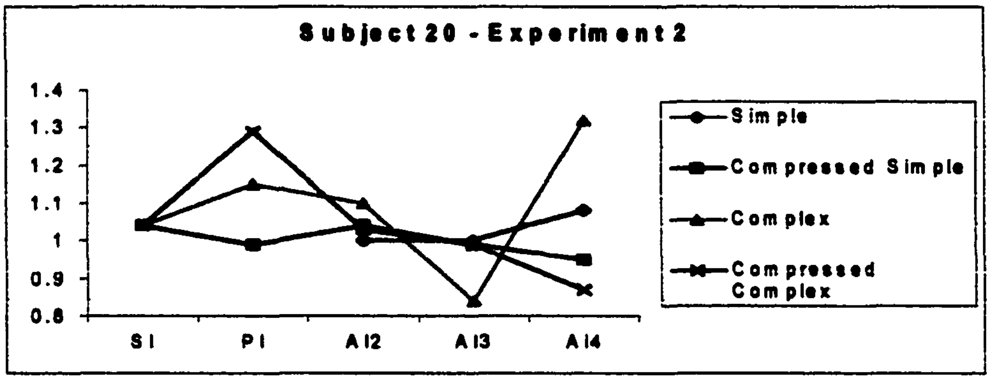
Figure 32. Stability, Perturbation, and Adaptation indices for Subject 20 in Experiment 1.



In Experiment 2, Subject 20 was relatively stable in the Simple Condition (SI = 1.04), but a substantial increase in RT was measured for AI4 (Figure 30). Performance in the Compressed Simple Condition was stable (PI = .99; AIs ranged from .99 to 1.04). In the Complex Condition, Subject 20 was perturbed (PI = 1.15) and he appeared to be adapting until AI4 when RTs increased dramatically (AI4 =

1.32). In the Compressed Complex Condition, as in Experiment 1, Subject 20 was perturbed (PI = 1.29) and then adapted.

Figure 33. Stability, Perturbation, and Adaptation indices for Subject 20 in Experiment 2.



Imaging Data

Subject 20 showed activation in all of the hypothesized regions except the superior temporal gyrus (Table 23). In the Compressed Simple Condition, the following regions showed intensities greater than 30% above Baseline in the perturbation blocks: the left and right middle frontal gyri, the left supramarginal gyrus, and the left cerebellum. During adaptation blocks in this condition, the following regions showed increases in intensity well above Baseline: the left angular gyrus, the right cerebellum, the left and right fusiform gyri, and the left and right occipital lobes. The only region showing a considerable difference between intensities in the perturbation versus the adaptation blocks was the left supramarginal gyrus (mean change for perturbation blocks = 47%; mean change for adaptation blocks = -4%; difference = 51%).

For the Complex Condition, only the left supramarginal gyrus showed an increase in intensities greater than 30% that was evident only in the perturbation blocks (mean change for perturbation blocks = 48%) and also differed from the level observed in the adaptation blocks (mean change for adaptation blocks = 16%; difference = 31%). For the adaptation blocks in the Complex Condition, the only region showing increases in intensity greater than 30% above Baseline were the left and right superior frontal gyri (medial aspect). The only region, other than the left supramarginal gyrus, for which a large difference was measured between the perturbation and adaptation blocks in this condition, was the left superior parietal lobule (mean change for perturbation blocks = -14%; mean change for adaptation blocks = 26%; difference = 42%).

In the Compressed Complex Condition, active regions showed substantial increase in intensity for both the perturbation and adaptation blocks. No regions showed increased intensities specific to adaptation blocks and only a few showed increases specific to perturbation blocks. Those showing large increases in intensity only in the perturbation blocks were: the left inferior frontal gyrus, the left supramarginal gyrus, and the left and right superior parietal lobules. Differences between perturbation and adaptation blocks were substantial for a few regions, and in all the intensities of the perturbation blocks were greater than those of the adaptation blocks. Those regions were:

1. the left inferior frontal gyrus (mean change for perturbation blocks = 37%; mean change for adaptation blocks = -18%; difference = 55%)
2. the left superior parietal lobule (mean change for perturbation blocks = 44%; mean change for adaptation blocks = -10%; difference = 54%)
3. the left cerebellum (mean change for perturbation blocks = 21%; mean change for adaptation blocks = -26%; difference = 47%)
4. the left parahippocampus (mean change for perturbation blocks = 16%; mean change for adaptation blocks = -19%; difference = 45%).

Summary

Subject 20's were in line with the hypothesized patterns of behavior. That is, he was perturbed in the more complex conditions and adapted to being perturbed. Further, this subject showed several regions that increased in intensity specific to being perturbed in the Compressed Complex Condition. These included the left inferior frontal gyrus and the left superior parietal lobule that also were commonly active in the other subjects for this condition.

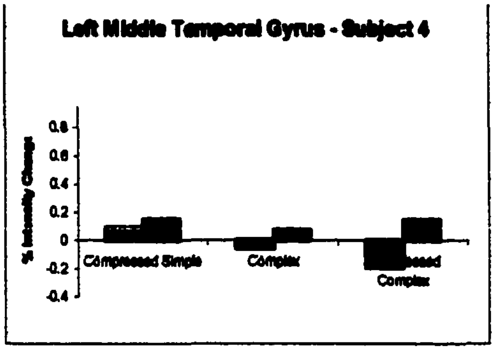
Table 24. Regions showing greater than 30% percent intensity change for each condition for Subject 20.

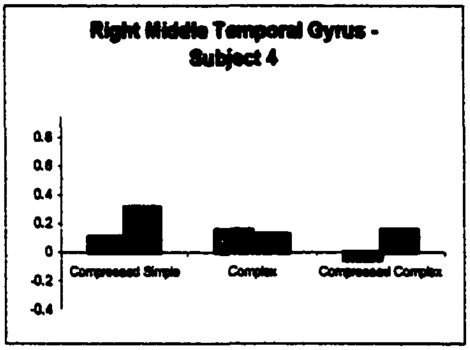
Region	Compressed Simple		Complex		Compressed Complex	
	Left	Right	Left	Right	Left	Right
Middle Temporal Gyrus (P)	*	*	*		*	
Middle Temporal Gyrus (A)	*	*	*		*	
Inferior Frontal Gyrus (P)					*	
Inferior Frontal Gyrus (A)						
Middle Frontal Gyrus (P)	*	*			*	*
Middle Frontal Gyrus (A)					*	*
Superior Frontal Gyrus, Medial (P)		*			*	*
Superior Frontal Gyrus, Medial (A)		*	*	*	*	*
Angular Gyrus (P)						
Angular Gyrus (A)	*					
Supramarginal Gyrus (P)	*	*	*		*	
Supramarginal Gyrus (A)		*				
Superior Parietal Lobule (P)		*			*	*
Superior Parietal Lobule (A)		*				
Cerebellum (P)	*					
Cerebellum (A)		*				
Fusiform Gyrus (P)						
Fusiform Gyrus (A)	*	*				
Occipital Lobe (P)						*
Occipital Lobe (A)	*			*		*
Parahippocampus (P)	*	*				
Parahippocampus (A)	*	*				

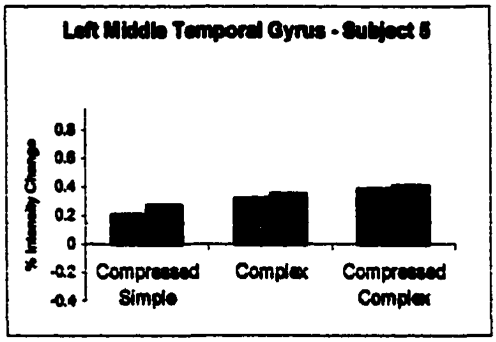
APPENDIX H

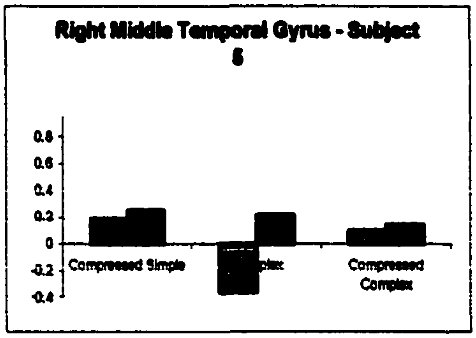
Graphs of percent change from Baseline in each brain region for each condition by block type.

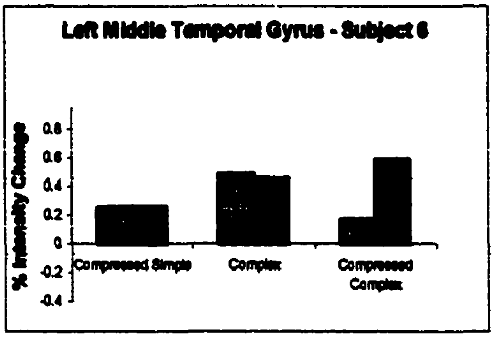
Middle Temporal Gyrus

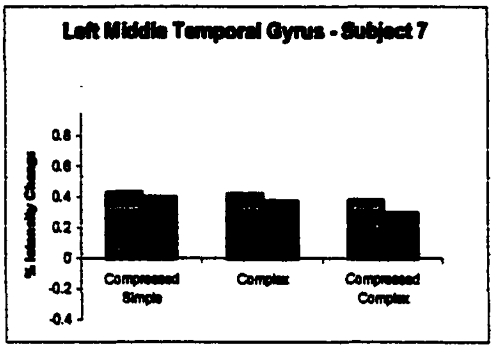


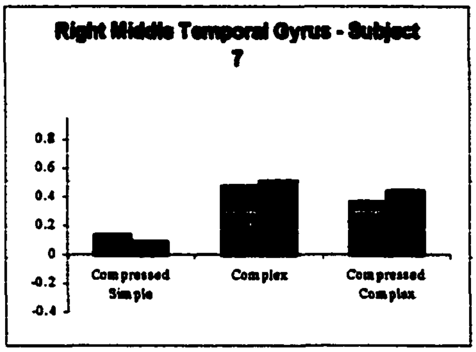


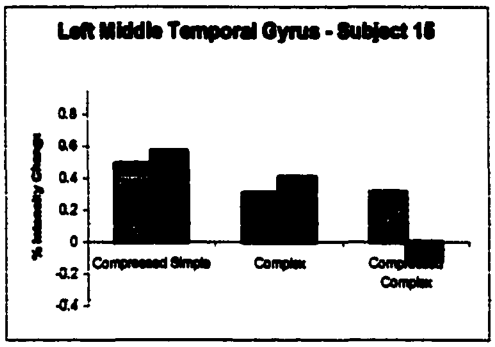


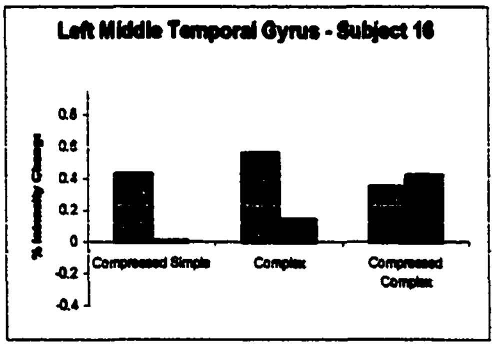


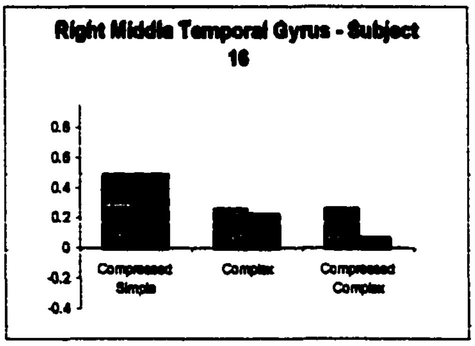


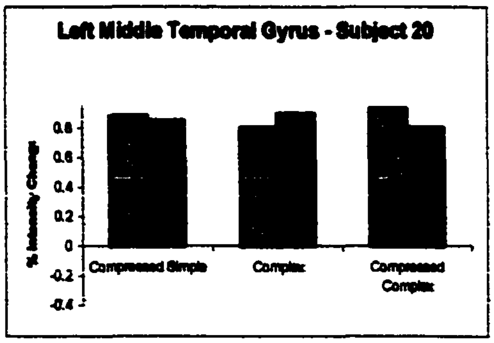

Left Middle Temporal Gyrus - Subject 7
% Intensity Change
0.8
0.6
0.4
0.2
0
-0.2
-0.4
Compressed Simple
Complex
Compressed Complex

