

ORIGINAL ARTICLE

Donald T. Stuss · Michael P. Alexander

Executive functions and the frontal lobes: a conceptual view

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Abstract Several problems in understanding executive functions and their relationships to the frontal lobes are discussed. Data are then presented from several of our studies to support the following statements: (1) the examination of patients with focal frontal lobe lesions is a necessary first step in defining the relation of executive functions to the frontal lobes; (2) there is no unitary executive function. Rather, distinct processes related to the frontal lobes can be differentiated which converge on a general concept of control functions; (3) a simple control-automatic distinction is inadequate to explain the complexity of control-automatic processes; (4) the distinction between complex and simple tasks cannot explain the differences in functions between the frontal lobes and other brain regions; and (5) the most important role of the frontal lobes may be for affective responsiveness, social and personality development, and self-awareness and unconsciousness.

Introduction

The understanding of executive functions has been difficult for multiple reasons. In this review we outline some methodological and conceptual obstructions, present our current position, and provide supporting

evidence for this viewpoint. We conclude with suggestions for future research directions.

A major problem has been the inconsistent and interchangeable use of both psychological and anatomical definitions of executive and frontal functions. While study of the effects of damage to the frontal lobes has been the most common way to study frontal lobe functions, many researchers still use the term “frontal functions” as a synonym for “executive functions”, without objective reference to anatomy. Yet the relationship between “executive” or “supervisory” functions to “frontal lobe” functions is not clear. Even those who research the effects of frontal lobe damage have often not clearly defined the anatomical limits of the pathology.

It is understandable why this has occurred historically. The executive functions of human cognition are among the most interesting of processes. Researchers interested in these issues are, however, faced with a dilemma. While executive functions can be studied as pure psychological processes, the constant association between executive and frontal functions suggests some type of relationship. A significant difficulty in studying frontal lobe functions, however, exists: there is no clinical condition with specific and easily limited relation to the frontal lobes (with the possible exception of frontal lobe dementia in the early stages). It is time consuming (years!) to obtain a sufficient number of patients with well-defined focal frontal lobe lesions to address the issues of specificity of functions to the frontal lobes in general, not even considering distinctions within the frontal lobes. If one superimposes the possibility that different processes required to complete a single task may be related to different areas in the entire brain, as well as to potentially different regions *within* the frontal lobes, it is easy to understand why understanding the functions of the frontal lobes, and the relation of different tasks to the frontal lobes, has been so difficult.

Further problems exist because of experimental methodological issues. Evaluating patients for frontal

D. T. Stuss (✉) · M. P. Alexander
Rotman Research Institute,
Baycrest Centre for Geriatric Care,
3560 Bathurst St., Toronto, Ontario M6A 2E1,
Canada
e-mail: rotman@rotman-baycrest.on.ca

D. T. Stuss · M. P. Alexander
Departments of Psychology
and Medicine (Neurology and Rehabilitation Science),
University of Toronto, Toronto, Canada

M. P. Alexander
Department of Neurology, Harvard University,
Beth Israel Hospital, Cambridge, Massachusetts, USA

lobe dysfunction, or using neuropsychological tests to correlate with performance on experimental tasks as a means of extrapolating to the underlying brain mechanism (as in normal aging studies), has been difficult because of our available tests. Many "executive" tests are multi-factorial, and performance could be impaired for reasons other than dysfunction in the frontal lobes (Stuss, Shallice, Alexander & Picton, 1995). This is particularly true if the test is more "complex", as was considered necessary to elicit frontal lobe dysfunction. Thus, it would be no wonder that patients with posterior lesions who might have visual neglect, or comprehension problems, might fail on a frontal lobe test (Anderson, Damasio, Jones & Tranel, 1991). This multi-factorial nature is also at least partially responsible for the low correlations among frontal lobe tests. Closely allied to this concept is the sensitivity and specificity of such frontal lobe tests. Tests that may be sensitive may not be specific. Tests that are specific may not be sensitive. It is also important to realize that many tests used to assess frontal lobe damage were developed for other reasons. Moreover, the current knowledge of how to dissociate processes within a task, developed in cognitive psychology, was usually not available when these tests were developed.

Another methodological warning relates to the very meagre evidence on the validity and reliability of the tests of frontal functions. If one considers how difficult it is to find such patients and how difficult it may be to obtain appropriate localizing information (and how this was unavailable in the past), it is no wonder that few studies with precise characterization of the lesion location and the patient have been completed.

