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Sequential Memory: A Developmental Perspective on Its Relation to Frontal Lobe Functioning

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The multidimensional nature of the frontal lobes serves to organize and coordinate brain functionings playing a central and pervasive role in human cognition. The executive processes implicated in complex cognition such as novel problem solving, modifying behavior as appropriate in response to changes in the environment, inhibiting prepotent or previous responses, and the implementation of schemas that organize behavior over time are believed to be mediated by the frontal regions of the brain. Overall, the functioning of the frontal lobes assists individuals in goal directed and self-regulatory behavior. Additional theories of frontal lobe functioning have focused on its involvement in temporal, or time-related domains. The organizational and strategic nature of frontal lobe functioning affects memory processes by enhancing the organization of to-be-remembered information. Among the specific memory systems presumed to be based on anterior cerebral structures is the temporal organization of memory. An essential component of memory that involves temporal organization is sequential ordering entailing the ability to judge which stimuli were seen most recently and the temporal ordering of events in memory. Focal lesion studies have demonstrated the importance of the frontal lobes on retrieval tasks in which monitoring, verification, and placement of information in temporal and spatial contexts is of critical importance. Similarly, frontal lobe damage has been associated with deficits in memory for the temporal ordering, or sequencing, of events. The acquisition of abilities thought to be mediated by the frontal lobes, including sequential memory, unfolds throughout childhood, serving to condition patterns of behavior for the rest of the brain. Development of the frontal regions of the brain is known to continue through late adolescence and into early adulthood, in contrast to the earlier maturation of other cortical regions. The developmental patterns of the frontal lobes are thought to involve a hierarchical, dynamic, and multistage process.

KEY WORDS: memory; executive function; sequencing; brain maturation.

Sequential memory is an important component process of learning that is believed to be mediated by the frontal lobes. In the discussion that follows, we will review the current conceptualization and role of the temporal order of memory, similarly referred to as sequential memory, and how it relates to frontal lobe functioning. In an effort to provide a context in which to discuss sequential memory, a review will occur first on frontal lobe functioning including an overview of the abilities mediated by the anterior portions of the brain. A developmental perspective is emphasized with a discussion on the maturation of frontal lobe functioning during childhood and its continuation into adolescence. Then, an overall review of frontal lobe involvement in memory will lead up to an analysis of its significant role in sequential memory.

FRONTAL LOBE FUNCTIONING

Frontal lobe functioning plays a central and pervasive role in human cognition. Through executive and organizational processes, the frontal lobes assimilate and fuse perceptual, volitional, cognitive, and emotional processes (Joseph, 1996). The executive processes implicated in complex cognition such as novel problem solving, modifying behavior as appropriate in response to changes in the environment, inhibiting prepotent or previous responses, and the implementation of schemas that

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organize behavior over time are believed to be mediated by the frontal regions of the brain. Overall, the multidimensional nature of the frontal lobes serves to organize and coordinate brain functioning, which has the effect of assisting individuals in goal-directed and self-regulatory behavior. Much of this was recognized early in research on frontal lobe functioning as Luria (1969) instructed us in the title of his address to the 19th International Congress of Psychology, "Cerebral organization of conscious acts: A frontal lobe function."

Investigations have examined neuroanatomical, neurochemical, neurophysiological, and behavioral correlates of frontal lobe functioning in both humans and nonhuman animals. Clinical and experimental research has converged to indicate the fractionation of frontal subprocesses and the initial mapping of these subprocesses to discrete frontal regions (Stuss and Levine, 2002). Various areas of prefrontal cortex seem to contribute to specific and differential functions (Pandya and Yeterian, 1998). Supportive evidence for regional specialization at an early age comes from the study of nonhuman primates (e.g., Goldman, 1971), where differential effects of orbital and dorsolateral frontal lesions were found in delayed response performances. Although disturbances in the integrity of frontal lobes result in a wide range of potential behavioral and cognitive disturbances (Joseph, 1996), it has been found that lesions to different regions of the prefrontal cortex are associated with distinct behavioral outcomes, denoting considerable specialization of function within the frontal lobes (also see Reynolds, 1981).

Regional Specificity and Functional Diversity

Much of what is known about frontal functions is based on patients with dorsolateral prefrontal cortex dysfunction (Stuss and Levine, 2002). The dorsolateral region, which is part of the archicortical trend originating in the hippocampus, has been found to be associated with spatial and conceptual reasoning processes; these cognitive processes form the basis of what is referred to as executive functioning (Goldman-Rakic, 1987; Milner, 1963). Furthermore, the function of the dorsolateral prefrontal cortex has been associated with planning and the temporal organization and sequencing of behavior (Fuster, 1997; Pandya and Yeterian, 1998). Related to this role, the dorsolateral prefrontal cortex also appears to play a significant role in the integration of perception with action across time (Quintana and Fuster, 1999). Comparative studies of human infants and rhesus monkeys also have suggested a critical role for the dorsolateral frontal region in the development of delayed responding and Piaget's AB task (Diamond and Doar, 1989; Diamond and Goldman-Rakic, 1989).

The ventral prefrontal cortex, which is part of the paleocortical trend emerging from the orbitofrontal (olfactory) cortex, is connected with limbic nuclei and is involved in emotional processing (Stuss and Levine, 2002). This region is intimately associated with the anterior cingulate and the amygdala and is involved in inhibition, emotion, and reward processing suggesting a role in behavioral self-regulation. The inferior (ventral) medial frontal regions have been functionally dissociated from ventrolateral and polar regions. Hypometabolism in this region has been implicated in disorders of self-regulation that are associated with disinhibition, such as attention-deficit/hyperactivity disorder (e.g., see review by Goldstein, 1999) whereas lesions to the superior surface may result in overcontrolled behavior. The ventromedial regions play a role in decision making, whereas the ventral lateral portion is involved in working memory, planning, and sequencing of behavior, language, and attention (Pandya and Yeterian, 1998). Personality and affective disorders have been associated with orbital prefrontal lesions (Stuss and Levine, 2002). It has been proposed that the orbital frontal region has a specialized role in activating the somatic states necessary for applying knowledge in the social domain (Damasio et al., 1990). Finally, the frontal poles, particularly on the right, are believed to be involved in autonoetic consciousness and self-awareness (Stuss and Levine, 2002).

Further functional and anatomical divisions within the frontal lobes can be specified, including the superior mesial region of the frontal lobes. This region is strongly connected with cortical and subcortical motor structures including the primary motor cortex, lateral premotor cortex, and basal ganglia (Grattan and Eslinger, 1991). Superior medial lesions can cause an apathetic syndrome, as in akinetic mutism, involving the complete or near complete absence of responsiveness and spontaneity (Cummings, 1993). The superior mesial frontal lobe region is believed to contribute to the modulation of both the experience and expression of emotions and may play a strong activation role that is crucial for initiating and driving cognitive, attentional, and motor systems (Grattan and Eslinger, 1991).

Executive Functioning

The cognitive construct of "executive function" has been adopted as a general descriptor of the behaviors reflecting frontal lobe activity. In fact, often the terms "frontal" and "executive" are used interchangeably (Stuss and Levine, 2002). However, although executive function has a more concrete neuroanatomical context than a purely theoretical one, it has been suggested that executive function should not be confounded with "prefrontal" except at a hypothesis generating level because of the nonfrontal contributions to executive function and functions of the prefrontal lobes that extend well beyond the list of cognitive abilities for which executive function is an umbrella (Denckla, 1996). Such functions are highly integrative and have been described as high-level cognitive functions that are involved in the control and direction of lower-level functions (Stuss and Levine, 2002). Although the precise characteristics defining the domain of executive function are in flux with a certain degree of conceptual ambiguity (Pennington et al., 1996), there is likely universal agreement regarding the importance of executive function skills to everyday function (Welsh, 2002). In a survey of editorial board members of journals central to clinical neuropsychology, these individuals rated behavior associated with social cognition and behavioral control in the social context as those behaviors most closely aligned with frontal lobe functioning (Barringer and Reynolds, 1995; Reynolds and Kamphaus, 2002).

Theories regarding prefrontal function center around goal-directed behavior and involve the ability to maintain an appropriate problem-solving set for the attainment of a future goal (Welsh and Pennington, 1988) in a flexible manner (Funahashi, 2001). Executive function facilitates future-oriented behavior by allowing for planning, flexible strategy employment, impulse control, and organized search (Welsh et al., 1991). The term "executive function" has been used in association with attempts to characterize the deficits of patients whose frontal lobes and/or frontally interconnected subcortical regions have been impaired by damage, disease, or disordered development (Denckla, 1996). The critical features of executive functions for active problem solving include delayed responding, future orientation, strategic action selection, intentionality, anticipatory set, freedom from interference, and ability to sequence behavioral outputs (Denckla, 1994). Related definitions of executive function emphasize the role of inhibition, working memory, temporal organization, and use of strategies in the attainment of goal-directed behaviors (Fuster, 1997; Lyon and Krasnegor, 1996; Pennington and Ozonoff, 1996). Formal operational reasoning seems to reflect adequate frontal lobe development (Shute and Huertas, 1990). The ability to identify patterns among environmental stimuli and make accurate inferences from those patterns, described by Piaget as formal operational reasoning, is related to adequate frontal lobe development. The functions of the frontal lobes appear to reflect the systematic problem solving that is involved in formal operational thinking.