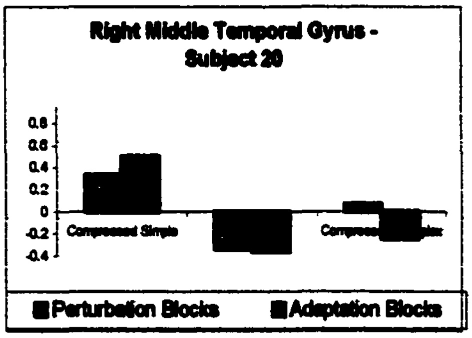

Right Middle Temporal Gyrus - Subject 7
0.8
0.6
0.4
0.2
0
-0.2
-0.4
Compressed Simple
Complex
Compressed Complex


Left Middle Temporal Gyrus - Subject 15
% Intensity Change
0.8
0.6
0.4
0.2
0
-0.2
-0.4
Compressed Simple
Complex
Compressed Complex

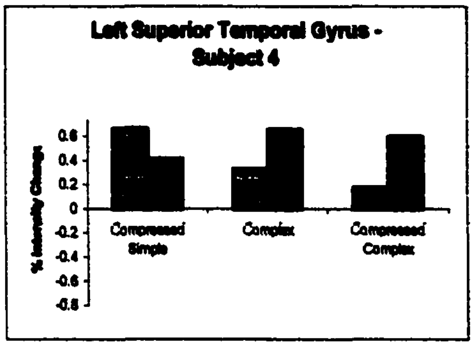

Left Middle Temporal Gyrus - Subject 16
% Intensity Change
0.8
0.6
0.4
0.2
0
-0.2
-0.4
Compressed Simple
Complex
Compressed Complex

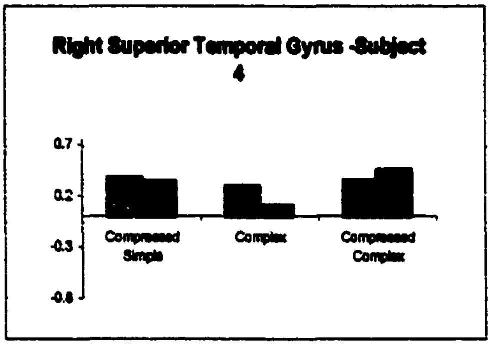

Right Middle Temporal Gyrus - Subject 16
0.8
0.6
0.4
0.2
0
-0.2
-0.4
Compressed Simple
Complex
Compressed Complex

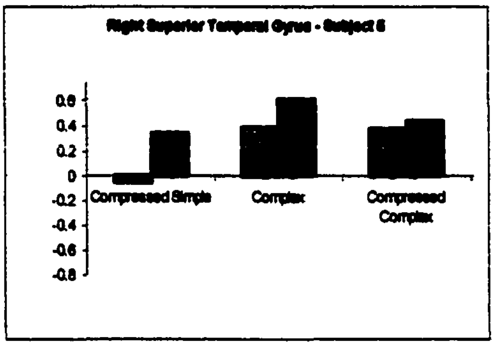

Left Middle Temporal Gyrus - Subject 20
% Intensity Change
0.8
0.6
0.4
0.2
0
-0.2
-0.4
Compressed Simple
Complex
Compressed Complex

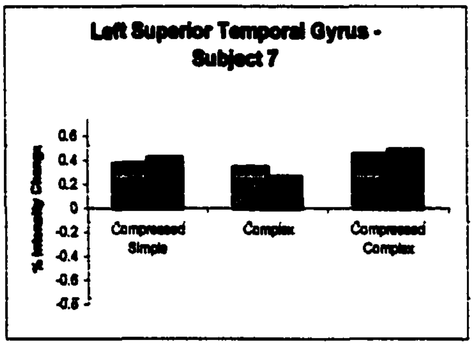

Right Middle Temporal Gyrus - Subject 20
0.8
0.6
0.4
0.2
0
-0.2
-0.4
Compressed Simple
Compressed Complex
■ Perturbation Blocks
■ Adaptation Blocks

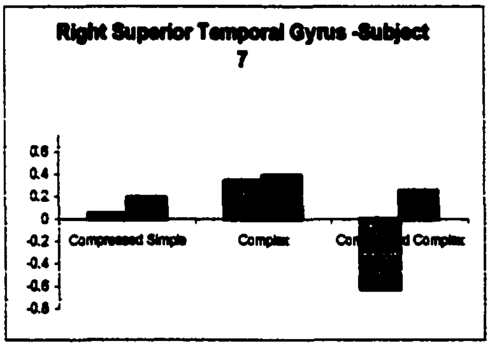
Superior Temporal Gyrus

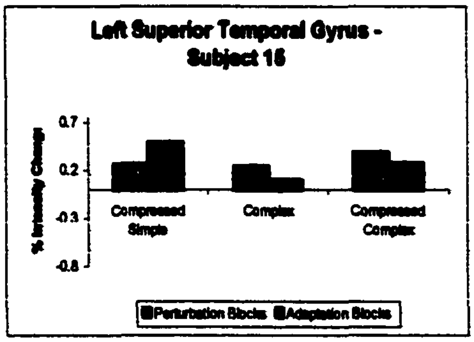


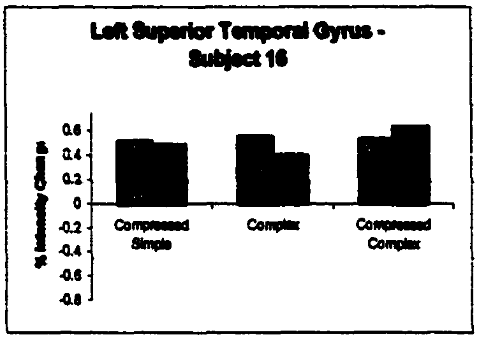


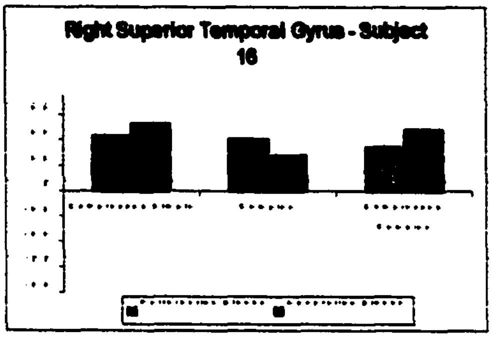




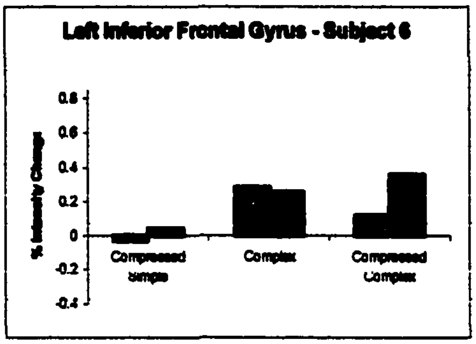


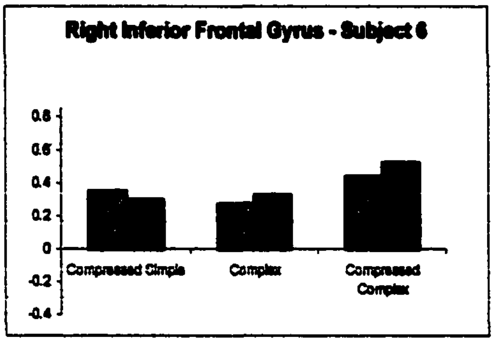


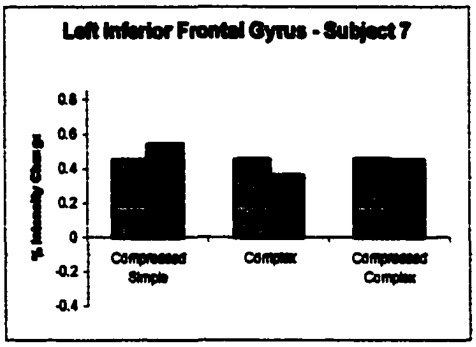

Left Superior Temporal Gyrus - Subject 16
% Intensity Change
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
-0.8
Compressed Simple
Complex
Compressed Complex