The experience of the examiner and the structure of the testing situation are also important factors, which may confound the examination of functions of the frontal lobes. It is relatively easy to "become the frontal lobes" of a patient or research participant (Stuss, 1987). Indeed, such external structure is one mechanism for rehabilitating these deficits. A final consideration relates to the individual differences among patients. Each patient brings a different background to the testing situation, which may influence the performance on any specific test.

The quality of the dependent measures themselves may raise an obstacle. We (Stuss, 1991c; Stuss, Stethem, Hugenholtz, Picton, Pivik & Richard, 1989; Stuss, Pogue, Buckle & Bondar, 1994b) reported that individuals suffering from traumatic brain injury were variable in their performance on a particular reaction time task. That is, they could do the task one day, but not another. This was hypothesized to be related to dysfunction in the frontal lobes, in that the ability to complete a task was intact, but the patients were unable to sustain the top-down effort to complete the task consistently. In an ongoing study (Stuss, Murphy & Binns, 1999), the primary relation of visual performance to the frontal lobes seems to be supported. That is, the noise is the data. Such variability very likely

might confound experimental studies of frontal lobe functions.

Perhaps the most significant problem in the study of executive or frontal functions has been conceptual in nature. Terms such as "executive" functions, "dysexecutive control", "supervisory system" and "control" functions are not easily operationalized. It therefore has been difficult to devise precise experimental manipulations to study these processes. Moreover, we have been bound by previous distinctions made to try to understand these terms. For example, one distinction has been made between "complex" and "routine" tasks in an attempt to characterize the differences between frontal and posterior processes. A consistent idea in many theories of frontal lobe functions has been that these frontal processes are activated when control of more automatic processes, located in more posterior brain regions, is required. This control is invoked when the level of complexity of a task requires more than routine processing, when old information must be considered in new ways, or when the information to be processed is novel. A similar distinction has been between control and automatic processes. Yet many routine, overlearned acts can be very complex, and a high degree of control may be required. Moreover, what is complex for one person can be simple for another, and a relatively simple task can be made complex by the interpretation of the subject. Most clinicians and researchers have had the experience of an intelligent control subject totally failing on the Wisconsin Card Sorting Test because they hypothesized much more complex sorting strategies than were required.

A reflection of this difficulty in defining the terms is the significant debate over the unity or diversity of function of the frontal lobes. Many theorists have considered the supervisory or executive functions in a unitary manner. Duncan (1995), who argued that the supervisory system was a term representing a unified function of fluid intelligence, or "g", most explicitly posited this idea. Others, in contrast, suggest that there are many frontal functions (Baddeley, 1996; Rolls, 1996; Shallice & Burgess, 1991; Stuss & Benson, 1984, 1986; Stuss et al., 1995).

It is therefore no wonder that the study of executive functions, let alone the functions of the frontal lobes, has been so difficult, particularly in humans. Here we outline our position on the study of frontal lobe functions, both from methodological and conceptual standpoints, and then provide data that led us to these statements.

Our position

We have limited our research to patients with focal lesions of the frontal lobes, and have attempted to characterize the lesion location and extent as well as possible in naturally occurring (with the possible exception of resection for tumors or epilepsy) lesions in

human patients. In our opinion this is the first step in limiting the terms of reference in the study of executive and frontal functions. These results in patients with focal frontal lobe lesions can eventually be compared to concepts of executive function defined purely in a psychological sense, and also to the discussion of executive functions found in more diffuse orders (Goldberg & Bilder, 1987) or in the literature on aging (Stuss, Craik, Sayer, Franchi & Alexander, 1996). In this stepwise manner, operational definitions of the functions of the frontal lobes and of executive functions can be developed. They may not necessarily be totally equivalent.

We emphasize that there are specific processes related to different brain regions within the frontal lobes. There is no frontal homunculus, no unitary executive function. Rather, there are distinct processes that do converge on a general concept of control functions. The idea of a supervisory system is very applicable, if the emphasis is on a system constructed of multiple parts. From a clinical viewpoint, the position that there is no frontal homunculus suggests that there is not a single frontal lobe syndrome with point-to-point correspondence to a homunculus. While a generally consistent frontal lobe syndrome can be found in some patients, this syndrome label described patients with extensive damage to the frontal lobes often late after injury, during an epoch in medical history when adequate imaging for earlier diagnosis and treatment was not available.