Executive function has been linked closely with emotion regulation, suggesting that the two functions are closely related, and perhaps both different aspects of the same frontal–subcortical circuits (Slattery et al., 2001). Emotion regulation has been defined by Slattery et al. as the process by which children gain increasing control over affective and behavioral responses. Such processes of emotion regulation are closely linked to components of metacognition. Lezak (1995) and others have integrated cognitive and social/self-monitoring systems in the construct of "meta-cognition."

Temporal Organization

Other significant theories regarding frontal functioning have been put forward. The temporal organization of behavior, speech, and reasoning has been considered "the most general function of the lateral prefrontal cortex" (Fuster, 2002, p. 99). The capacity to integrate information in the time domain is described by Fuster as the critical element in both the representation and execution of goal directed actions. Fuster (1997) provides a theory of hierarchical organization of the function of the frontal lobes which suggests that the role of the frontal lobes is the temporal organization of behavior which is subserved by three secondary processes including the temporally retrospective functioning of short-term or working memory, the temporally prospective function of prepatory set, and inhibitory control. All three processes are not strictly speaking located in the frontal lobes, but all three need the prefrontal base to operate. The "executive role" of executive function is carried out by orchestrating the activity in the other neural structures that perform those three functions more directly. Fuster emphasizes that working memory and prepatory set have opposite and symmetrical temporal perspectives that operate together in tandem through their respective neural substrates to mediate cross-temporal contingencies.

Hypotheses positing a role in temporal processing have long characterized theories regarding frontal lobe functioning. Luria (1966, 1969) argued for sequencing as a key aspect of frontal lobe functioning and included tasks of sequencing skill in his clinical examinations. The frontal lobes do appear to be specialized for processing the temporal order and frequency of environmental stimuli (Grattan and Eslinger, 1991). Such processes have been examined on tasks requiring individuals to judge the recency and frequency of experimentally presented stimuli. In studies involving individuals with injury to the frontal lobes, impairment in recency discrimination was evident when presented with visual (Milner and Petrides, 1984), auditory (Lewinsohn et al., 1972), and tactile (Corkin, 1965) stimuli. Funahashi (2001) has provided support for this function of the frontal lobes by demonstrating the presence of extensive functional interactions among temporal information-storage processes.

Further theories regarding the role of the frontal lobes in the processing of such temporal information have included Tulving's idea (Tulving, 2002) of chronesthesia, a form of consciousness that allows individuals to think about the subjective time in which they live and that makes it possible for the to "mentally travel" in such time. This ability is closely related to such neurocognitive functions as remembering past happenings, thinking about the past, expecting, planning, and thinking about the future. Other ideas concerning the contributions of the anterior regions of the brain to the processing of temporal information have included Barkley's hypothesis that deficits in working memory, particularly in nonverbal or spatial working memory, should lead to deficits in one's subjective sense of time (Barkley, 1997). This is based on the hypothesis that retaining a sequence of events in working memory, and making comparisons among the events in the sequence, leads to a sense of temporal continuity (Brown, 1990; Michon and Jackson, 1984).

A number of these theories converge on the idea that the frontal lobes play a significant role in organizing thought and behavior over time. Certainly continued research in this area, with an emphasis on interdisciplinary collaboration, will provide elaboration and further insight into this important role of the frontal regions of the brain. A comprehensive examination of the role of the frontal lobes in such temporal domains is needed. For example, Stuss and Knight (2002) have proposed that Tulving's idea of mental time travel should be considered in the context of Fuster's temporal integration and contrasted with the different temporal domains considered in the workings of memory.

Strengths and Weaknesses of Frontal Lobe Functioning Research

Research on frontal lobe functioning has provided insight into the complexity and diversity of cognitive abilities mediated by this region of the brain, as well as demonstrating the great influence of such functions on an individual's overall functioning. Unfortunately, research in the area of frontal lobe functioning, including explorations of executive function and temporal organization, have yielded a somewhat amorphous picture of these cognitive abilities. For example, there is no agreed upon unitary definition of executive function. In addition, the term "executive function" has often been confused with other cognitive processes, such as attention and memory, and used interchangeably with other similar concepts, such as self-regulation or other mental control processes (Eslinger, 1996). Executive function is a multidimensional construct encompassing varied processes and impacting behavior in complex ways. Similarly, descriptions of the frontal lobes' involvement in temporal or time related domains need continued development. Certainly the integrative and organizational nature of frontal lobe functioning makes it inherently difficult to tease apart such abilities. Given that frontal functioning has been investigated from multiple perspectives, continued integration of neuropsychological, cognitive, behavioral, developmental, and neurophysiological perspectives should be sought. In addition, a focus on the adaptive value of such functions should be taken, as suggested by Barkley with his encouragement to take a broader, more functional look and evolutionary perspective on executive functions (2001).

Relation of Frontal Functioning to Behavior and Psychological Functioning

Frontal lobe functioning contributes significantly to overall psychological and behavioral functioning, and frontal lobe dysfunction has been implicated in several childhood disorders. In fact, deficits in executive function have been found to be typical of developmental disorders in general (Pennington et al., 1996). Research has specifically examined the extent to which executive function deficits may be implicated in specific disorders such as attention deficit hyperactivity disorder (ADHD), learning disabilities, autism, and conduct disorder. Attention–Deficit/Hyperactivity Disorder (ADHD) is one of the most common of childhood disorders that have been linked to executive dysfunction (Chelune et al., 1986; Heilman et al., 1991; Mattes, 1980; Pennington and Ozonoff, 1996). Deficits in executive functioning also have been associated with higher levels of aggressive behavior and conduct disorder, as well as substance abuse (Dery et al., 1999; Giancol et al., 1996; Pennington and Ozonoff, 1996; Wiers et al., 1998). Others have suggested that children with learning disabilities demonstrate deficits on measures of frontal lobe functioning (Graham and Harris, 1993; Kelly et al., 1989; Meltzer, 1993). Autism is another developmental disorder that has been studied widely in relation to executive dysfunction (e.g., Griffith et al., 1999). However, comorbidity with mental retardation, Tourette Syndrome, and ADHD often obscures the interpretation of executive function deficits identified in individuals with autism (Pennington and Ozonoff, 1996).

DEVELOPMENT OF FRONTAL LOBE FUNCTIONING

The acquisition of abilities thought to be mediated by the frontal lobes unfolds throughout childhood, serving to condition patterns of behavior for the rest of the brain. Development of the frontal regions of the brain is known to continue through late adolescence and into early adulthood, in contrast to the earlier maturation of other cortical regions. The developmental patterns of the frontal lobes are thought to involve a hierarchical, dynamic, and multistage process (Case, 1992; Thatcher; 1992). The developmental progression of performance on frontal-mediated tasks has been shown to be stage-like with mastery of some tasks occurring between 6 and 8 years of age, and adult-level performance on other tasks occurring by the age of 12 or in the immediate postpubescent period (Passler et al., 1985). Further development of the frontally mediated executive functions may continue through age 16 (Riccio et al., 1994) with continued development through early adulthood (Golden, 1981). Research regarding the development of the nervous system, as well as research on the development of behavior, has resulted in a greater understanding of how the brain and behavior develop together. Such findings have shown complex developmental patterns, with many growth functions demonstrating non-linear, dynamic patterns, rather than monotonic growth (Fischer and Rose, 1997).

Physical Maturation of the Frontal Lobes

Neuroanatomical, neurophysiological, and neurochemical changes are involved in the continued development of the frontal lobes throughout adolescence and into adulthood (Eslinger, 1996; Sowell et al., 2001). At birth, the primary areas of the brain are developed including the connective apparati of the frontal lobes (Stuss, 1992). However, the secondary and tertiary systems involving learning, memory, emotion, cognition, language, and attention continue to develop beyond birth. Such changes appear to parallel the changes in cognitive abilities seen during adolescence (e.g., Gibson, 1991; Goldman-Rakic, 1987; Huttenlocher, 1994).