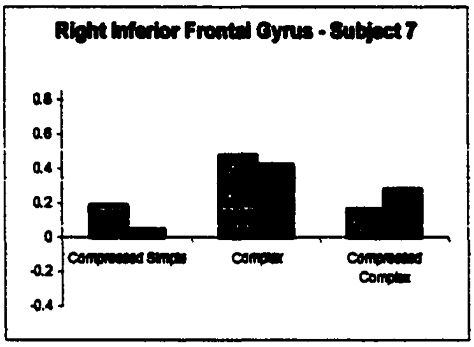

Right Superior Temporal Gyrus - Subject 16

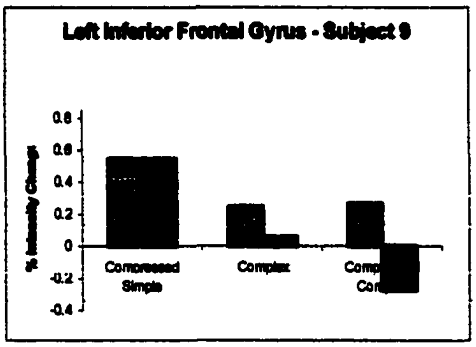
Inferior Frontal Gyrus

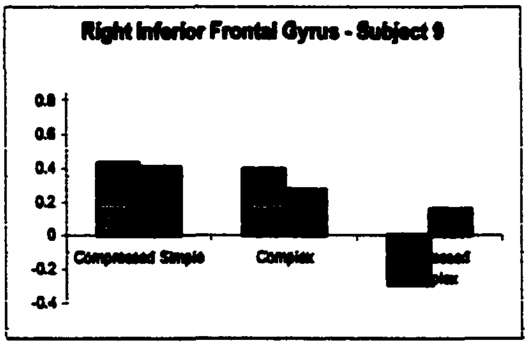

Left Inferior Frontal Gyrus - Subject 6

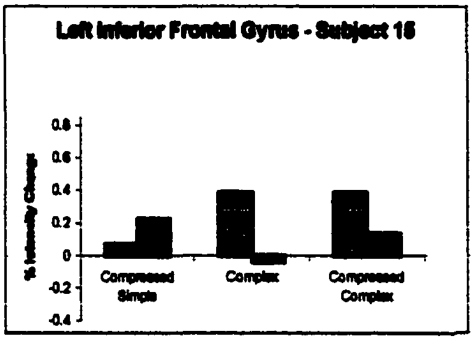

Right Inferior Frontal Gyrus - Subject 6


Left Inferior Frontal Gyrus - Subject 7

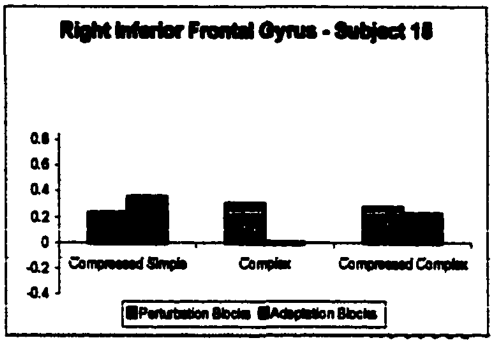

Right Inferior Frontal Gyrus - Subject 7


Left Inferior Frontal Gyrus - Subject 9

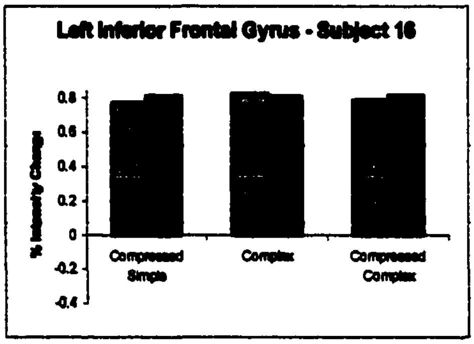

Right Inferior Frontal Gyrus - Subject 9



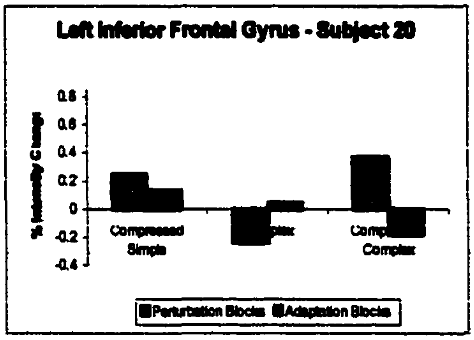
Left Inferior Frontal Gyrus - Subject 15



Right Inferior Frontal Gyrus - Subject 15

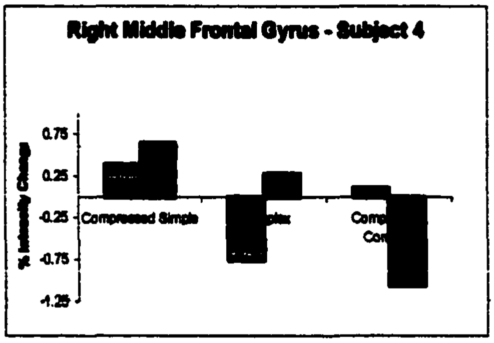


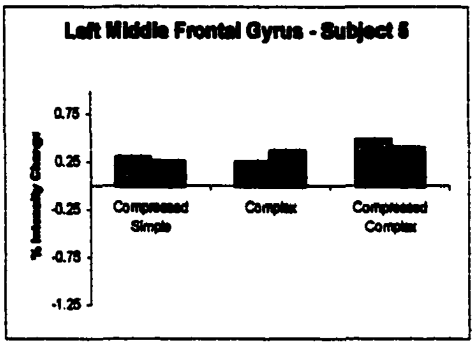
Left Inferior Frontal Gyrus - Subject 16

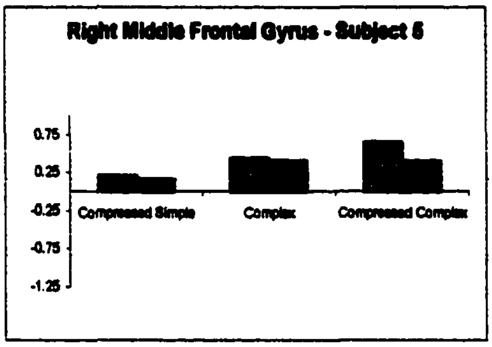


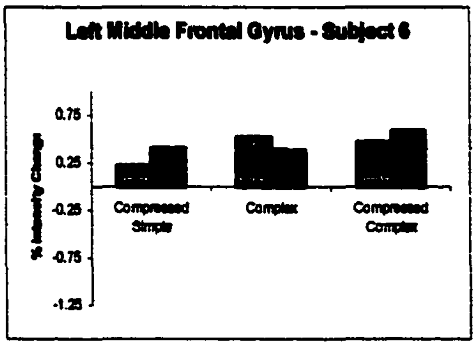
Left Inferior Frontal Gyrus - Subject 20

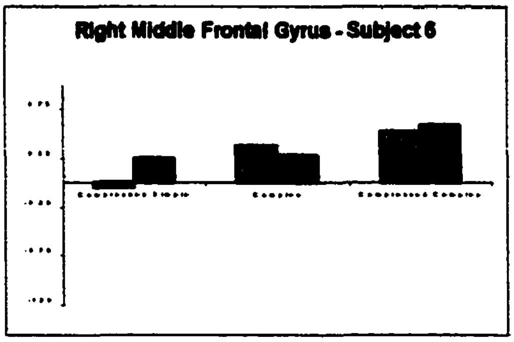
Middle Frontal Gyrus

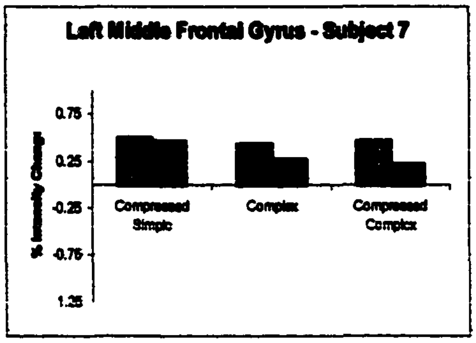

Right Middle Frontal Gyrus - Subject 4

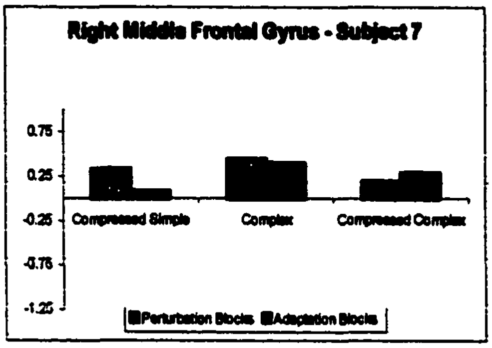

Left Middle Frontal Gyrus - Subject 5

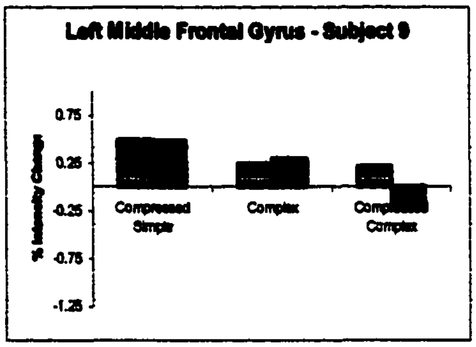

Right Middle Frontal Gyrus - Subject 5

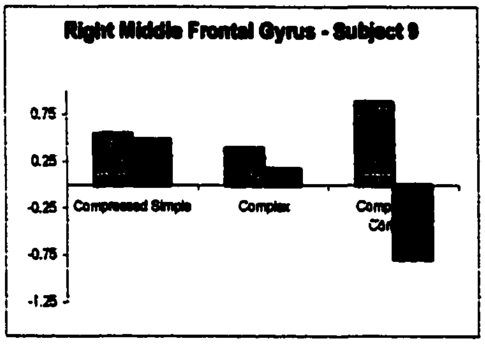

Left Middle Frontal Gyrus - Subject 6

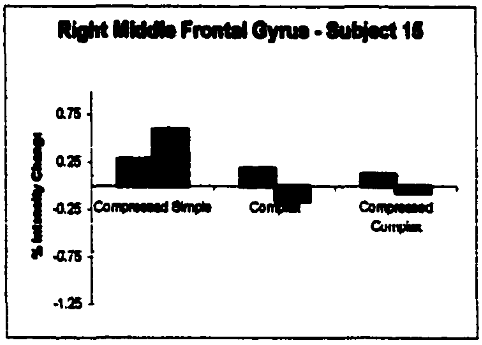

Right Middle Frontal Gyrus - Subject 6

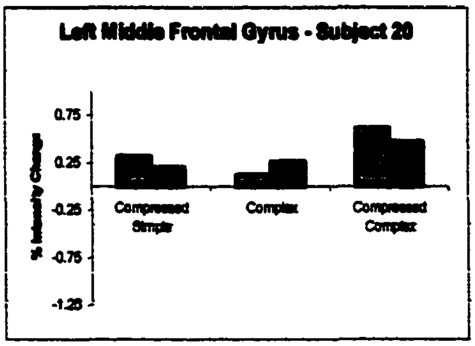

Left Middle Frontal Gyrus - Subject 7

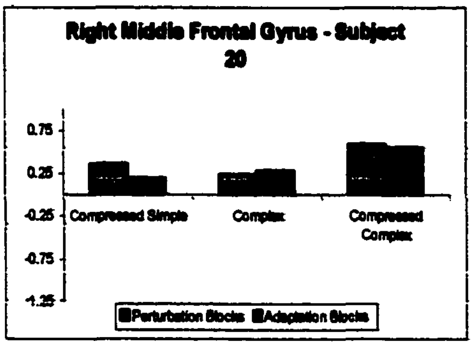

Right Middle Frontal Gyrus - Subject 7


Left Middle Frontal Gyrus - Subject 9

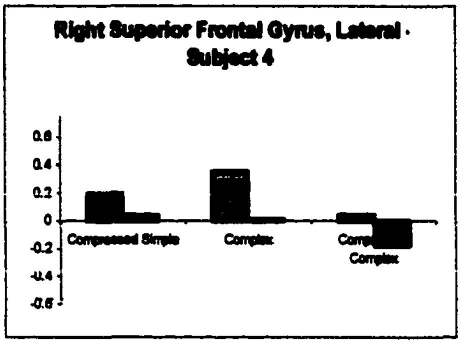

Right Middle Frontal Gyrus - Subject 9


Right Middle Frontal Gyrus - Subject 15

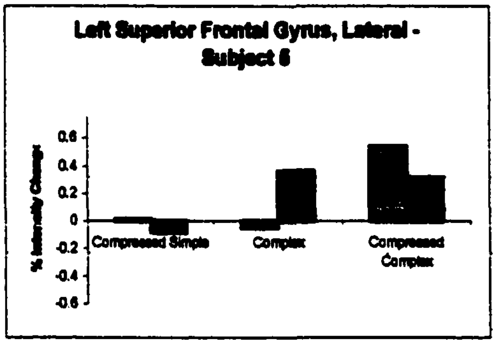

Left Middle Frontal Gyrus - Subject 20


Right Middle Frontal Gyrus - Subject 20

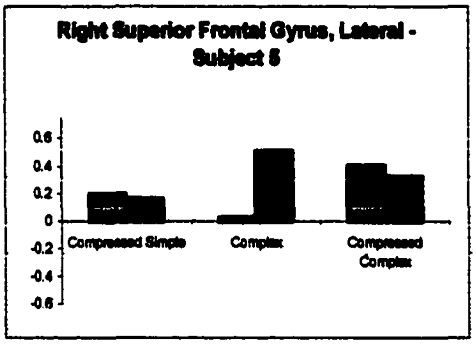
Superior Frontal Gyri (Lateral)