While the immediately preceding point would seem to support the concept of a dissociation of control – automatic processes, we suggest that this dissociation requires considerable refinement. There are many types and levels of control, and to argue just for a frontal/posterior dissociation related to control/automatic processes is inadequate. We hope to demonstrate that the interaction is much more complex, and that simple frontal/posterior dissociations do not capture the complexity of human cognitive processing.

In a similar vein, we propose that the distinction between complex and simple tasks cannot by itself explain the differences in functions between the frontal lobes and other brain regions. The distinction is a relative one, and complexity must be defined. The processes of the frontal lobes are necessary for more than just complex tasks. Stated differently, apparently simple processes related to the frontal lobes can be identified. More importantly, the manipulation of complexity in experimental tasks may help to determine how an integrated brain works.

Our final emphasis is on an old concept of the frontal lobes – the frontal lobes are very intimately linked to the limbic system and affect. Indeed, the most important role of the frontal lobe may not be for executive cognitive processes, but for affective responsiveness, social and personality development, and self-awareness and consciousness.

The remainder of the review presents selected data from our studies in patients with focal lesions (with one exception) to demonstrate the above statements.

Supporting evidence

Cognitive functions of the frontal lobes

Memory

The historical controversy about the role of the frontal lobes in memory is classically dichotomized into two separate camps: damage to the frontal lobes does not/does result in a memory disturbance. We have examined the role of the frontal lobes in memory functions in different ways.

1. List-learning performance. A study of the performance of patients with focal frontal lobe lesions on a list-learning task was one of the first studies we performed that led us to a different approach in demonstrating separation of processes within the frontal lobes (Stuss, Alexander, Palumbo, Buckle, Sayer & Pogue, 1994a). The first observation was that left frontal and bifrontal lesions did result in a significant recognition deficit. Since this was contrary to most published results and the most common view of the role of the frontal lobes in memory, we pursued the reasons behind this significant difference in recognition performance [a subsequent meta-analysis by Wheeler, Stuss and Tulving (1995) has brought into the question this “accepted” view].

The procedure we used to address the underlying reasons why our results were incongruent with standard teaching was as follows: list all patients in order of performance, from best to worst; use a criterion to differentiate the good vs. impaired performers, such as split-half division, or a standard comparison to the control group (e.g., exceeds two SDs); and finally establish and test hypotheses as to why the specific individuals were impaired. We used lesion location and differentiation of processes (by correlational analyses with other neuropsychological measures) to examine our hypothetical reasons as to why some patients with frontal lobe lesions had a recognition deficit, and some did not.

This approach led us to isolate two separate and independent factors that led to an apparently similar recognition deficit: damage to the septal region, affecting the limbic memory system related to explicit memory; damage to the left frontal lobe, affecting language systems. There are important implications of this finding. Impairment on a specific test or process may not be related to one brain region. Rather, the neural systems underlying the task must be understood. This approach has proven successful in understanding disorders such as neglect (Heilman, Watson & Valenstein, 1985). While patients with a different location of lesions are impaired on a task, they are likely impaired for different reasons. A corollary conclusion is that it is inadequate to discuss patients with frontal lobe damage as a group, even using patients with a common etiology. Most of the patients with septal damage had suffered the consequences of anterior communicating artery aneurysm rupture. However, not all patients with such ruptures suffered

Group	ENCODING/ SECONDARY MEMORY			RETRIEVAL		RETRIEVAL	
	REC	FR	SM	PM	S-O	DR	CONS
Unilateral Right	↑	↑	↑	↑	↓	↓	↓
Unilateral Left	↓	↓	↓	↑	↓	↑	↑
Bilateral	↓	↓	↓	↑	↓	↑	↑

Fig. 1 Three different groups of patients with focal frontal lobe lesions are compared on a word-list learning task. The measures on the *left* reflect primarily encoding – recognition, free recall and secondary memory; on the *right*, two measures more associated with retrieval – monitoring (double recalls) and retrieval set (inconsistency of recall); in the *middle* are depicted primary memory, and the subjective organization (pair frequency) score. The direction of the arrows indicates normal (↑) or impaired (↓) performance. None of the patient groups had a primary memory deficit. All groups were significantly deficient on subjective organization. Only the patients with left frontal and limbic-septal pathology had a significant recognition deficit. Retrieval problems were observed in patients with right frontal lobe damage. These lesion data reflecting left-right frontal differences in encoding and retrieval are consistent with the imaging HERA model (see text) (*REC* recognition, *FR* free recall, *SM* secondary memory, *PM* primary memory, *S-O* subject organization, *DR* double recall, *Cons* consistency)

septal damage (see also DeLuca, 1992; DeLuca & Diamond, 1995).