The structure and function of the prefrontal cortex changes significantly during the early childhood period (Espy et al., 2001). Such changes include the pruning of synaptic connections (Huttenlocher, 1979) and the maturation of subcortical prefrontal myelination (Kinney et al., 1988). Low rates of cortical local cerebral metabolic rates for glucose (lCMRGlc) are observed in newborns and they continue to rise until exceeding adult levels at age 3, leveling of at this high level between ages 4 and 9, and declining thereafter, reaching adult values in the second decade of life (Chugani, 1994). The "sculpting" of the neuronal substrate through the selective elimination of excess connectivity results in a decline in local cerebral metabolic rates for glucose (lCMRGlc), which eventually results in more efficient information processing (Chugani, 1994). Additional changes involving a cycle of brain electrical signal development between the ages of 1 and 5 years have been identified using resting electroencephalogram (EEG) recordings which have demonstrated an increased coherence in electrical activity between the short distance anterior electrode recording sites, lengthened frontolateral connections that become synchronous prior to frontal dorsomedial and central sites in the left hemisphere, and lateral to medial differentiation of long-distance connections to shorter fibers in the right hemisphere (Thatcher, 1992). Thatcher has proposed that two cycles or "waves" of development may be identified, in which electrical activity in the frontal cortex is increasingly coordinated with electrical activity in other cortical systems in a dynamic fashion.

Continued changes occur as development proceeds into late childhood and adolescence (Davies and Rose, 1999). Morphological maturation of the prefrontal cortex is reached around puberty, but quantitative and qualitative changes may continue into later years (Stuss, 1992). It has been suggested that the pathways of the prefrontal lobes are among the last of all brain areas to fully myelinate with this process continuing up to about age 20 (St. James-Roberts, 1979). In addition, developmental changes in neuronal density and synaptogenesis of the frontal lobes have been reported throughout adolescence including a reduction in synaptic density (Huttenlocher and de Courten, 1987; Rakic et al., 1986). A decrease in cortical gray matter also occurs with accompanied increases in cerebrospinal fluid (CSF) within the sulci of the frontal regions (Jernigan et al., 1991). Research findings also have suggested relatively stable brain volume with age-related changes in the gray and white matter components of the cerebrum between childhood and young adulthood (Caviness et al., 1996; Giedd et al., 1996; Jernigan et al., 1991). Jernigan et al. (1991) found increases in cerebrospinal fluid (CSF) within the sulci of the frontal regions which accompanied grey matter decreases during adolescence; smaller reductions in volume also were observed in subcortical grey matter nuclei. Concurrent functional changes that occur during adolescence include a change in frequency and amplitude of electroencephalographic activity (Thatcher et al., 1987), a decrease in cerebral blood flow (Kennedy et al., 1970) and a decrease in cortical metabolic rate (Chugani and Phelps, 1986).

An underlying factor that could regulate the development of brain and cognitive processes into the adolescent years is the increased secretion of gonadal hormones (Davies and Rose, 1999). There has been increasing evidence showing that gonadal steroid hormones have an organizing effect on neural mechanisms underlying cognitive functions (Bachevalier and Hagger, 1991; Kimura, 1992). In addition, changes in the regulation of neurotransmitter receptor synthesis and maintenance occur in the prefrontal cortex, including increases in dopamine and serotonin (Fuster, 1997; Goldman-Rakic and Brown, 1982) and modification in the biosynthesis of neurotransmitters and peptides occur during adolescence (Davies and Rose, 1999).

Integrated Development of Frontal Lobe Functioning

Overall, the neuroanatomical, neurophysiological, and neurochemical studies that have examined frontal lobe development have provided converging support for a model of protracted frontal lobe development that parallels and likely provides a major neural substrate for acquiring the skills and knowledge necessary for higher cognition and social behavior (Grattan and Eslinger, 1991). These relatively late changes in brain morphology and physiology are likely related to children's maturing cognitive abilities during the same time period. The development of "frontal functions" may relate not only to anatomical/biochemical maturation of the frontal lobes but also to the integrative demands of tasks on multiple brain regions (Stuss, 1992). Functional development of abilities mediated by the frontal lobes may be considered a multistage process, with different functions maturing in different ways, at different times. The greatest period of development appears to occur at the 6- and 8-year-old levels, with more moderate effects between the ages of 9 and 12 and performance approximating adult levels during adolescence and sometimes even into the early 20s, depending on task demands (Anderson et al., 2001; Chelune et al., 1986; Chelune and Baer, 1986; Korkman et al., 2001; Levin et al., 1991; Lin et al., 2000; Paniak et al., 1996; Passler et al., 1985; Welsh et al., 1991).

A hierarchical model of frontal lobe function has been proposed by Stuss (1992) which describes the progressive development of three levels of monitoring within the frontal lobes. At the first level, automatic and "overlearned" operations act upon sensory/perceptual input. Such actions comprise routine activities that are used repetitively. Executive and supervisory functions of the frontal lobe constitute the second level of processing. These functions synthesize information to organize goal-directed behavior. Self-reflection and the awareness of oneself and the environment, represents the highest level of monitoring. These three levels of hierarchical function are hypothesized to reflect developmental stages of brain maturation. The sensory/perceptual and automatic processing is believed to reflect actions of the posterior and subcortical systems. Executive and supervisory functions are proposed to correlate with the development of connections between the frontal lobe and the limbic and posterior regions, whereas self-awareness is believed to reflect development of the prefrontal region.

Early Childhood

Rudiments of frontal functioning are present early in development including the behavioral development of self-control and the capacity to regulate and voluntarily direct goal-oriented behavior in response to environmental contingencies (Welsh and Pennington, 1988). As measures sensitive to dorsolateral prefrontal function, the delayed response and the similar A-not-B tasks have provided insight into the early emergence of frontal functioning in infancy. Diamond and Goldman-Rakic (1989; Diamond, 1985; 1990; Diamond and Doar, 1989) demonstrated successful delayed response performance by 8-month-old infants who were able to correctly retrieve objects in delayed response paradigms when delays were between 1 and 2 s. By 12–13 months of age, the infant could perform successfully at 10-s delays before making the classic "A-not-B" error. The "A-not-B" error occurs over two successive trials involving the first trial presentation of an object that is hidden and successfully retrieved by the child at location A. On the next trial, the object is hidden at location B within full view of the child, yet the child returns to location A to find the object. From approximately 7 $^1/_2$–11 months, an infant tends to search for the object in the place that was previous reinforced, rather than the most recent hiding place. Another infant behavior, object retrievals is believed to be localized to the frontal lobes. During this task, the goal object is placed within a plexiglass box and can be retrieved only if a reach along the line of sight is inhibited. A new plan must be initiated in which the reach finds its way to an opening on the side of the box. The task demands self-control and planning, but does not require short-term memory because the object is always in view. At $6^1/_2$–7 months, the human infants' reach for the goal object is completely guided by visual information and cannot be inhibited or flexibly modified (Diamond, 1985). However, the infant is able to complete task at 11–12 months of age.

Childhood

Between the ages of 1.5 years and 5 years, and again between the ages of 5 and 10 years, a sequence of changes takes place in children's behavior which indicates a fundamental reorganization of their attentional, executive, and self-reflexive processes (Case, 1992). It has been suggested that it may be more difficult to identify deficient executive processes in younger children than in older children (Becker et al., 1987; Chelune and Baer, 1986; Chelune et al., 1986; Levin et al., 1991; Passler et al., 1985; Riccio et al., 1994; Welsh et al., 1991). The interaction of simple task demands and immature executive functions in early development may make it difficult to observe such functions in their less mature form (Gioia, et al., 2001). However, beginning in infancy, children begin to use processes included under the umbrella of frontal lobe functioning such as attentional control and future oriented intentional problem solving (Gioia et al., 2001). The period between 18 months and 4 years seems to be a time when the emergence of certain executive functions, working memory, inhibitory processes can be observed on tasks such as visual search, radial maze test of working memory, and self-control paradigms (Welsh, 2002).

Between the ages of 5 and 8, basic cognitive abilities are demonstrated reliably in the areas of recognition memory, concept formation, set-shifting, and rudimentary planning skills (Luciana and Nelson, 1998). By age 10, the ability to inhibit attention to irrelevant stimuli and perseveratory responses is fairly complete with mastery evident by age 12 (Passler et al., 1985). There is consistent evidence that executive functions of inhibition and flexibility mature between age 10 and 12 and performance on verbal working memory tests mature in this same age range (Welsh, 2002). Chelune and Baer (1986) found that performance on the Wisconsin Card Sorting Test (WCST; Heaton et al., 1993), a commonly used measure of frontal lobe functioning, improved most between ages 6 and 8 years, with no significant changes after age 10. Welsh et al. (1991) found similar results with adult level performance obtained on a visual search task at 5 years of age, the three-disc version of the Tower of Hanoi (TOH) at age 6, and the WCST at age 10. During the period from 5 to 7 years of age, Welsh et al. (1991) documented rapid advances in systematic problem solving. A 9- to 12-year age group showed increases in performance on the California Verbal Learning Test–Children's Version (CVLT-C) and the Tower of London test. Findings of a study by Klenberg et al. (2001), which examined differences in the development of attention and executive processes in four hundred-3 to 12-year-olds, indicated that at age 6, children had maturing abilities to inhibit responses, and at age 10 children demonstrated improved auditory and visual attention. Flexibility and monitoring are believed to be developed by late childhood (Anderson et al., 2001). Goal setting also was shown to display a developmental increase around age 12 (Anderson et al., 2001).