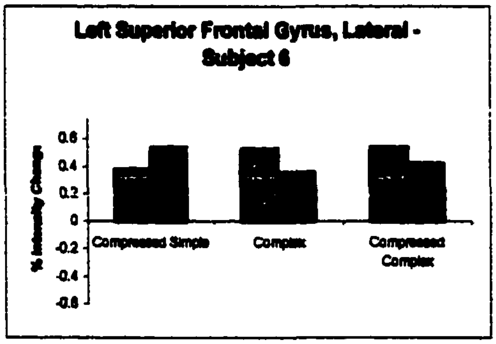
Right Superior Frontal Gyrus, Lateral - Subject 4



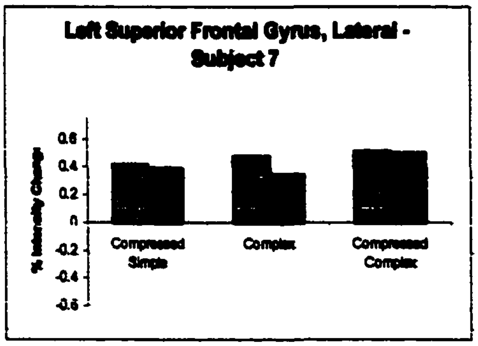
Left Superior Frontal Gyrus, Lateral - Subject 5



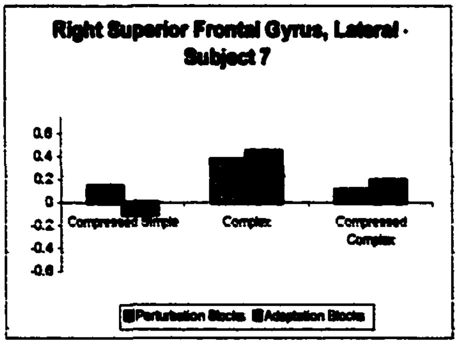
Right Superior Frontal Gyrus, Lateral - Subject 5



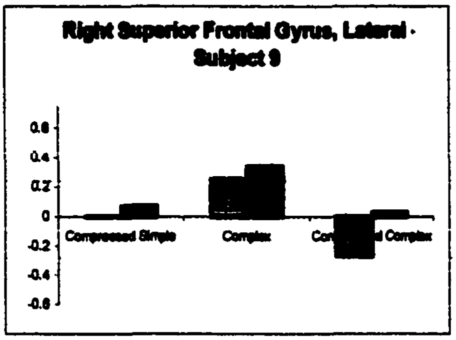
Left Superior Frontal Gyrus, Lateral - Subject 6

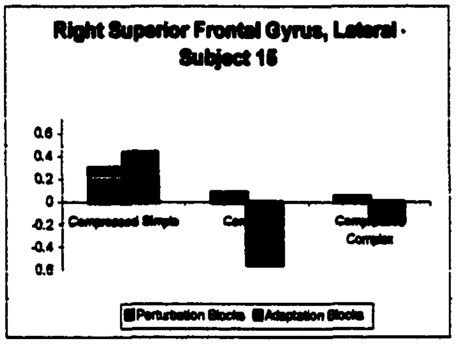


Left Superior Frontal Gyrus, Lateral - Subject 7

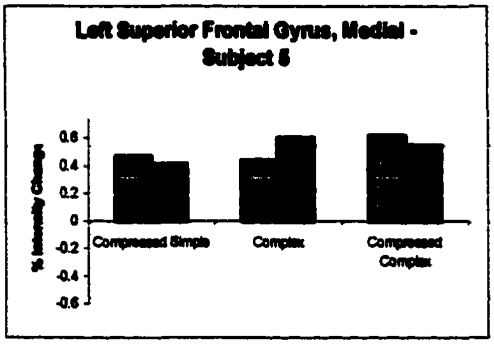


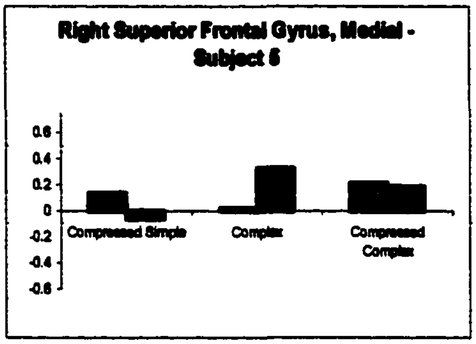
Right Superior Frontal Gyrus, Lateral - Subject 7

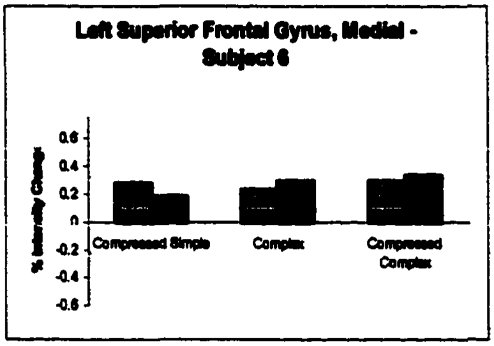

Right Superior Frontal Gyrus, Lateral - Subject 9
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
Compressed Simple
Complex
Co
d Complex

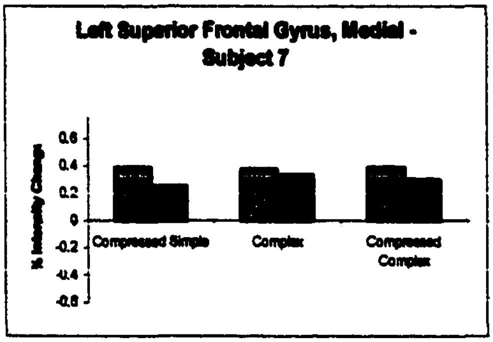

Right Superior Frontal Gyrus, Lateral - Subject 15
0.6
0.4
0.2
0
-0.2
-0.4
0.6
Compressed Simple
Co
Comp
Complex
Perturbation Blocks
Adaptation Blocks

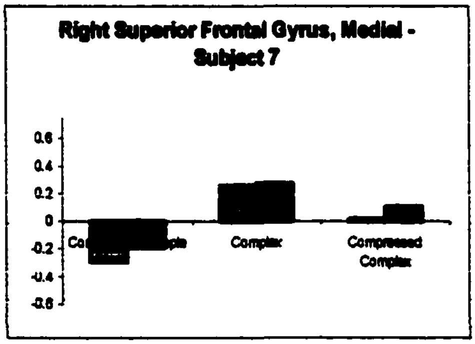
Superior Frontal Gyri (Medial)

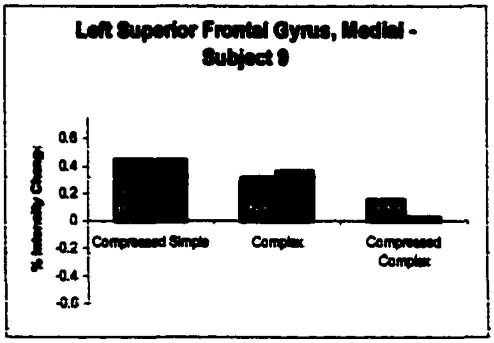

Left Superior Frontal Gyrus, Medial - Subject 5

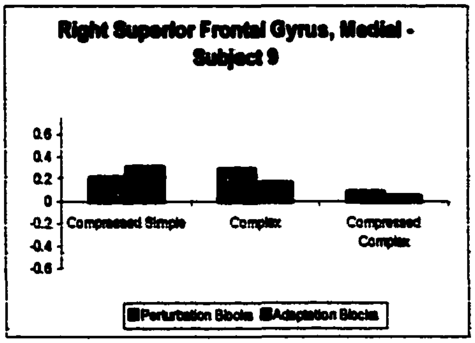

Right Superior Frontal Gyrus, Medial - Subject 5

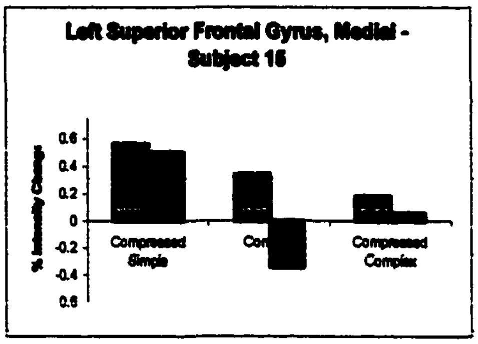

Left Superior Frontal Gyrus, Medial - Subject 6


Left Superior Frontal Gyrus, Medial - Subject 7

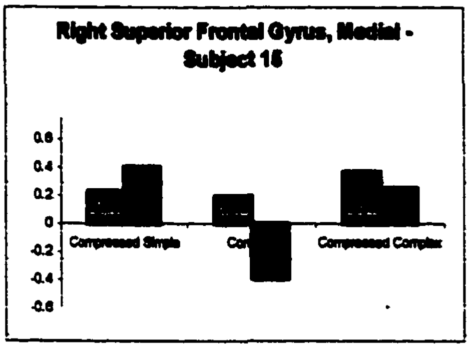

Right Superior Frontal Gyrus, Medial - Subject 7


Left Superior Frontal Gyrus, Medial - Subject 9

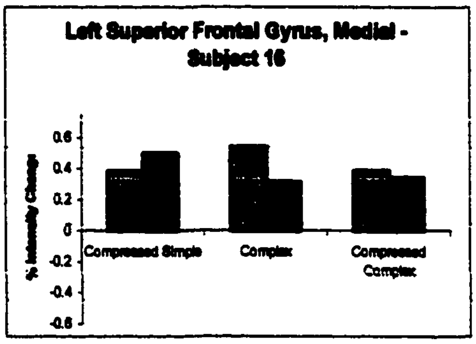

Right Superior Frontal Gyrus, Medial - Subject 9



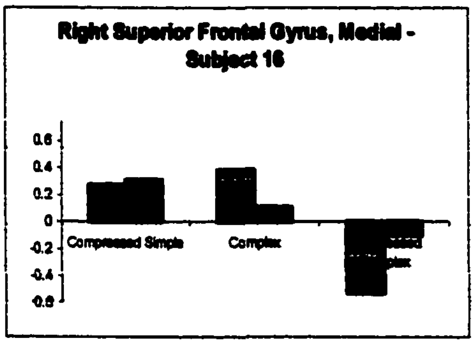
Left Superior Frontal Gyrus, Medial - Subject 15



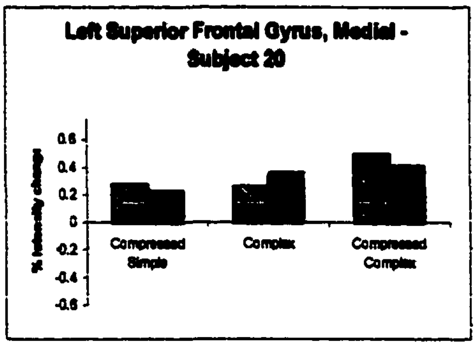
Right Superior Frontal Gyrus, Medial - Subject 15



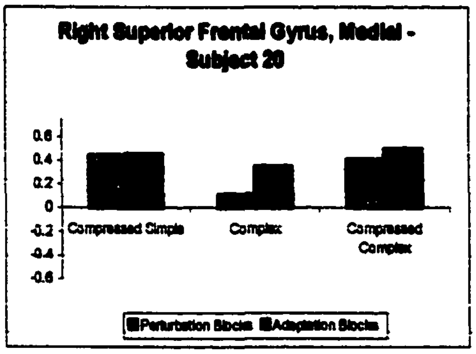
Left Superior Frontal Gyrus, Medial - Subject 16