Influenced by cognitive psychology, we also isolated other measures within the list-learning task, and examined if the defined patient groups were differentially impaired (recall the procedure: from task to process to mechanism). The results are outlined in the Fig. 1. Several observations can be made from these data. There is a difference between the effect of damage to the right and left frontal lobes. Pathology in the left frontal lobe appears to affect encoding, while the right frontal lobe is more involved in retrieval processes such as monitoring of output (recalling words that had already been recalled – double recalls) and maintaining consistent recall over trials (retrieval set?). The patients with right frontal lobe damage did not have significant problems in recall. This left/right frontal difference in encoding and retrieval is also consistent with imaging studies (Nyberg, Cabeza & Tulving, 1996; Tulving, Kapur, Craik, Moscovitch & Houle, 1994). On the other hand, all patients with frontal lobe damage were impaired on the Tulving and Colotla (1970) subjective organization score, which reflects top-down organizational strategies. That is, on the one test, if different processes are assessed, there is apparent support for both the heterogeneity and homogeneity of frontal lobe processes. We demonstrate a similar finding in the study on attention described below.

2. The role of frontal functions in implicit and explicit recall. This study addressed the control/automatic distinction in relation to “frontal” processes. Implicit memory tests are considered to be measures of automatic functions. As such, if one used the strict distinction between control and automatic processes and the relation to frontal and posterior brain regions, an implicit memory task should not depend on equations of the frontal lobes. One might expect that impairment of memory after frontal injury would only occur in a demanding explicit memory task. Winocur, Moscovitch and Stuss (1996) tested this assumption using a correlational method in which performance on tests that have been more related to frontal or medial-temporal functions was correlated with performance on word-stem and word-fragment tasks that required either explicit recall or implicit memory. Young and old subjects were compared.

A double dissociation was observed. The neuropsychological test related to medial-temporal areas correlated with the explicit version of the task, but a test of frontal function was significantly correlated with the implicit version, but *only* the word-stem completion. The explanation offered for this finding was that word-stem completion requires generative search processes as well as perceptual identification processes. This is illustrated in Fig. 2. Nyberg, Moscovitch and Winocur (1997) replicated and extended these findings. This study nevertheless needs to be replicated in patients with focal lesions.

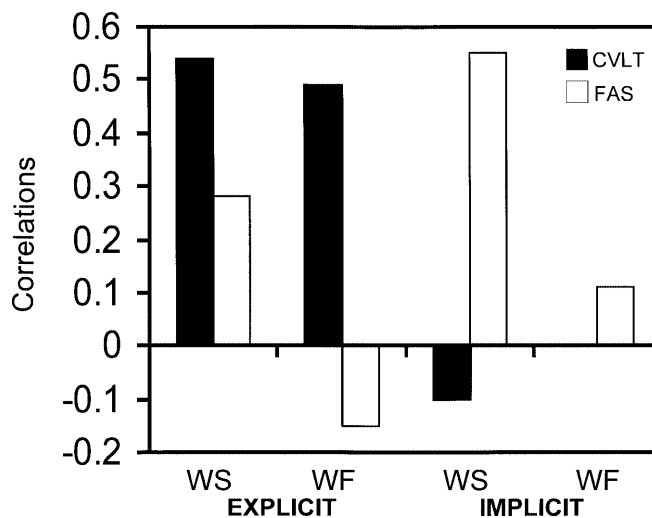


Fig. 2 The ordinate depicts the amount of correlation. The abscissa indicates two types of memory tasks, word-stem (*WS*) and word-fragment (*WF*) completion. On the *left side* is the explicit recall version of the task, on the *right* the implicit recall version. Each test result is correlated with the California Verbal Learning Test (*CVLT*) (used here as reflecting more the limbic-hippocampal memory system) and verbal fluency (*F-A-S*, taken as the measure of “frontal” lobe functioning). Explicit recall is correlated with the *CVLT*; implicit recall is significantly correlated with the *F-A-S* score, but *only* stem completion

These findings have significant implications: (1) no test of memory is process pure (see also Jacoby & Kelly, 1991). Supposedly executive processes are required for performance on some implicit tests of memory. Automatic implicit processes may influence performance on explicit tests; (2) the control-automatic distinction is a complex interactive one; (3) the necessity of strategic processes in what appears to be a simple task calls into question a simple distinction between simple and complex functions, and frontal and posterior processes.