An important consideration in regards to the development of executive and frontal functioning is the fact that such functions are intertwined with the development of interacting systems including memory, language, emotions, and attention (Gioia et al., 2001). Development of attention during this same period likely contributes to increased frontal functioning. It has been shown that children show a maturationally based increase in attentional capacity from 1 to 4 units during the period from 4 to 10 years of age, with this increase acting to energize and constrain the novel behavior they exhibit (Case, 1992). More specifically, this developmental trend was demonstrated by children's performance on counting and spatial span tasks. The developmental progression was characterized by a linear increase from 1 to 3 units for the age range from 4 to 7 years, a deceleration at about the age of 8 years and an asymptote which began at about the age of 10 or 11 years.

Adolescence

A number of skills mediated by the frontal lobes show a protracted period of development beyond age 12. Planning, visual working memory, the coordination of working memory and inhibition, verbal fluency, and motor sequencing are among such abilities showing continued development well into adolescence (Anderson et al., 2001; Klenberg et al., 2001; Levin, et al., 1991; Lin et al., 2000; Paniak et al., 1996; Welsh et al., 1991). In contrast to the findings by Chelune and Baer (1986) which suggested that there were no significant changes on WCST performance after the age of 10, more recent findings have suggested a more protracted developmental course which continues well into adolescence with performance leveling off around age 20 (Heaton et al., 1993; Lin et al., 2000; Paniak et al., 1996). Performance on a four-disc version of the Tower of Hanoi, verbal fluency, and a motor sequencing task had not reached adult levels by 12 years of age in a study conducted by Welsh et al. (1991). In the same study, increases in performance on the California Verbal Learning Test—Children's Version and the Tower of London were noted in a 13–15 years of age group. Furthermore, into adolescence, continuing improvements are made in verbal and visuomotor fluency indicating improved strategy usage (Klenberg et al., 2001). Attentional control and processing speed also have indicated gradual development through adolescence with a significant increase in development around the age of 15 years (Anderson et al., 2001). Major gains in adolescents similarly have been noted on several measures involving the organization of memory (Levin et al., 1991). The capacity to cluster responses on the CVLT, a response pattern which Levin et al. suggested reflected sensitivity to semantic features, increased in adolescents relative to the 7- to 8-year-olds. In comparison with 9- to 12-year-olds, adolescents also exhibited increased productivity in generating words or inventing designs in accord with rules. Continued development of executive functions into early adulthood has been indicated with functional gains found in the efficiency of working memory capacity, planning, and problem-solving abilities evident not only between the ages of 15 and 19 years, but again throughout the 20–29 age period (De Luca et al., 2003).

Strengths and Weaknesses of Developmental Research

Developmental research on frontal lobe functioning has begun to provide a picture of a complex and protracted course of development with early spurts in executive abilities beginning from as young as 12 months of age, with the majority of functions beginning to develop around the age of 8 and continuing into adolescence, and with some evidence suggesting continued development into early adulthood. Because frontal functions include a number of diverse cognitive abilities, the development of frontal functioning may in fact be represented by different developmental trajectories. Despite the hypothesis that the development of frontal functioning occurs throughout adolescence and into early adulthood, research documenting such continued development is limited. This may, in part, be due to the presence of ceiling effects, characterizing many of the common measures of frontal functioning. Further examination of the hypothesized protracted course frontal functioning development into early adulthood is necessary to better document such continued maturation. The integrative nature of the frontal lobes adds another difficulty evident in the developmental research of frontal functioning. For example, although improvements in executive performance are evident throughout adolescence and potentially into early adulthood, such improvements may be the result of one or multiple factors including improved strategic development, superior inhibitory control, mastery of temporal integration, or increased processing efficiency. Continued research is needed to help better understand the developmental timetable in the functional connectivity between the prefrontal cortex and other neural regions in which it is interconnected.

Developmental Gender Differences in Frontal Lobe Functioning

In considering the developmental trajectory of frontal lobe functioning, the question arises regarding whether or not females and males display similar patterns of development. The frontal lobes have been shown to exhibit morphological gender differences and asymmetries including a more pronounced protrusion of the right frontal pole over the left frontal pole in males and a cortical thickness of similar size in the right versus left frontal lobes in females, but differing in males (Goldberg, 2001). In addition, biochemical differences have been found including a symmetrical distribution of estrogen receptors across the frontal lobes in females and an asymmetrical distribution in males (Glick et al., 1982). Given such differences, there certainly exists the possibility that the frontal lobes are functionally different in males and females and that development occurs at different rates. The research on gender differences in frontal lobe functioning has not yielded consistent results, and continued efforts in this area are needed. Although little is known about the possible developmental differences in frontal lobe functioning related to gender, the existence of a possible gender crossover in selected executive functions occurring around ages 12 or 13 has been suggested, with girls becoming more effective than boys on a range of tasks including subtests of inhibition, more complex tasks of selective attention, and verbal fluency tasks (Anderson et al., 2001; Klenberg et al., 2001). Although some studies have found a gender difference, favoring girls, some of this discrepancy has been attributed to increased verbal skills. On executive function tasks of a more visuospatial nature, it was found that males consistently outperformed females (De Luca et al., 2003).

FRONTAL LOBE INVOLVEMENT IN MEMORY

The organizational and strategic nature of frontal lobe functioning affects memory processes by enhancing the organization of to-be-remembered information (Moscovitch, 1992). Memory is the capability to acquire, retain, and use knowledge and skills; however, within this broad definition exist many diverse forms of memory and a broad array of memory processes. The term “memory” is really too vague to be very useful in clinical and scientific analyses of memory’s many manifestations (Wheeler et al., 1995). Memory does involve many regions of the brain and certain regions of the brain are much more important for some types of memory than for others. Although the results of many studies do not encourage the view that restricted frontal lobe lesions are sufficient to produce classical amnestic syndromes, there are specific memory systems presumed to be based on anterior cerebral structures including working memory, the temporal organization of memory, and source memory (Schacter, 1987).

Focal lesion studies have demonstrated the importance of the frontal lobes on retrieval tasks in which monitoring, verification, and placement of information in temporal and spatial contexts are of critical importance (Milner et al., 1985). Similarly, frontal lobe damage has been associated with deficits in the memory for the temporal ordering of events (Kesner et al., 1994; McAndrews and Milner, 1991; Milner et al., 1991). Other specific memory impairments associated with frontal lobe damage include a failure to show normal release from proactive interference in category shift paradigms (Cermak et al., 1974), impaired free recall of words (Incisa della Rocchetta, 1986), and impaired recall of remotely learned information (Mangels et al., 1996). In a meta-analysis of the relation between the frontal lobes and memory as measured by tests of recognition, cued recall, and free recall, it was found that contrary to popular belief, there is strong evidence that frontal damage disrupts performance on all three types of tests, with the greatest impairment in free recall, and the smallest in recognition (Wheeler et al., 1995). Some have viewed the memory impairment associated with frontal lobe dysfunction as secondary to other cognitive disorders, such as deficits in attention, inferential reasoning, and cognitive mediation, whereas others have viewed the memory impairment as a primary deficit in frontal lobe mechanisms (Shimamura, 1995).

The frontal lobes' involvement in memory tends to be associated with executive functions and organizational abilities, whereas medial temporal regions (e.g., hippocampus) are thought to mediate memory encoding functions. New learning is preserved in patients with frontal lobe lesions, in contrast to the severe learning impairment associated with lesions involving the medial temporal lobe or diencephalic midline (e.g., thalamic nuclei); such lesions produce organic amnesia, in which patients have difficulty remembering information and events that occur after the onset of amnesia (Shimamura, 1995). Patients with frontal lobe deficits are typically not impaired on cued recall or recognition memory, which rely primarily on effective storage and consolidation of declarative information (Pennington et al., 1996). Instead, memory disorders following frontal lesions are associated with impaired organizational and strategic processes (Moscovitch, 1992).