Right Superior Frontal Gyrus, Medial - Subject 16

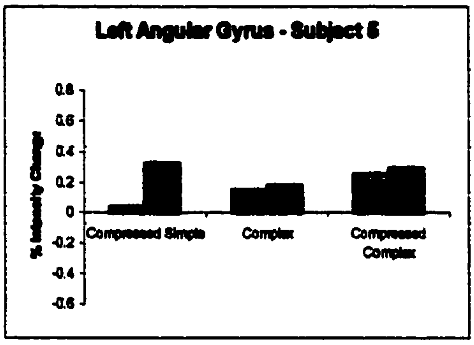


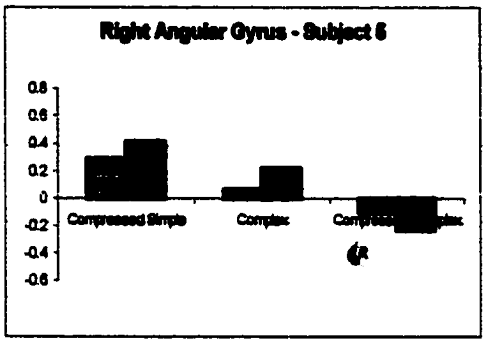
Left Superior Frontal Gyrus, Medial - Subject 20

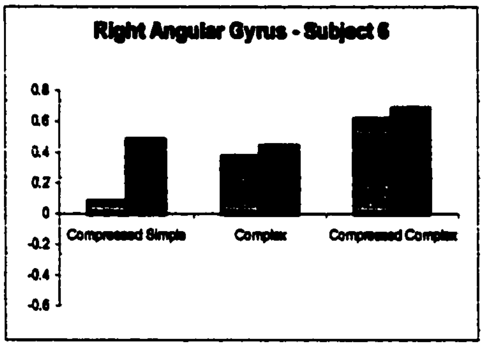


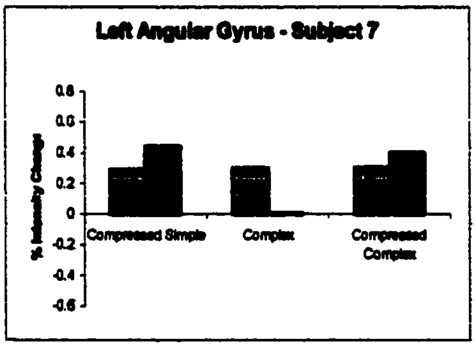
Right Superior Frontal Gyrus, Medial - Subject 20