Attention

Most clinicians will attest to the attentional disturbance in patients with frontal lobe damage. Yet clinical observation does not necessarily translate into factual data. One example illustrates this. D. Frank Benson, while on sabbatical at the Maudsley Hospital in London, England, was scheduled to give a lecture on an ongoing study at the Boston VA on the long-term effects of orbitofrontal leucotomy. The data had not been analyzed but the first author of this paper very confidently informed Dr. Benson that there could be no doubt: the major impairment after orbitofrontal leucotomy was a severe attentional disorder. Some months later the test data, including demanding tests such as the Stroop, were analyzed. There were *no* significant differences between the normal control group and the leucotomized patients, whose lesions were quite large (Stuss, Benson, Kaplan, Weir & Della Malva, 1981).

There are several reasons for this discrepancy between the clinical observations and the research data. As noted above, the test structure could have been such that “frontal” demands might have been minimized. It is also possible that the tests used did not require the processes related to the region of the frontal lobes most often damaged after frontal leucotomy. There have been only a few studies investigating the specificity of attentional disturbances, and their relation to particular frontal brain regions.

The frontal lobes have been hypothesized to play a central and different role from posterior brain regions in attentional functions (Posner, 1988; Mesulam, 1981; Shallice, 1988). We (Stuss, Toth, Franchi, Alexander, Tipper & Craik, 1999) pursued the question of the role of the frontal lobes in attention by employing a spatial-selection task that differentiates different types of putative anterior attentional processes. The objectives of the study were to dissociate possible anterior attentional processes; to evaluate the effect of task complexity; and to examine the specificity of supposed anterior attentional processes to the frontal lobes. The three measures were the following:

Interference: The difference in response time to select a target presented alone, compared to responding to that target when it was presented simultaneously with a distractor. (What is the effect of extra irrelevant information?)

Negative priming: The effect of a change in the location of a target, particularly when the target is presented in the location where a distractor had been in a previous trial. (What is the effect of previous inhibition of irrelevant information on subsequent processing?)

Inhibition of return: The response inhibition measure indexes the extra time required to respond to a target when the location of that target is identical to the location of the previous trial when the response had to be suppressed to that location. (What is the effect of inhibiting a motor response on subsequent trials?)

The results, summarized in Fig. 3, suggest the following conclusions:

1. Different anterior attentional processes can be isolated, and these attentional processes can be related to different brain regions within the frontal lobes.
2. Apparently simple processes can be related to the frontal lobes.
3. There is an interaction between anterior and posterior attentional processes, suggesting that the only way to discuss the results is to use the concepts of neural functional systems.
4. Task demands, including task complexity, alter the interaction of neural systems.
5. Inhibition is not simply a function of the frontal lobes.

Verbal fluency

Research with the standard tests of “frontal lobe functions” reveals the inadequacy of some popular beliefs

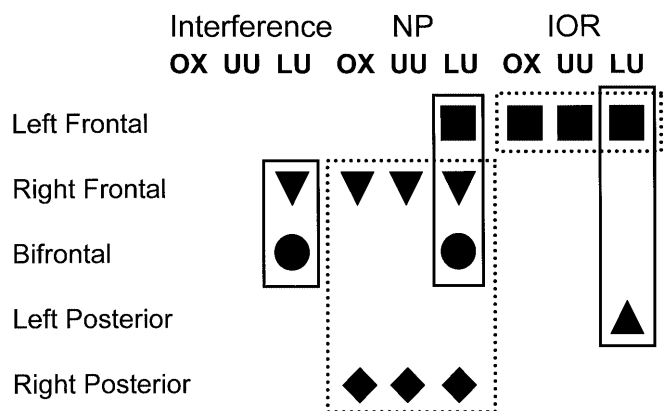


Fig. 3 This figure summarizes the performance of patients with lesions in defined brain regions on three different measures of attention, measured at three different levels of task complexity. Three measures (see text): *INT* interference, *NP* negative priming, *IOR* inhibition of return. Three levels of task difficulty: *OX* a constant mapping of one target (*o*) and one distractor (*x*); *UU* four capital case letters are used, the target changing for each trial and identified at a central location; *LU* the same letters, but this time the target is identified in lower (*L*) case but the target appears in upper (*U*) case, requiring at least some processing beyond perceptual matching. Significant impairment for each group is identified by the placement of a particular symbol within a task and level of difficulty. The boxed areas help identify all the brain regions resulting in a significant impairment on a task

about executive functions. We devised a novel analysis of lesion site on one of these “standard” tests, verbal fluency.