The frontal lobes are organizational structures that are critical for selecting and implementing encoding strategies that organize the input to the hippocampal component and the output from it, determining its correct temporal sequence and spatial context with respect to other events and for using the resulting information either to guide further mnemonic searches, to direct thought, or to plan future action (Moscovitch, 1992). Thus, it has been stated that the frontal lobes are necessary for converting information to-be-remembered from a reflexive, noneffortful act triggered by a cue to a reflective goal-directed activity that is under voluntary control (Moscovitch, 1992). In studies that have found an association between frontal lobe lesions and impaired recall of words, such deficits could be overcome when the material was presented in a preorganized fashion and when appropriate retrieval cues were supplied (Incisa della Rocchetta and Milner, 1993). These findings were consistent with the hypothesis that frontal lobe lesions result in deficits in situations where retrieval requires deliberate and strategic effort. Furthermore, in adults with prefrontal dysfunction related to dopamine dysregulation, deficits have been observed in semantic clustering and learning, but retention of information over a period of delay, which is largely mediated by medial temporal structures of the brain, remains relatively intact (Daum et al., 1995; Massman et al., 1990; Taylor et al., 1990). Similarly, patients with either left or right frontal lobe lesions display deficits in the categorization of pictures, suggesting an impairment in organizing ability and planning (Incisa della Rocchetta, 1986). Less use of semantic clustering and poor learning across trials, but intact retention of previously encoded information were found in children 11 years of age or older with phenylketonuria (PKU), a disorder commonly associated with deficits in executive functioning (White et al., 2001). Such a finding was not found for children with PKU in a younger group (less than 11 years of age), but the researchers hypothesized that this was expected because the use of higher order organizational learning and memory strategies does not typically develop until 10 or 11 years of age; frontal lobe functioning increases in importance with age as well and seems to be more crucial to organizational behavior in postpubescent individuals.

Some of the earliest findings concerning the effects of frontal lobe lesions resulted from primate studies involving delayed response and delayed alternation tasks. Impairment in such tasks resulted after bilateral excision of the frontal cortex (Jacobsen, 1935; Jacobsen and Nissen, 1937). During these tasks, the animal is confronted with two identically covered food-wells and must choose either the left-hand one or the right, on the basis of information received a few seconds before. In delayed response, the predelay cue is the sight of one food-well being baited before both wells are screened from view. During delayed alternation, the animal must avoid the location that was correct on the previous trial. In both of the above cases, the animal must respond on the basis of the most recent information. Early research using such techniques demonstrated that monkeys with extensive bilateral frontal lesions perform poorly on the delayed response tasks and on both spatial and object alternation tasks (Jacobsen, 1935; Malmo, 1942; Mishkin and Pribram, 1955, 1956). Several studies have shown that the capacity for short-term spatial memory is critical to success on delayed response and delayed alternation tasks (Goldman, 1971; Mishkin and Manning, 1978).

Endoding and Retrieval

Further support for the significant role played by the prefrontal cortex in encoding and retrieval memory processes has been provided by findings from neuroimaging studies (Buckner and Petersen, 1996; Kapur et al., 1994; Nyberg et al., 1996; Tulving et al., 1994). Tulving et al., (1994) found left frontal activation is primarily associated with memory encoding (which may be a sequential processing advantage), and right frontal lobe activation is primarily associated with retrieval of episodic memories (possibly representing a simultaneous processing advantage); based upon such data, the researchers proposed a hemispheric encoding–retrieval asymmetry (HERA) model of memory. Tulving and colleagues also found that relative to shallower encoding, deeper processing was accompanied by a prominent left prefrontal activation and resulted in higher recognition of studied material. Functional neuroimaging studies of episodic memory consistently report an association between memory encoding operations and left prefrontal cortex activation with encoding-related activation being described in dorsolateral, ventrolateral, and anterior prefrontal regions. Further findings indicate that a key function of the left dorsolateral prefrontal cortex in encoding relates specifically to the use of executive processes necessary for the creation of an organizational structure; whereas, activity in more ventral and anterior left prefrontal cortex regions appear to reflect a less specific component of episodic memory encoding (Fletcher et al., 1998). Storage of verbal material into episodic memory also has activated this area, demonstrating an association between semantic processing, higher subsequent memory performance, and increased activity in the left inferior prefrontal cortex (Kapur et al., 1994).

In several studies using positron emission tomography (PET), strong right hemisphere frontal activations were evident during effortful retrieval of recent studies material (e.g., Kapur et al., 1995, Nyberg et al., 1995; Tulving et al., 1994). Fletcher et al., (1998) found similar results with activation of the right prefrontal region during retrieval of information from episodic memory no matter whether stimuli was verbal or spatial in nature, or auditorally or visually presented. Fletcher et al.'s findings suggested that the dorsal region showed greater activation when monitoring demands were emphasized, whereas the ventral region showed greater activation when external cueing was emphasized, thus providing evidence for the functional specialization of the right prefrontal cortex for discrete cognitive processes during episodic memory retrieval. An area in the left-inferior prefrontal cortex also has been observed to be active across a wide range of tasks requiring an individual to retrieve words or information about words from semantic memory (Buckner and Petersen, 1996). Neuroimaging studies have shown that the left inferior prefrontal cortex is active during semantic retrieval of words and it has been suggested that areas within this region might be used to access and maintain a representation of words during their retrieval (Buckner and Petersen, 1996). The studies conducted by Buckner and Petersen suggested that left prefrontal areas are used during more elaborate forms of production when words must be generated in a nonautomatic or internally guided fashion. Some criticism, however, has been received regarding PET methodology's limitation in determining exactly what aspects of encoding and retrieval are reflected in prefrontal activation (McDonald et al., 2001). Because encoding and retrieval processes are complex and can be further analyzed into more specific components, it is not known what aspects of encoding and retrieval are reflected in left and right prefrontal activations. Certainly, the role of the prefrontal lobes in conscious awareness and in attentional, supervisory, executive, and strategic function may contribute to the contributions in encoding and retrieval. For example, efficient monitoring and control likely facilitate the processing of memory activation, both at the time of encoding and retrieval (Shimamura, 2002).

Studies of frontal lobe patients have yielded results providing further insight of the role of the frontal lobes in memory processes. Research has suggested that frontal lobe dysfunction is associated with impaired free recall of words (Incisa della Rocchetta, 1986; Incisa della Rocchetta and Milner, 1993), despite intact ability to recall elements from prose passages. Incisa della Rocchetta (1986) found that patients with either left or right frontal lobe lesions were impaired in recalling the names of the objects represented in a set of pictures that they had previously attempted to group into taxonomic categories. Both left and right frontal lobe lesions were associated with deficits in sorting the pictures, but, whereas the recall deficit of the patients with right-sided lesions seemed to be mainly related to their impairment in categorization, the patients with left frontal lobe excisions were impaired in recall, irrespective of whether or not the items previously had been sorted correctly suggesting that left frontal lobe lesions disrupt retrieval processes in addition to categorization. Jetter et al., (1986) similarly found impairment in free recall of words from lists in patients with frontal lobe lesions as did Janowsky et al., (1989a) when the words were unrelated. However, despite the impairment in free recall, subsequent cued recall and yes–no recognition of words from the same list were unimpaired (Janowsky et al., 1989b; Jetter et al., 1986). Such results possibly suggest that retrieval processes are affected by frontal lobe lesions to a greater degree than storage processes (Incisa della Rocchetta and Milner, 1993).

Working Memory

Another component of memory commonly associated with the frontal regions of the brain is working memory. Working memory has been described as the maintenance of transient information over brief temporal intervals to direct future-oriented activity (Roberts et al., 1994). Working memory commonly is characterized as a system of memory stores which include a limited-capacity central executive and two slave subsystems that have been referred to as the articulatory loop and the visuospatial scratchpad (Baddeley, 1992; Baddeley and Hitch, 1974). Other definitions of working memory have been proposed. Pennington (1994) defined working memory as a "limited capacity computational arena" (p. 248) that allows an individual to hold temporarily on-line constraints relevant to the current context so that the interaction of those constraints can lead to adaptation and the selection of actions. The concept of working memory has been linked closely to executive function. It has been proposed that working memory processes observed in the prefrontal cortex, especially the neuronal mechanisms for the temporary storage of information and dynamic and flexible interactions among them, can explain how the prefrontal cortex exerts executive control (Funahashi, 2001).

Working memory has been regarded as an important component of, or prerequisite for, planning, selection of actions, and action regulation; all these functions depend on the ability to process information actively in working memory. Multiple theoretical definitions of working memory in relation to executive function have been described including being one component of some of the executive functions (Lehto, 1996), a core process of the executive functions (Roberts and Pennington, 1996), or as a multifunctional unit that includes a central executive function responsible for the control and regulation of cognitive processes (Baddeley, 2001). Frontal lobe patients often demonstrate the component processes necessary for working memory including intact recognition memory, sensory perception, and motor skills, but they lack the cognitive resources to organize, monitor, and/or strategize their behavioral actions to integrate the present environmental context with future outcomes (Luciana and Nelson, 1998).

Early studies initially suggested that patients with frontal lesions performed more poorly than the nonfrontal controls on both auditory and visual short-term memory tasks (Lewinsohn et al., 1972). Similarly, Petrides and Milner (1982), using self-ordered tasks requiring the organization of a sequence of pointing responses, two verbal and two nonverbal, found patients with excisions from the left frontal lobe exhibited significant impairments on all four tasks. Patients with excisions from the right frontal lobe showed deficits only on the two nonverbal tasks. Individuals with temporal lobe lesions that involved little damage to the hippocampal complex were unimpaired on all tasks, whereas those with more radical hippocampal excision exhibited material-specific deficits that varied with the side of the lesion. These self-ordered tasks require the individual to organize and carry out a sequence of responses and thus, the self-ordered test makes considerable demands on an active, working memory (Petrides and Milner, 1982). The deficits on self-ordered tests by individuals with frontal lobe excisions can be attributed to poor organization strategies, attentional deficits, or poor monitoring of responses. Upon questioning patients with frontal lobe lesions about their approach used to complete the task, Petrides and Milner found that the frontal lobe patients were less likely than other participants to report that they had used a particular strategy and if they had used a strategy, it was likely ill-defined and less consistently used.