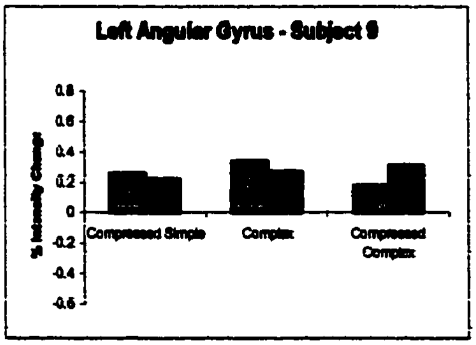
Angular Gyri

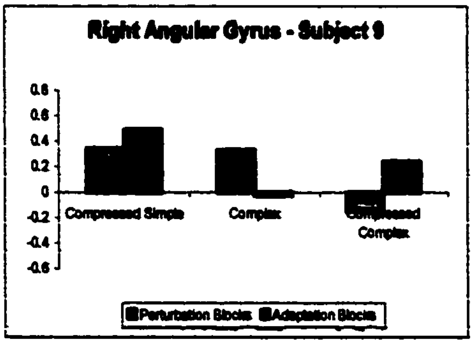


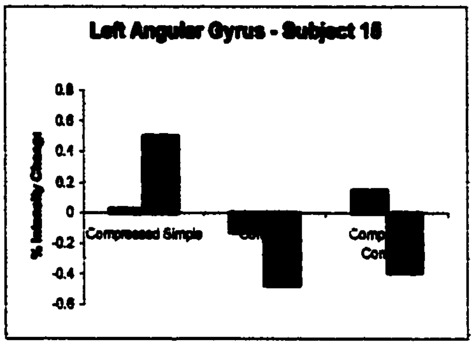


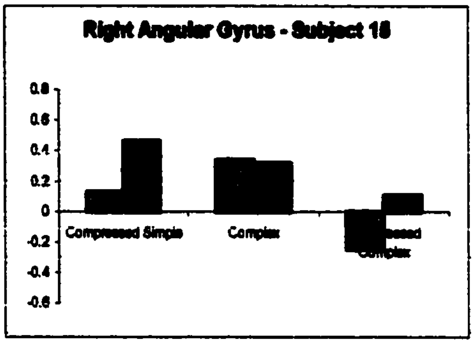


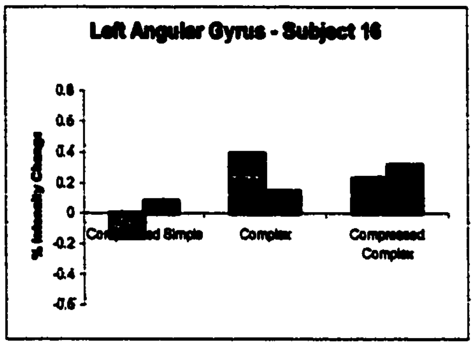


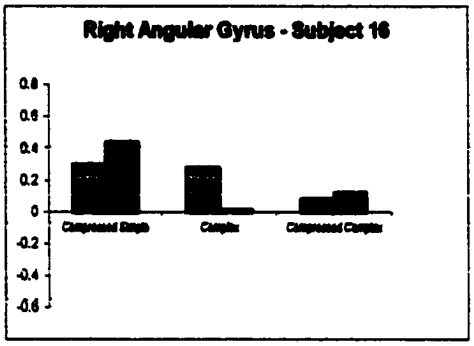


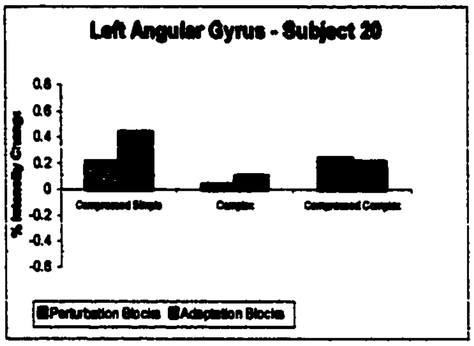



Left Angular Gyrus - Subject 15

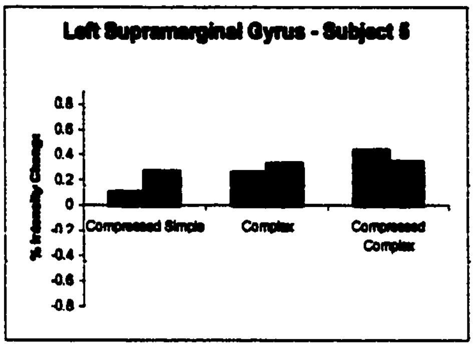

Right Angular Gyrus - Subject 15

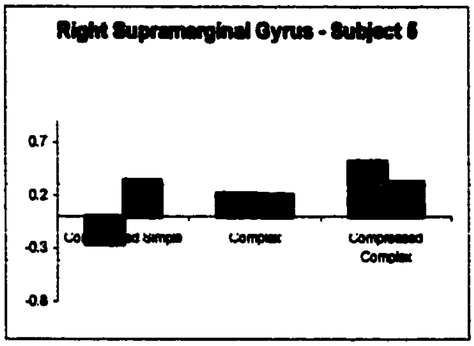

Left Angular Gyrus - Subject 16

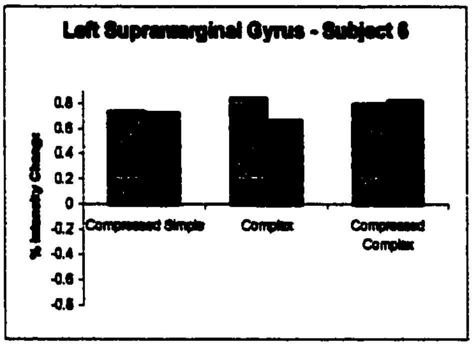

Right Angular Gyrus - Subject 16

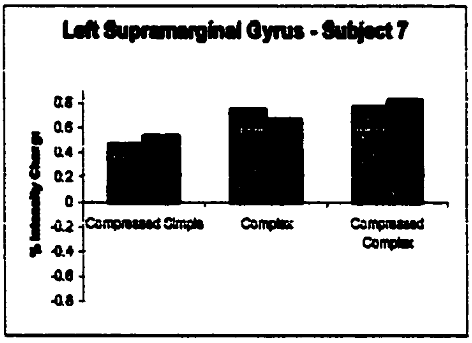

Left Angular Gyrus - Subject 20

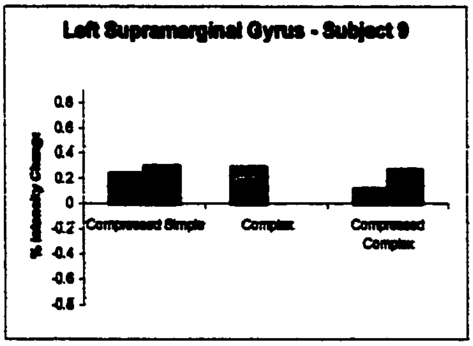
Supramarginal Gyri

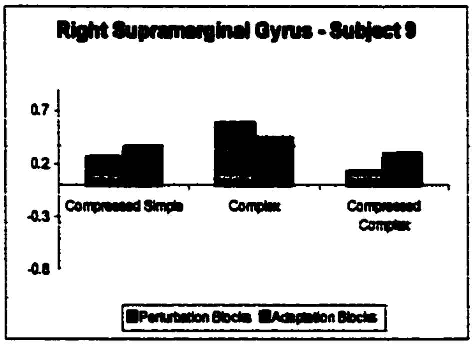

Left Supramarginal Gyrus - Subject 5

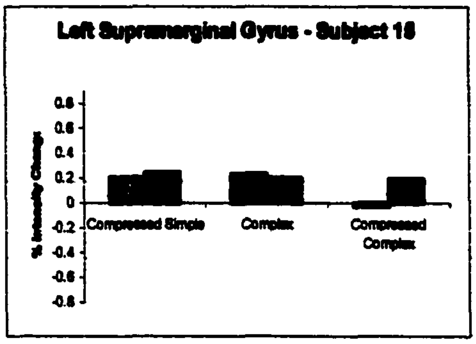

Right Supramarginal Gyrus - Subject 5

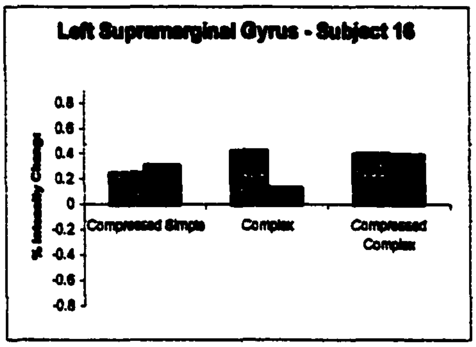

Left Supramarginal Gyrus - Subject 6

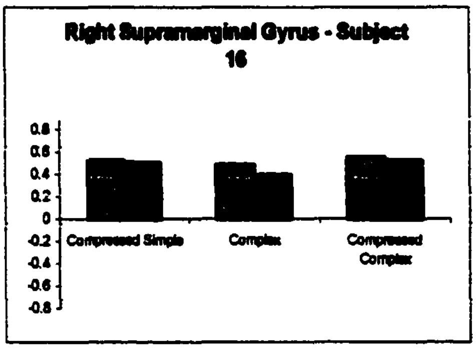

Left Supramarginal Gyrus - Subject 7

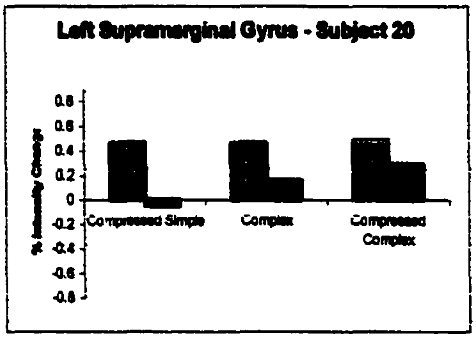

Left Supramarginal Gyrus - Subject 9

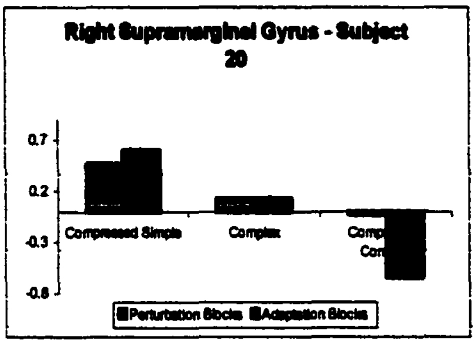

Right Supramarginal Gyrus - Subject 9


Left Supramarginal Gyrus - Subject 18

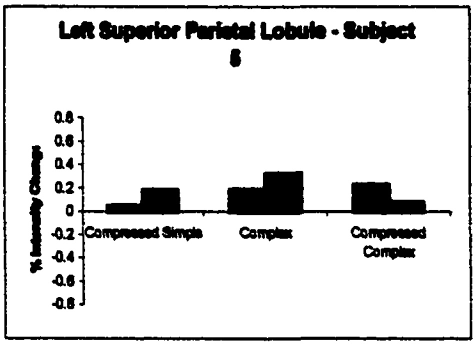

Left Supramarginal Gyrus - Subject 16

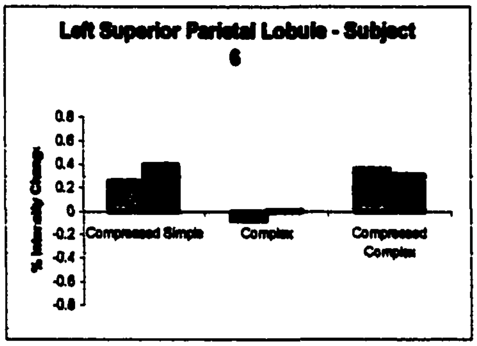

Right Supramarginal Gyrus - Subject 16

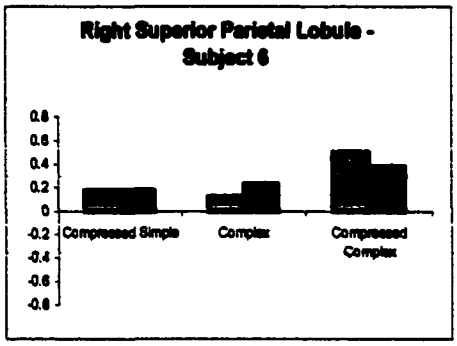

Left Supramarginal Gyrus - Subject 20

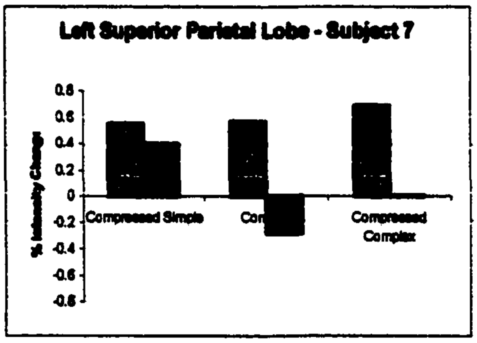

Right Supramarginal Gyrus - Subject 20

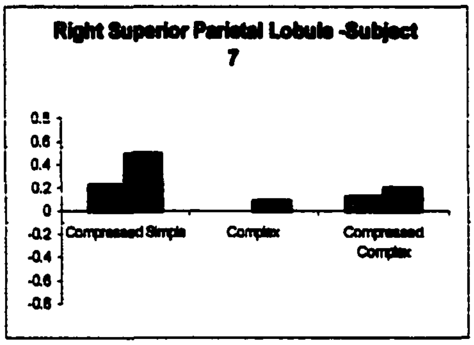
Superior Parietal Lobule

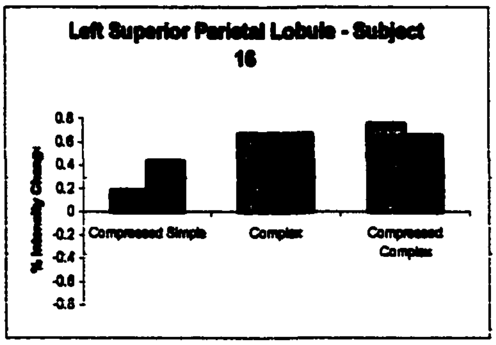

Left Superior Parietal Lobule - Subject 5

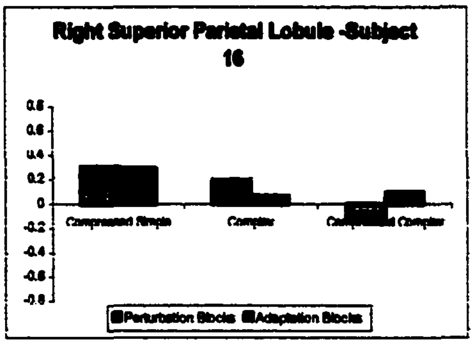

Left Superior Parietal Lobule - Subject 6

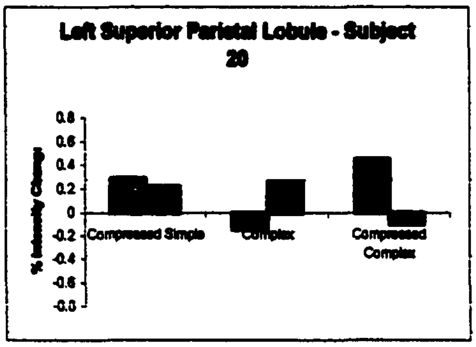

Right Superior Parietal Lobule - Subject 6

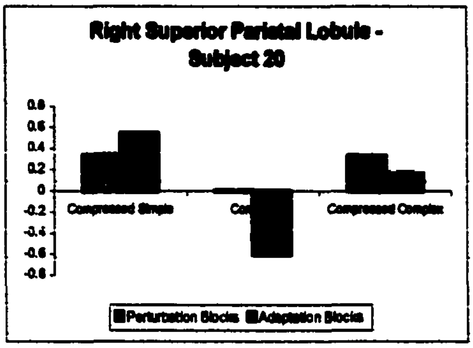

Left Superior Parietal Lobe - Subject 7


Right Superior Parietal Lobule -Subject 7

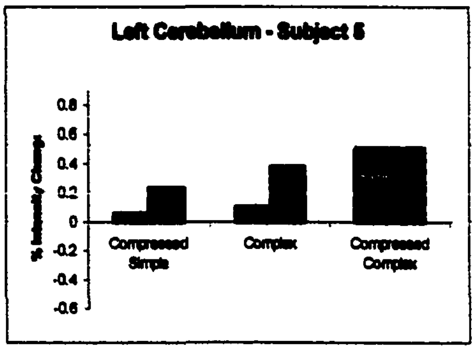

Left Superior Parietal Lobule - Subject 16

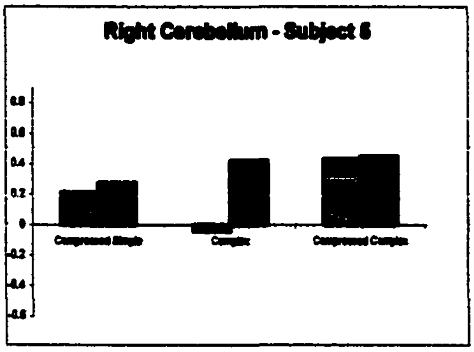

Right Superior Parietal Lobule -Subject 16

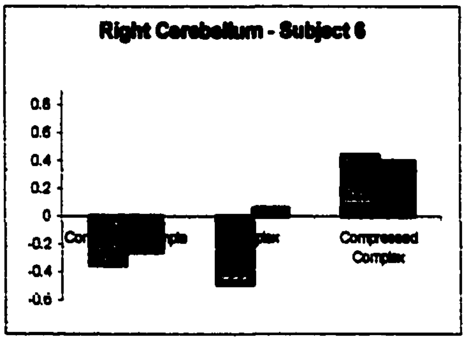

Left Superior Parietal Lobule - Subject 20
% Intensity Change
0.8
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
-0.8
Compressed Simple
Complex
Compressed Complex

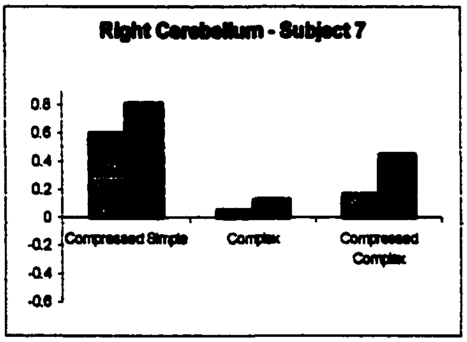

Right Superior Parietal Lobule - Subject 20
0.8
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
-0.8
Compressed Simple
Co
Compressed Complex
Perturbation Blocks
Adaptation Blocks