- a. Subdivide the frontal lobes based on past behavioral research, and recent anatomical demonstrations of frontal subsystems (e.g., Alexander, DeLong & Strick, 1986; Petrides & Pandya, 1994).
- b. Identify each of these regions as damaged (1) or not structurally damaged (0), each entered independently into the statistical analyses, to allow analysis of the contributions of each subsystem to a deficit performance when most subjects had lesions involving more than one subsystem.
- c. Use a regression technique that separates by extremes of performance. The Classification and Regression Tree (Breiman, Friedman, Olshen & Store, 1984) method follows a re-iterative process so that variables can be re-introduced until the maximum degrees of separation can be found.
- d. These new groups now can be analyzed for statistical differences in performance.

In the past, studies of brain-behavior relations compared frontal to posterior brain regions, or left and right hemisphere damage. Some studies have extended the distinction by isolating patients with damage to the right frontal, left frontal and bifrontal regions. While all of these methods of grouping the patient participant can produce interesting results, and indeed may be the only way to analyze the data if the sample size is not large enough to follow the methods proposed, these methods of patient classification for analyses do not allow examination of precise brain-behavior relations.

Figure 4 demonstrates how the two approaches differ. Patients with frontal lobe damage were originally classified as right frontal, left frontal and bifrontal. The CART technique resulted in a finer distinction of right and left frontal (both primarily dorsolateral), superior medial, and inferior medial groups. Using these new groupings provides a finer distinction among the patient subjects. The figure is somewhat misleading. The new groupings are *not* just a simple division. For example, the new superior medial and inferior medial groups may include individuals who had previously been identified as right or left frontal.

Analysis of strategic processes to complete tasks is another means of distinguishing processes related to different brain regions. Troyer and colleagues at the Rotman (Troyer, Moscovitch, Winocur, Alexander & Stuss, 1998) demonstrated this using the verbal fluency task. Patients with left dorsolateral or superior medial lesions switched less frequently, but produced normal cluster sizes. On phonemic fluency, temporal lobe patients performed normally for both switching and clustering. On semantic fluency, however, these temporal lobe patients were impaired in switching, and left temporal damage resulted in more problems in clustering.

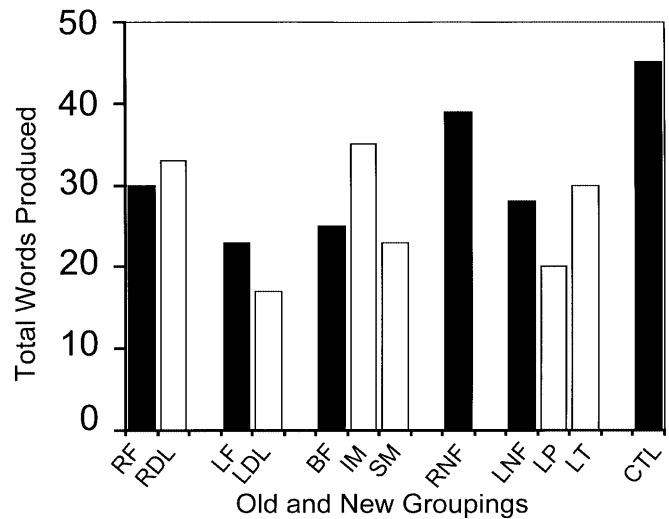


Fig. 4 This figure demonstrates how further lesion specification clarifies results in a phonological fluency task. The *black columns* represent the standard lesion classifications (*RF* right frontal, *LF* left frontal, *BF* bifrontal, *RNF* right nonfrontal, *LNF* left nonfrontal, *CTL* control). The *white* identifies the restructured groups (see text for method) (*RDL* right dorsolateral frontal, *LDL* left dorsolateral frontal, *IM* inferior medial, *SM* superior medial, *LP* left parietal; *LT* left temporal)

The role of the frontal lobes in humor, affect, and awareness. Perhaps the most important new trend in the study of the functions of the frontal lobes is an old emphasis: the study of personality and affective changes after damage to this area. The knowledge about Phineas Gage being “no longer Gage” after his accident has been almost universally disseminated (Ripley’s “Believe it or not TV show”; Damasio, Grabowski, Frank, Galaburda & Damasio, 1994). Prefrontal lobotomies and leucotomies were performed to effect behavioral and personality change, not alterations in cognition. Yet much of the more recent research on frontal lobe functions has been directed to the cognitive role of this brain region. The role of the frontal lobes in cognition is logical, considering the anatomical connectivity of the frontal lobes with posterior knowledge and perceptual systems; however, there are perhaps even more logical reasons to study the neuropsychiatry of the frontal lobes.