Failure to Release From Proactive Interference

Other research examining memory deficits in patients with frontal lobe damage has demonstrated difficulties releasing from proactive interference resulting in the inability to recall more recent events because of interference from the memory of earlier events (Cermak et al., 1974; McDonald et al., 2001; Moscovitch, 1992). Proactive interference plays a significant role in one's ability to recall information and it affects one's performance on such tasks as a memory span test (May, et al., 1999). In fact, it has been suggested that working memory span tasks may measure the ability to reduce the competition or interference from items presented on previous trials, whereby an individual retrieves only the most recently presented set (Lustig et al., 2001). Increased proactive interference is likely related to the general deficit in inhibiting irrelevant information that appears to be indicative of many aspects of frontal lobe dysfunction (Shimamura, 1995). Proactive interference effects likely contribute to the impairment in the ability to encode or register semantic information exhibited by patients with frontal lobe lesions. Proactive interference effects also have been demonstrated by individuals with frontal lobe epilepsy as well as amnesic Korsakoff patients with extensive frontal lobe involvement (Butters and Cermak, 1974).

Source Memory

An additional relationship between memory and frontal lobe functioning involves source memory. Source memory involves the contextual factors associated with learning, such as where and when information was presented. A relationship has been documented between performance on tasks of frontal lobe function and source memory in neurological patients as well as normal controls (Schacter et al., 1984). Furthermore, neuroimaging studies have suggested that the left prefrontal cortex is particularly active during the retrieval of source information (Rybash and Colilla, 1994). In addition, significant impairment in source memory ability is evident in individuals with frontal lobe lesions (Janowsky et al., 1989b). Similarly, the incidence of source errors in children is related to their performance on other measures of frontal lobe functioning independent of their age and general memory (Rugg et al., 1999). It has been suggested that disorders of source memory may be mediated by the impairment of memory for spatial–temporal context observed in patients with frontal lobe lesions (Shimamura et al., 1991).

Sequential Memory

Another contextual component of memory, believed to be mediated by the frontal lobes, is the encoding and representation of temporal information. Most broadly speaking this involves the assigning of a time tag to stimulus events. An essential component of memory that involves this temporal organization of memory is sequential ordering. Sequential ordering within memory is one function that has been described within a broader domain of frontal functioning, temporal processing (Stuss and Knight, 2002). Sequential memory has been equated with memory for temporal order (Ardila and Rosselli, 1994) and includes the ability to judge which stimuli were seen most recently or to recreate the order in which stimuli were presented. It has been suggested that a breakdown in the temporal organization of memory system leads to an inability to order actions in appropriate temporal sequences, which in turn, leads to difficulty with planning, goal-directed behavior, and sequencing (Raskin, 2000).

Initial Conceptualization of Frontal Lobes' Involvement in Temporal Domains of Memory

Early hypotheses regarding this role of the frontal lobes in memory were proposed by Milner (1968) on the basis of the findings of a study conducted by Prisko (1963) which used a modification of Konorski's delayed paired-comparison technique (Konorski, 1959). Two easily discriminable stimuli in the same sensory modality were presented in succession, 60 s apart. The participants had to identify whether the second stimulus was the same as or different from the first. The patients with frontal lobe lesions, unlike the temporal lobe groups, were impaired on those versions of the task in which a few stimuli recurred in different pairings throughout the test. However, they made virtually no errors on the one task in which new stimuli were used on each trial. Such findings led Milner to propose that frontal lobe lesions might interfere with the ability to structure and segregate events in memory, and thus, in a situation lacking strong contextual cues, patients with such lesions would be less able than normal subjects to give salience to a stimulus that had been presented 60 s ago over one that had appeared earlier in the same series of trials (Milner, 1968).

Additional support for the role of the prefrontal cortex in the temporal organization of memory was gained from the interpretation of the impairments displayed in delayed-response and delayed-alternation tasks that are associated with frontal lobe damage. Although several studies have shown that the capacity for short-term spatial memory is critical to success on delayed-response and delayed-alternation tasks (Bjork and Cummings, 1984; Goldman, 1971; Mishkin and Manning, 1978), others have emphasized the tasks' requirement for adequate registration and retention of temporal information (McAndrews and Milner, 1991; Milner, 1995; Pribram and Tubbs, 1967). Such a conclusion was based on the fact that the same two events and possible choices occur repeatedly, and the animal must remember which event occurred on the most recent trial in order to respond correctly (McAndrews and Milner, 1991). On both tasks the correct location varies from trial to trial and thus, the animal must be able to suppress the potentially interfering memory of earlier trials and respond on the basis of the most recent information.

Further research continued to support a major involvement of the frontal cortex in various aspects of the temporal organization of memory, much of which emerged from the study of patients who had sustained a unilateral frontal lobe excision for the control of cerebral seizures. The prefrontal cortex has been shown to participate in monitoring and remembering temporal order of contextually similar events as well as being involved in the planning and monitoring of the execution of self-determined sequences of responses (McAndrews and Milner, 1991; Milner, 1971; Milner et al., 1985). In a study conducted by McAndrews and Milner (1991) it was found that both left and right frontal lobe groups were impaired on order judgments for named items. Furthermore lesions in the mid-dorsolateral frontal cortex were associated with impaired verbal recency judgments, whereas neither left nor right anterior–temporal lobectomy affected such judgments (Milner et al., 1991). Similar results were provided by a study conducted by Petrides (1991) which demonstrated that the primate mid-dorsolateral frontal cortex is a critical component of a neural circuit underlying the monitoring of the serial order of stimuli. The group with mid-dorsolateral lesions performed close to the level expected by chance when the serial order judgments involved stimuli that had occupied middle positions in the presentation sequence. The ordering deficit on temporal memory tasks also is seen when frontal patients recount well-rehearsed scripts' of daily life situations (Godbout and Doyon, 1995) and in reconstructing a motor sequence (Kolb and Milner, 1981).

Lateralization Associated With Sequential Memory

Research studies have utilized stimuli of different modalities to demonstrate some degree of lateralization associated with memory for temporal order. Kesner et al. (1994) found that relative to controls, the individuals with prefrontal cortex damages were not impaired for spatial location recognition memory, but were slightly impaired for spatial order recognition memory. Specifically, right and bilateral prefrontal cortex groups performed worse than the left prefrontal cortex on the order recognition task. In the same study, using verbal stimuli, results indicated that relative to controls, individuals with prefrontal cortex damage were not impaired for word recognition memory, but they were impaired for word order recognition memory. Other analyses suggested that the bilateral prefrontal cortex damaged group performed worse than the right or left prefrontal cortex damaged groups. When memory for abstract pictures was examined, data were consistent and suggested no impairment for recognition memory, but impairment for abstract pictures (order) recognition memory amongst the individuals with prefrontal cortex damage. Similar findings were found using memory for hand positions. Overall, a certain degree of lateralization was present in Kesner et al.'s study in that patients with right prefrontal cortex damage showed an item-order dissociation for words, spatial locations, and abstract pictures, whereas patients with left prefrontal cortex damage showed an item-order dissociation only for words and abstract pictures.

Impairment in Sequential Memory in Clinical Groups

Additional evidence regarding the involvement of the prefrontal cortex in the coding of temporal sequence, order or succession in memory has come from clinical groups that are commonly associated with frontal lobe dysfunction. Patients with Korsakoff's syndrome, like other amnesic patients are impaired on many standard tests of memory; yet they also have a disproportionately large impairment on tests of temporal order memory (Meudell et al., 1985; Shimamura et al., 1990). In Korsakoff's syndrome, damage typically involves the dorsal medial nucleus of the thalamus and atrophy of the frontal lobes (Joseph, 1996). Shimamura et al. (1990) examined temporal order of memory in patients with frontal lobe lesions, amnesic patients with Korsakoff's syndrome, other non-Korsakoff amnesic patients, and control participants by presenting a list of 15 words and asking the individuals to reproduce the list order from a random array of the words; in addition, the participants were asked to place in chronological order 15 public events that had occurred between 1941 and 1985. Patients with frontal lobe lesions had particular difficulty remembering the sequential order of the words in the list and the patients with Korsakoff's syndrome were quite impaired relative to the group of non-Korsakoff amnesic patients. However the difference was not significant; the researchers hypothesized that the failure to find a significant difference between the two amnesic groups was due largely to one patient with Korsakoff's syndrome who performed quite well. In addition, patients with Korsakoff's syndrome were markedly impaired when asked to arrange facts in chronological order. It was suggested that performance on the fact sequencing test might be mediated in part by semantic associations, which would likely be more elaborate than the semantic associations for recently presented words.