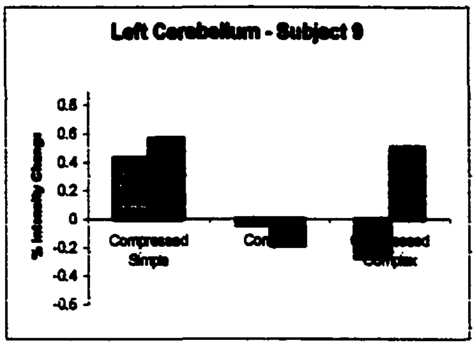
Cerebellum

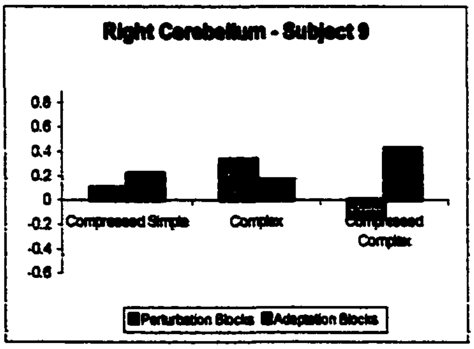

Left Cerebellum - Subject 5

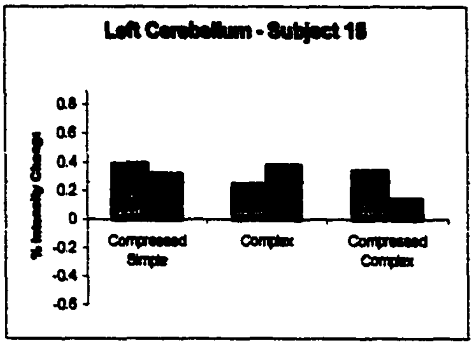

Right Cerebellum - Subject 5

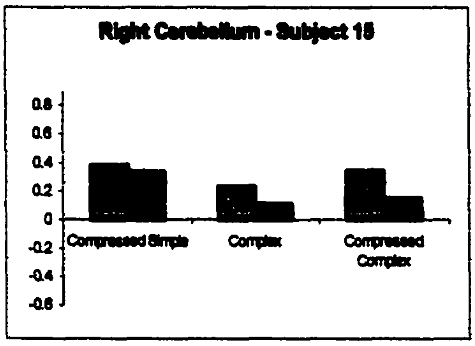

Right Cerebellum - Subject 6

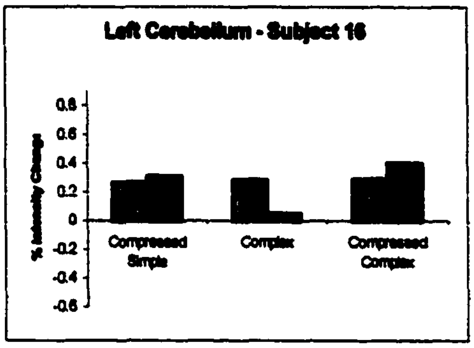

Right Cerebellum - Subject 7

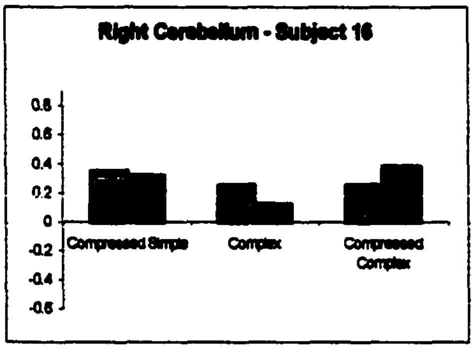

Left Cerebellum - Subject 9

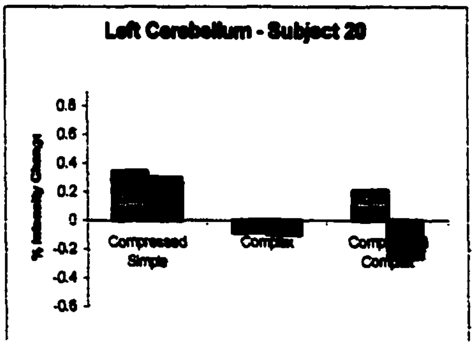

Right Cerebellum - Subject 9

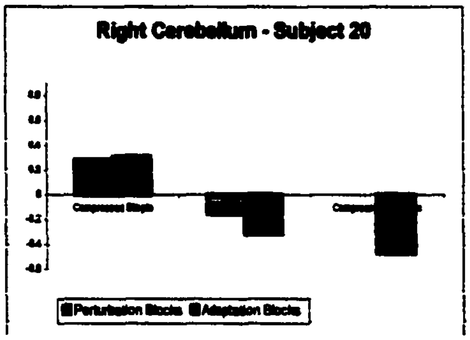

Left Cerebellum - Subject 15


Right Cerebellum - Subject 15

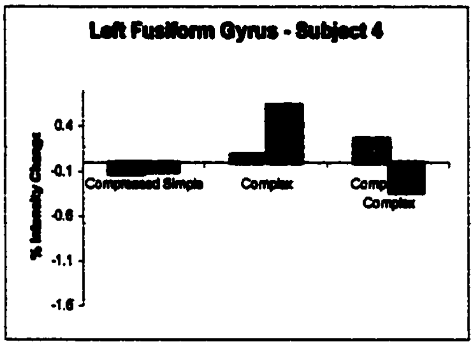

Left Cerebellum - Subject 16

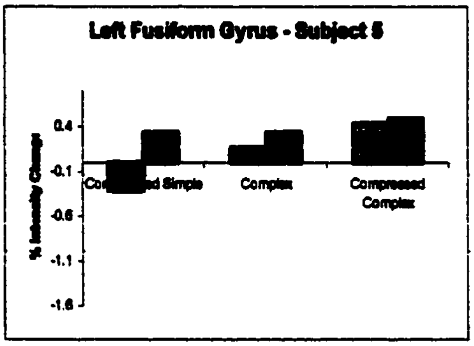

Right Cerebellum - Subject 16

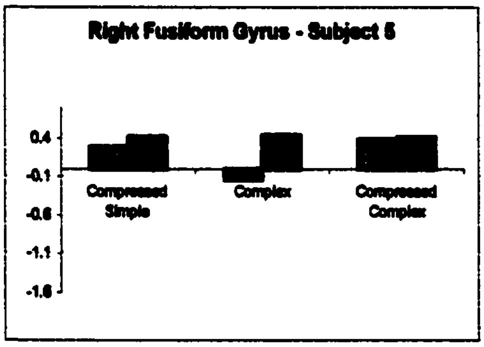

Left Cerebellum - Subject 20

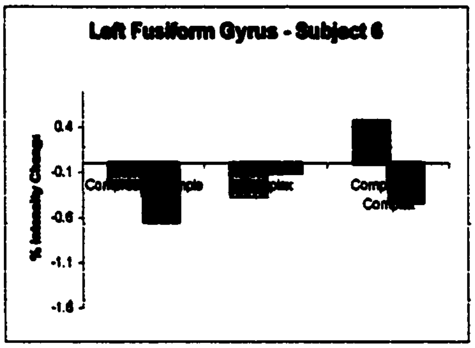

Right Cerebellum - Subject 20

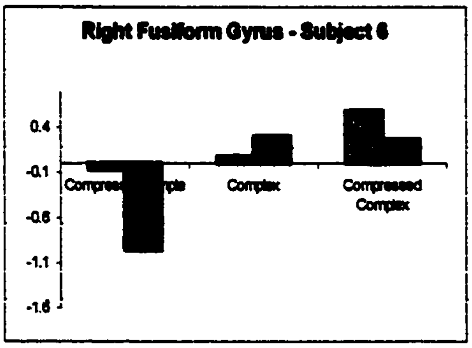
Fusiform Gyri

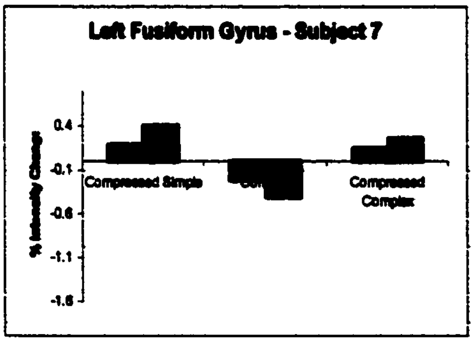


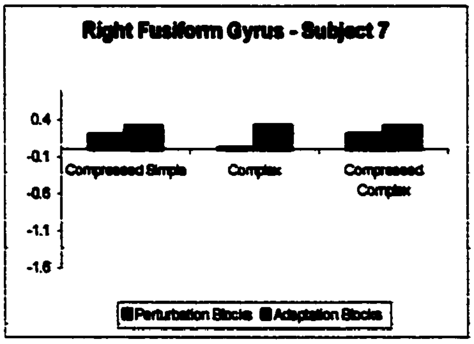


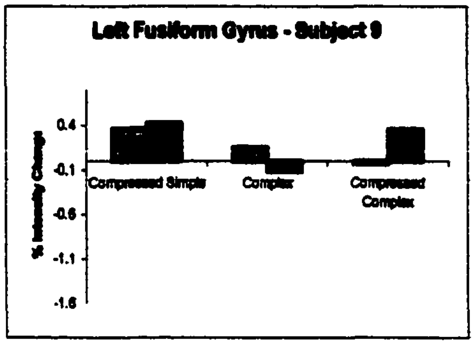




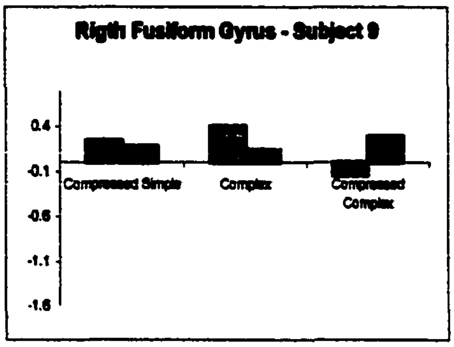




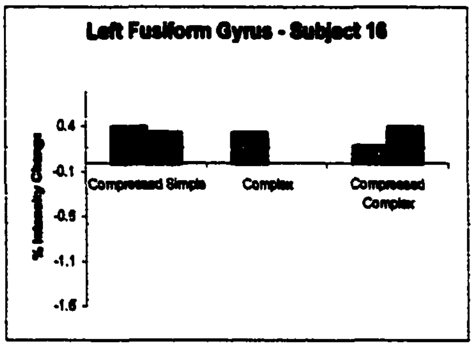




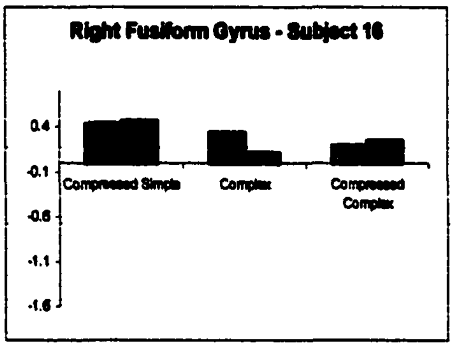
Left Fusiform Gyrus - Subject 9



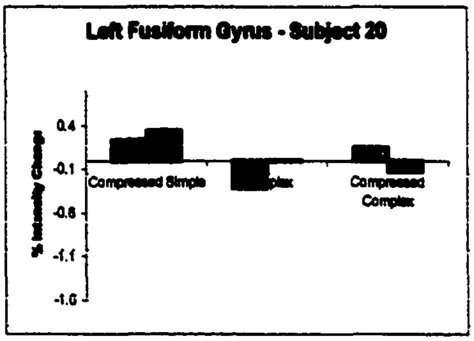
Rigth Fusiform Gyrus - Subject 9



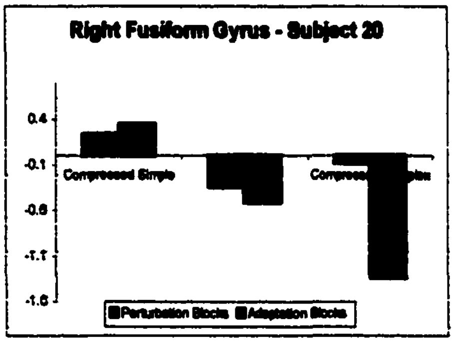
Left Fusiform Gyrus - Subject 16



Right Fusiform Gyrus - Subject 16

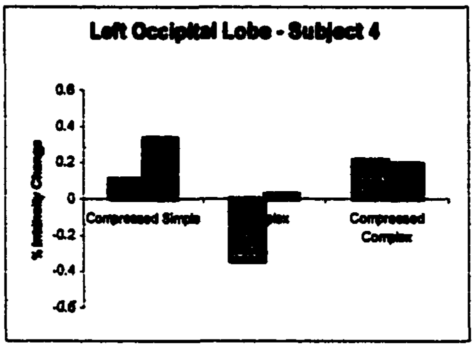


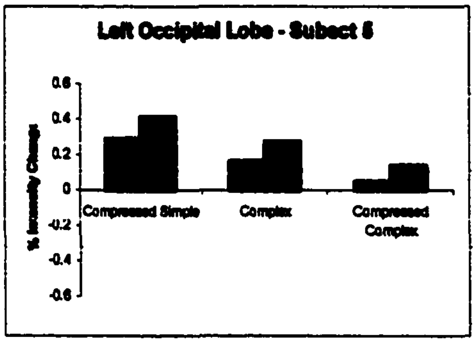
Left Fusiform Gyrus - Subject 20

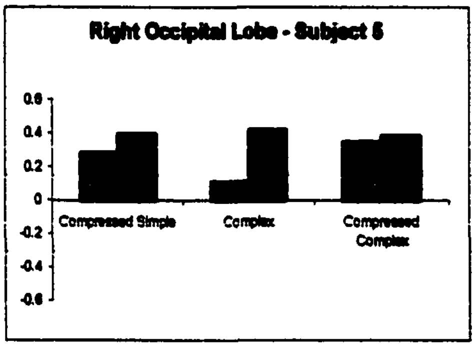


Right Fusiform Gyrus - Subject 20

Occipital Lobes