One pathway for the frontal lobes to influence emotional responsiveness is via the amygdala (Adolphs, Tranel, Damasio & Damasio, 1995; Markowitsch, Calabrese, Wurker, Durwen, Kessler, Babinsky, Brechtelsbauer, Heuser & Gehlen, 1994) which is essential for modulation of emotion (Angrilli, Mauri, Palomba, Flor, Birbaumer, Sartori & di Paola, 1996). Nauta (1973) proposed that the amygdala and the dorsomedial thalamic nucleus present information from the limbic system specifying the status of affective feeling and of the viscerio-endocrine periphery state to the frontal lobes. Only in frontal lobes are affective state and perceptual and associational activity integrated. Affective information provides navigational markers to the valence value for decision making (Nauta, 1973). A

similar proposal has been proposed more recently by Damasio and colleagues (Damasio, Tranel & Damasio, 1991) who label these somatic markers.

Evolutionary development of the frontal lobes is another reason to emphasize the affective role of the frontal lobes. The largest evolutionary developmental difference between man and the highest of non-human primates is in Brodmann area 10 of the frontal lobes (Petrides and Pandya, 1994). This is an area that evolved from the olfactory base of animals, that brain region related to the four "Fs" of animal interactions: fear, flight, fight and procreate.

We summarize our observations on disorders of self-awareness, and a study on humor appreciation, as supportive evidence for the importance of the frontal lobes in these domains.

Self-awareness

Many of the models of brain functioning have a hierarchical component to them, and we have postulated such a model for self-awareness (Picton & Stuss, 1994; Stuss & Benson, 1986; Stuss, 1991a, b; Stuss, Picton & Alexander, in press). This model has several properties: (1) There are four operational levels: arousal-attention; perceptual-motor; executive mediation; self-awareness. (2) Each operational level feeds forward to higher levels, providing a tentative digest of the analyses and associations within that level. (3) Each operational level also feeds backward to lower levels to modulate, bias, constrain or facilitate the analyses and operations that will occur. (4) Direct contact with the external environment is restricted to the perceptual-motor level. (5) The two highest levels are instantiated in frontal lobes. The executive mediation level is predominantly localized to ventrolateral and dorsolateral frontal regions. It incorporates action planning, inhibition and facilitation of parietotemporal association cortices and working memory capacities. Open and closed neural loops through basal ganglia and cerebellum provide neural space for unfolding complex plans and for learning frequently used plans. (6) Self-awareness emerges from convergence of emotional states and memory – not simply explicit remote memory of experience or explicit semantic knowledge – but memory of abstract mental states that allow construction of expectancy and thus memory for the future. Human consciousness is an unstable template of experience and emotion.

Our interest in disturbed self-awareness initiated with our report of a patient who had Capgras Syndrome (belief that an imposter has taken the role of a significant other) secondary to bilateral frontal lobe damage, more extensive on the right, and right anterior temporal lobe damage (Alexander, Stuss & Benson, 1979). He was initially confused and amnesic. During the period of recovery, he began to report a "new", second family, virtually identical to his first family. This belief persisted, despite his recovery on most cognitive abilities, with the

exception of frontal lobe functions. Following James (1891/1952), we postulated that his belief in two families was based on the warmth, intimacy and immediacy of the two separate memories that occurred at separate times. The emotional salience and impact of two episodic memories (personal, individual) allowed these memories to be "affectively burnt in" (Stuss & Alexander, 2000). The impaired executive functioning precluded any personal review, validation or correction of the situation. This case exemplifies a disorder of model construction and monitoring at the level of the frontal lobes, different from the knowledge-based disorders of awareness in patients with posterior lesions. Indeed, when the patient was presented the situation as a non-personal occurrence, as if he was judging the story told by someone else, he called it "amazing" and "unbelievable".