Theories Regarding Underlying Mechanisms of Sequential Memory

Several different theories have been proposed providing possible explanations for deficits observed on tasks requiring memory for temporal order. Although the presence of a temporal ordering deficit in patients with frontal lobe dysfunction is fairly well-documented, the process that accounts for this deficit is unclear (McDonald et al., 2001). Pribram and colleagues (Pribram et al., 1977; Pribram, and Tubbs, 1967) have proposed that deficits on delayed alternation reflect a failure to parse or segment the ongoing stream of experience into discrete "temporal moments" and similarly argued that the temporal characteristics of the delayed-alternation task constitute the main source of difficulty for monkeys with dorsolateral frontal lobe lesions. Such a theory was based upon studies that showed monkeys with dorsolateral frontal lobe excisions were unimpaired when the experimenter imposed external "temporal landmarks" by asymmetrically manipulating the duration of the delay period between trials. Milner has suggested (Milner, 1971; Milner et al., 1985) that frontal lobe damage might compromise encoding or retrieval of "time tags" hypothesized to be laid down as part of the mnemonic record of experienced events. This idea was first proposed by Yntema and Trask (1963) who suggested that memory may be assumed to contain items of information, each of which bears a number of tags that describe it and show how it is related to other items in memory. Included among these are time tags, which can be used to determine which of a series of stimuli occurred more recently. Nairne (1990) provided support for the theory that effortful, intentional encoding and search, as well as relatively automatic "time-tagging" processes are involved in memory for temporal order through a study involving long-term recall of order when participants were not expecting a memory test. Such results suggested that temporal information was encoded relatively automatically.

Ramsay and Reynolds (1995), in an extensive review of the clinical literature on forward and backward recall, found that forward recall of digits and other sequential material was more impaired among left hemisphere and frontal lesioned patients relative to backward recall. Forward and backward recall, even though order is crucial to both, apparently invoke different strategies for encoding and recall. Posterior and right hemisphere lesion patients tend to perform more poorly on backward recall relative to forward recall, suggesting a spatial or visualization strategy is involved. On the basis of such findings, it has been concluded that scores from forward and backward recall should not be combined (Reynolds, 1997). Strategy development and subsequent information processing strategies are likely to be more salient than the stimulus presentation in determining functional specialization, i.e., brain function is organized along the lines of process specificity and not stimulus specificity.

Other theories have emphasized that sequencing of memory is a specific component of a broader deficit. Schacter (1987) has suggested that deficits are associated with an impairment in automatic encoding of spatiotemporal information. Such a role is consistent with the frontal lobes' involvement in spatiotemporal context The role of active strategies and reconstruction in memory for temporal order also has been proposed (Winograd and Soloway, 1985; Michon, and Jackson, 1984; Moscovitch, 1989). It has been suggested that the impairment of temporal order memory in patients with frontal lobe lesions may be part of a broader deficit in the ability to organize and retrieve information (Shimamura et al., 1990). It is possible that a deficit in temporal order memory, such as that observed in patients with frontal lobe lesions is related to other cognitive deficits, such as deficits in planning, problem solving, metamemory, verbal fluency, and cognitive estimation (Shimamura et al., 1990).

Sequential Memory and Its Relation to Working Memory

The relationship between the temporal order involved in memory and working memory have been discussed. Pennington et al. (1996) suggest that the tasks in which patients with frontal lobe deficits have shown impairment on including tasks for temporal order, source memory, and free recall are tasks that place strong demands on working memory because they allow an individual to access, organize, and manipulate memories. Impairment in serial order does represent an inability to monitor flexible sequences of events that may change from trial to trial (Petrides, 1991). Case (1992) has suggested that the role of working memory is the maintenance of a temporally ordered sequence of information while inhibiting the intrusion of potentially competing sequences of information. Case proposed that tests of working memory should include three specific requirements: execution of a repetitive pattern of operations, storage of the products of these operations in the face of interfering stimuli, and the output of these products in a precise sequence. It has been proposed that the mid-dorsolateral frontal cortex constitutes a specialized neural network for the on-line maintenance and monitoring of precise cognitive presentations of intended acts, as well as of the order in which events or actions are occurring or can be made to occur (Petrides, 1991), and such specific functional contributions of the mid-dorsolateral frontal cortical areas which are well developed in the primate brain, give rise to a considerable capacity for planning.

Relation of Sequential Memory to Behavior and Psychological Functioning

An important component of frontal functioning that significantly contributes to learning is sequential memory. The accurate representation of temporal order is crucial for both perceptual and motor functions whether it be in comprehending a sentence or playing a musical instrument. The serial order of information often must be transiently kept in working memory before being translated to motor output such as when looking up a telephone number and dialing the individual digits in the proper order. Similarly, when recalling something, it is important not only to recall what happened, but when it happened. Memory for temporal order has been found to be sensitive to different pathological groups (Vakil and Blachstein, 1994). For example, auditory sequential memory impairments have been shown to be present in individuals with a reading disability (Howes et al., 1999; Siegel, 1994). Furthermore, there have been consistent research findings suggesting individuals with reading disabilities have difficulty recalling sequences of alpha-numeric stimuli presented in an auditory–verbal format (Shapiro et al., 1990; Waldron and Saphire, 1990; Watson and Willows, 1995). In validity studies performed during the standardization of the Test of Memory and Learning, (TOMAL; Reynolds and Bigler, 1994a) it was found that a sample of children and adolescents with learning disabilities, although scoring significantly below the standardization sample mean on all subtests but one, displayed their worst performance on a measure of attention and concentration, with performance nearly as low on the measure of sequential recall (Reynolds and Bigler, 1994b). Although these two scales overlap in content, both constructs are often thought to be impaired in children with learning disabilities.

It also has been shown that children and adolescents with ADHD perform significantly worse than controls on measures of sequential memory (August and Garfinkel, 1990). Similar results were obtained in a study conducted by Gorenstein et al., (1989) which found that children who displayed inattentive and overactive behaviors exhibited deficits on a sequential memory task. However, results have been equivocal as Chelune et al., (1986) did not find differences on sequencing processing tasks between children with ADHD and controls. The presence of such deficits have been investigated in other disorders including in a study by Lueger and Gill (1990) that found adolescents with conduct disorder displayed impaired sequencing on memory and motor tasks. Continued research is needed to better delineate the relationship between sequential memory ability and learning, as well as its relationship with different developmental disorders and overall functioning.

DEVELOPMENT OF MEMORY IN RELATION TO FRONTAL LOBE MATURATION

Overall, there is evidence that frontal lobe maturation is specifically related to improving memory functioning (Sowell et al., 2001). The maturation of the prefrontal cortex underlies an increase in efficiency of executive control which in turn facilitates memory and learning. The association between executive function and memory makes the two difficult to separate. It has been hypothesized that prefrontal maturation underlies an increase in the efficiency of executive control (Dempster, 1992). Learning and the complex phenomenon of being able to acquire new skills and knowledge and the requisite memory processes are inextricably linked with executive functions (Schneider and Pressley, 1997). It has been proposed that the development of hippocampally based recognition memory skills and the prefrontal organization of working memory processes proceeds dimensionally through the course of middle childhood with such development being initiated with the structural maturation of specific brain areas, then refinement of local circuitry within these regions, and finally, to the formation of widespread neural networks that integrate interactions between local circuits and distal sites (Luciana and Nelson, 1998).

Developmental studies have provided information regarding the development of memory. A form of preexplicit memory which is dependent on the hippocampus develops in the first few months and between 8 and 12 months, a more adult-like form of the explicit memory emerges, which draws broadly on limbic and cortical structures (Nelson, 1995). During toddlerhood, the development of memory-for- location is related to both increasing age and to individual differences in self-control, as well as a failure to use available relevant cues (Lee et al., 1983). Picture recognition memory reaches adult level performance by 4 years of age (Welsh et al., 1991). Young children's ability to retain information in memory undergoes substantial increases between 5 and 11 years of age, when short-term memory capacity approaches adult levels (Gathercole, 1998). Ardila and Rosseli (1994) found a steady increase in performance on all Wechsler Memory Scale subtests between the ages of 5 and 12. However, the use of higher order organizational learning and memory strategies does not typically develop until 10 or 11 years of age (Bjorklund and Douglas, 1997). Results of an examination of the development of learning and memory, suggested an initial growth spurt at around 7–8 years of age, which the authors stated was consistent with physiological literature suggesting the maturation of prefrontal areas and cortical connections in general (Anderson and Lajoie, 1996). The researchers did find that between the ages of 7 through 13, long-term memory (the capacity of the child to retain information over time) did not change greatly with age. In comparison to the older age groups, the 7- and 8-year-old groups exhibited shorter-memory spans, less efficient learning skills, and poorer delayed recall. In addition, they appeared to utilize fewer memory strategies, and exhibited poorer spontaneous retrieval and flatter learning curves than older children. A developmental transition from 8 to 9 years existed, with the 9-, 10-, and 11-year-old groups generally achieving higher scores than the younger groups. Older children, (12- and 13-year-olds), performed better in most areas, supporting the possibility of a further developmental spurt, associated with more effective processing and greater capacity, as well as an increasing ability to control memory and learning actively, to develop and implement memory strategies, and to organize material.