Left Occipital Lobe - Subject 4


Left Occipital Lobe - Subect 5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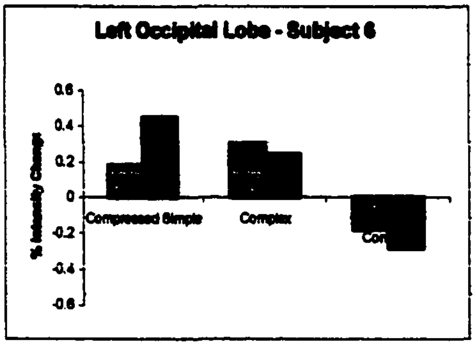
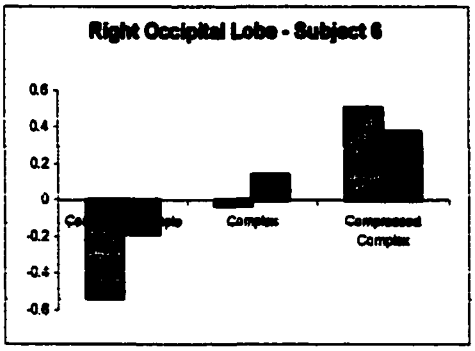

Left Occipital Lobe - Subject 6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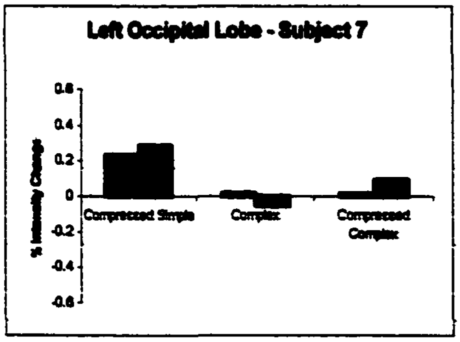
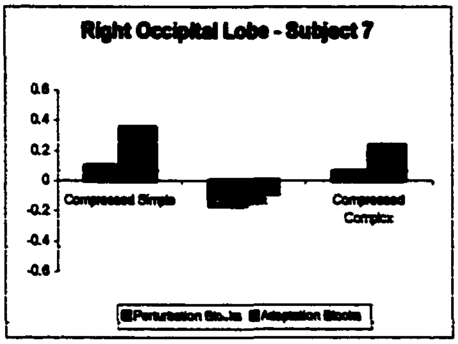
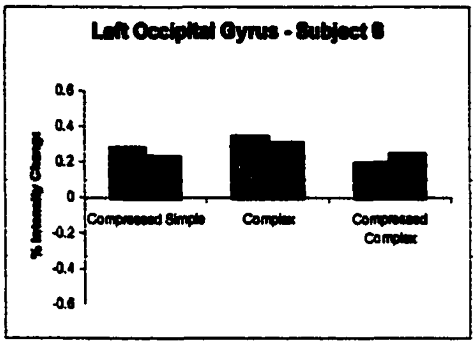
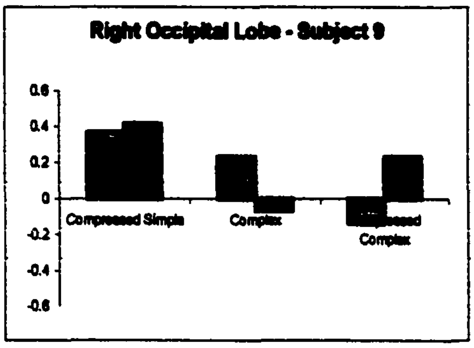
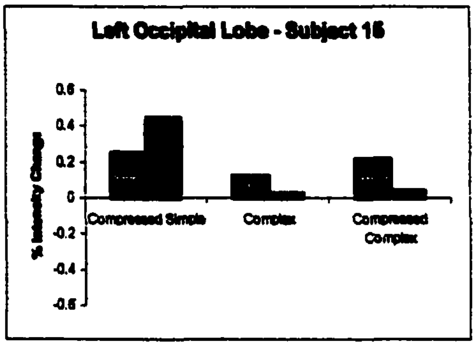
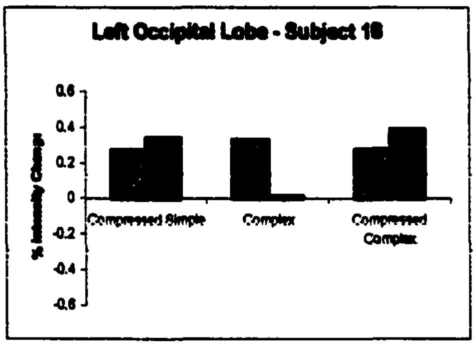

Left Occipital Lobe - Subject 7

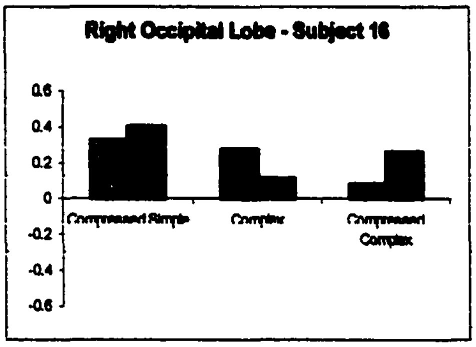

Right Occipital Lobe - Subject 7

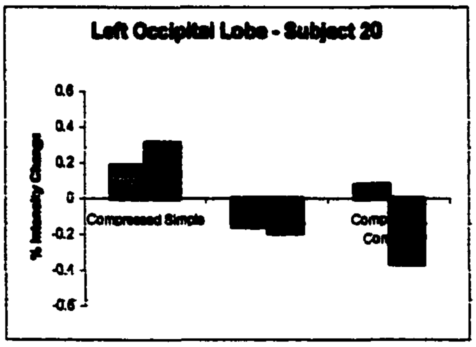

Left Occipital Gyrus - Subject 8

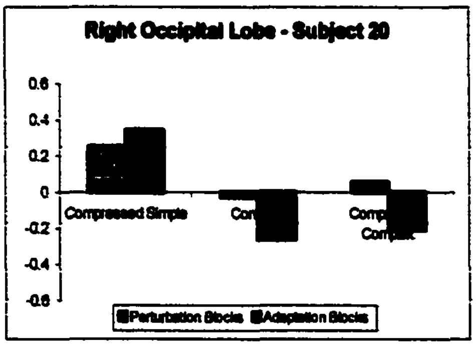

Right Occipital Lobe - Subject 9


Left Occipital Lobe - Subject 15

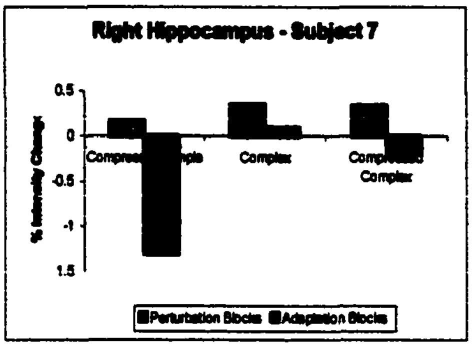

Left Occipital Lobe - Subject 16


Right Occipital Lobe - Subject 16

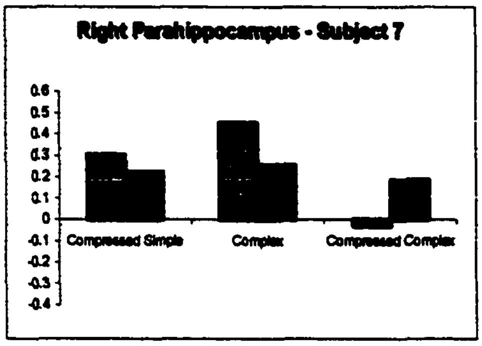

Left Occipital Lobe - Subject 20


Right Occipital Lobe - Subject 20

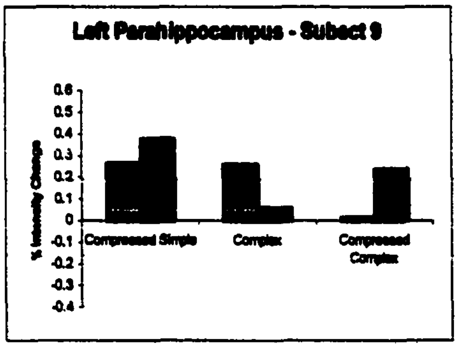
Hippocampus



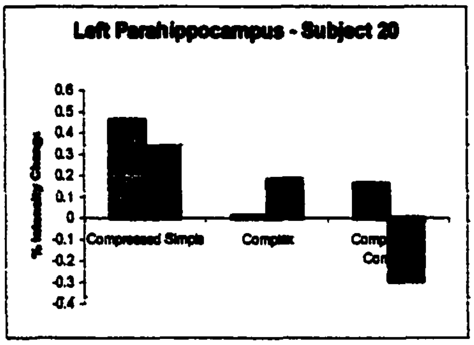
Parhippocampus



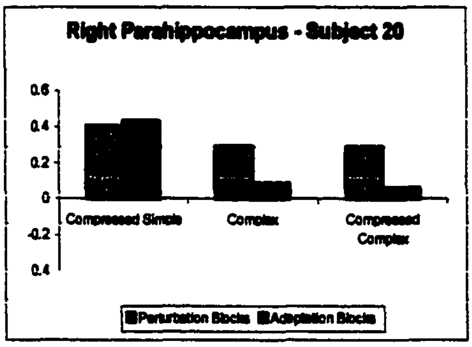
Right Parahippocampus - Subject 7



Left Parahippocampus - Subect 9

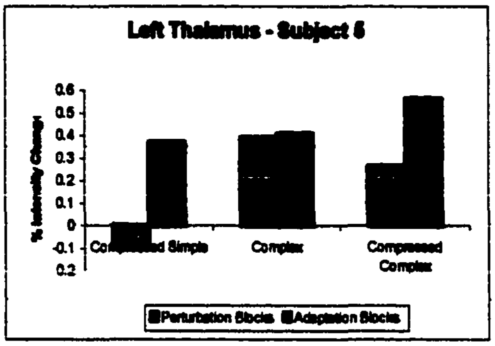


Left Parahippocampus - Subject 20



Right Parahippocampus - Subject 20

Thalamus


Left Thalamus - Subject 5
% Intensity Change
0.6
0.5
0.4
0.3
0.2
0.1
0
-0.1
0.2
Compressed Simple
Complex
Compressed Complex
Perturbation Blocks
Adaptation Blocks

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