Serial Recall

Examinations of the developmental trends of different components of memory have occurred. Children's level of performance on tests of phonological memory such as digit span and other serial recall tests increases dramatically over the early and middle years of childhood (Gathercole, 1998). Much of this development appears to arise from developmental increases in the speed of rehearsing and of retrieving material from memory and from the emergence of subvocal rehearsal as a strategy for actively maintaining the contents of the phonological store. The memory span for the maximum number of unrelated verbal items that can be remembered in correct sequence shows an average two- to threefold increase from between two and three items at 4 years of age to about six items at 12 years (Hulme et al., 1984). Similarly, in a sample of individuals, age 7 through 15, performance on digit span was slow to gradually increase throughout this age period (Isaacs and Vargha-Khadem, 1989).

Verbal Memory

Investigations of the developmental trends of verbal learning tests also have occurred and suggest a steady increase in performance throughout childhood and into adolescence (Bishop et al., 1990; Vakil et al., 1998) A steady increase in performance on the Rey Auditory–Verbal Learning Test (Rey AVLT) was evidenced in a sample of individuals ages 5–16 years of age (Bishop et al., 1990). However, in another study conducted by Vakil et al. (1998), more dynamic changes were displayed during the 8- to 10-years old range, as compared to the 11- to 17-years-old range. The researchers concluded the capabilities required to cope optimally with the different demands of the Rey AVLT, such as storage capacity or strategies, are stabilized around the age of 11. The mental operations developed by the age of 11, such as utilization of strategy, planning, and categorization are attributed to frontal lobe functioning (Shimamura, 1995).

Visual/Figural Memory

It has been suggested that the capacity to retain visuospatial characteristics of events (stimuli, or information), for short periods of time is mediated by a short-term memory system dissociated from the phonological loop, and may consist of dissociable visual and spatial/temporal subcomponents (Gathercole, 1998). Performance on a spatial span task increased significantly between 9 and 10 years of age, while performance on the backward spatial span increased between 7 and 8 years of age (Isaacs and Vargha-Khadem, 1989). In an investigation of the developmental progression of performance on the memory condition of the Rey-Osterrieth Complex Figure (ROCF), major improvement was observed at 7- to 8-year-old range; at 11–12 years, scores were 2.3 times higher than the average scores at 5 or 6 (Ardila and Rosselli, 1994).

Sequential Memory

Given the frontal lobe involvement in sequential memory, it may be hypothesized that such an ability would show a course of development similar to other measures of frontal lobe functioning. In the evaluation of the developmental patterns of a sequential verbal memory test, Ardila and Rosselli (1994) expected the test to be particularly sensitive to central nervous system maturation given that sequential memory has been associated with frontal lobe activity; however this was not the case. The sequential verbal memory scores did not improve steadily between 5–6 and 11–12 years. They began to decay very early, even at ages 9–10. The authors speculated that perhaps younger children store information in a "bit-by-bit recording" and in a less structured way; however, with advancing age, the child learns to organize the to-be-recalled information in a meaningful way, and some metamemory strategies are developed (Ardila and Rosselli, 1994). In an investigation of the developmental course of children's memory spans on both the digit span and Corsi blocks tasks, Issacs and Vargha-Khadem (1989), demonstrated a regular increase across the age range of 7–15 years with a total increase of about 1.5 items of span during this age range, with Corsi spans at each age lagging about one item of span behind digit span. The Corsi blocks task involves a three-dimensional display of nine blocks which is placed in front of the participant, who observes the experimenter tapping the blocks in an unsystematic sequence. The task is to repeat the activity, tapping the same blocks in the same sequence.

The development of temporal ordering also was investigated using a recency task. Significant age effects were evident with 6-year-olds performing significantly less accurately than 8-year-olds and 8-year-olds significantly less accurate than 10- and 12-year-olds, who did not differ from each other (Becker et al., 1987). Interestingly, unlike the other four frontal tasks given to the participants where 10- and 12-year-olds were performing nearly perfectly, on the temporal ordering task, their performance leveled out at about 60% accuracy. Because no adult norms were available, researchers did not know whether better accuracy could be achieved later (other tasks included go–no go, auditory sequential and visual simultaneous conflict tasks).

Developmental Gender Differences in Memory

Gender related developmental variation in memory has been investigated by a number of researchers. A number of studies have suggested that females demonstrate an advantage on verbal memory measures (Kramer et al., 1997; Sowell et al., 2001; Vakil et al., 1998) Sowell et al. (2001) found that girls performed significantly better than boys in learning a list of words. Such results were associated with a larger mesial temporal lobe volume (relative to brain size) in girls as compared to boys. The same study found no gender effects on figure recall task. A similar advantage for girls over boys on verbal memory measures was demonstrated by Vakil et al. (1998). The girls' advantage remained constant across all age groups. Kramer et al. (1997) suggested girls were more likely than boys to use a semantic clustering strategy and display more effective long-term memory mechanisms. It has been proposed that the edge females have over males in memory performance may be specific to verbal memory (Trahan and Quintana, 1990). However, the sex differences in verbal memory evidenced in the study conducted by Kramer et al. (1997) tended to be small, averaging approximately 0.5 words per trial during the learning trials and increasing to 0.9 words on the delayed trials of the CVLT-C.

In a review of the literature, Trahan and Quintana (1990) found mixed results regarding gender differences in performance on memory measures. The review suggested that several studies found a gender effect with females tending to perform somewhat better on verbal memory procedures, while males performed slightly better on measures of visual memory; however some studies have suggested that no consistent pattern of performance has yet emerged (e.g. Forrester and Geffen, 1991). Overall, the literature on gender related differences on verbal memory tasks in young children is relatively small and inconclusive.

SUMMARY AND CONCLUSIONS

As an organizer and coordinator of brain functioning, the frontal lobes play a central and pervasive role in human cognition. The organizational and strategic nature of frontal lobe functioning affects memory processes by enhancing the organization of to-be-remembered information. The frontal lobes appear to be specialized for processing the temporal order and frequency of environmental stimuli, and thus the temporal organization of memory is among the specific memory systems presumed to be based on anterior cerebral structures. Such a role in memory is consistent with the belief that the frontal lobes are critical in the broader domain of temporal processing. The acquisition of abilities thought to be mediated by the frontal lobes, including sequential memory, unfolds throughout childhood and adolescence, serving to condition patterns of behavior for the rest of the brain. Development of the frontal regions of the brain is known to continue through late adolescence and into early adulthood, in contrast to the earlier maturation of other cortical regions, and involves a hierarchical, dynamic, and multistage process (Case, 1992; Thatcher, 1992). This protracted development of the frontal lobes parallels and likely provides a major neural substrate for acquiring the skills and knowledge necessary for higher cognition and social behavior. The greatest period of development in frontal lobe functioning appears to occur at the 6- and 8-years-old levels, with more moderate effects between the ages of 9 and 12 and performance approximating adult levels during adolescence and sometimes even into the early 20s, depending on task demands. However, more research is needed to further document the continued development of frontal functioning into early adulthood. An important consideration in regards to the development of frontal functioning is the fact that such functions are intertwined with the development of interacting systems including memory, language, emotions, and attention. Such interrelatedness makes it difficult to separate and individually assess each of these functions.

Although research involving patients with frontal lobe damage has provided information regarding the role of the anterior portions of the brain in the temporal organization of memory, research has been limited regarding the development of such a processing ability throughout childhood and adolescence. Further developmental studies can provide a source of information for deciding how different frontal functions are actually related to each other and to the brain, as well as provide a better idea of how these brain functions develop together. A developmental perspective is important because a better understanding of the changes that take place in memory throughout childhood and adolescence will provide insight into a portion of the many processes and systems involved in human memory. Such an understanding of the development of memory is of great importance to psychologists. Because learning and the complex phenomenon of being able to acquire new skills and knowledge are inextricably linked with sequential memory and frontal functioning, the assessment of memory provides a crucial method for understanding the profiles of learning difficulties. Through gaining knowledge of the developmental patterns associated with sequential memory, a better understanding of the unfolding of organizational strategies used in learning will be gained. In the clinical examination of children and adolescents with CNS compromise, a development-based understanding of frontal functions, especially as related to memory, is crucial to accurate diagnosis. Memory disturbances of various forms may implicate different brain systems at different ages and may be complicated even further by gender, although the latter effects are likely to be small.

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