That there may be a higher level of self-awareness related to frontal functions, distinct from dysfunction in the frontal "executive" abilities, was first suggested by basic research in animal self-awareness using the "mirror" test. Gallup (1991) found no evidence that a monkey can use a mirror to recognize its own reflection as an image of itself. Yet monkeys clearly have executive abilities of some kind, recognized by the extensive research on frontal lobe executive functions using the monkey. While monkeys do not have the ability to use a mirror as a mirror, higher order primates, such as chimpanzees, orangutans and human children after a certain age easily perform this act of visceral consciousness.

We examined a patient after operation for removal of a right frontal astrocytoma (Stuss, 1991a, b). On neuropsychological examination, performance was excellent, even with standard frontal lobe tests. This patient had more than adequate knowledge of his life and work difficulties. Yet there was a lack of awareness of the implications of the disorder; an impairment in using intact knowledge to guide personal decision; and a deficit in acting in his own self-interest. It is plausible, although perhaps unprovable, that he had a deficient mental model of the entire self. Without that he could organize no clear purposes to motivate his actions.

Experience must be monitored over the past and present and anticipated or imagined in the future. The depth of this temporal integration varies with the hierarchical level. Ingvar (1985) and Fuster (1997) have also asserted that the frontal lobes generate "memories of the future". Wheeler, Stuss and Tulving (1997) proposed that the prefrontal regions, particularly on the right, provide essential organization for episodic memory guiding the recall of experience with its associated emotions and connecting the recollections with plans and expectations for the future (see also Craik, Moroz, Moscovitch, Stuss, Winocur, Tulving & Kapur, 1999; Levine, Black, Cabeza, Sinden, McIntosh, Toth, Tulving & Stuss, 1998). Only humans appear to have a reflective consciousness of the self as an entity across time (Stuss, Picton & Alexander, in press).

Humour

Both the patient with the Capgras Syndrome and the patient who had lost integrated awareness of his experiences, past and future, had damage in the right frontal region. Shammi and Stuss (1999) extended the study of the role of the frontal lobes (particularly right frontal) in emotional, affective behavior by studying the ability to appreciate verbal and non-verbal humor in patients with various focal lesions. The patients who were impaired had lesions in a rather selective region – the superior right frontal polar/medial region. Patients with posterior lesions were not impaired on the tasks, with one exception. The patients with right posterior lesions had difficulty on a cartoon appreciation task, which required scanning of a picture, and detection of details. The ability to appreciate certain forms of humor correlated with specific cognitive abilities (e.g., language with the verbal tasks; visual search with the cartoons). Beyond simply understanding humor, these patients do not feel or appreciate humor even when they recognize its existence. The right frontal lobe is required for the subtle convergence of cognition and affect essential to humor.

Conclusions and discussion

The question of the unity versus diversity of the functions of the frontal lobes has been a long-standing controversy, but the data presented here support the proposition that distinct processes are related to different regions of the frontal lobes. Under certain circumstances (still to be delineated but complexity of task seems to be one superficially similar factor), impairments can be found after damage in many if not most areas of the frontal lobes. When functions of the frontal lobes are tested with complex tasks, this brain region appears functionally homogeneous. Increasing the complexity of a task may demand multiple processes in different frontal lobe regions. Processing capacity reflected in working memory may be so taxed at high levels of complexity that more general frontal lobe resources are recruited. In addition, the simple/complex dichotomy as related to posterior/frontal processes must be considered with caution. Complex tasks are multi-factorial, and patients with lesions in many different regions of the brain may be impaired on these. This is probably a major reason for some of the controversy in studies of the validity of “frontal lobe” tests.

Our studies suggest several methods to assist in establishing more specific behavioral distinctions within the frontal lobes: finer lesion location; use of cognitive neuropsychology to help differentiate processes; assessment of a large number of patients with localized lesions; and starting with performance first, and then evaluating the determinants of performance.

Taken to its reductionist endpoint, our argument suggests that there is no discrete central supervisory

system; there is no ghost in the mind's machine. The central supervisory system is the sum of the processes recruited at any moment, for any task. We have identified some of the processes and marshaled evidence for their relationship to specific frontal regions. Activation studies in normals with functional magnetic resonance imaging (fMRI), positron emission tomography and event-related potentials (ERPs) also point to specific brain regions for particular elements of supervisory processes. Newer methods of analysis of activation paradigms may disentangle the supportive from the essential element of a brain network activated by specific supervisory processes. Linear, sequential models of supervisory networks will blend with simultaneous emergent models.

For the processes that underlie self-awareness, current evidence from both lesion studies and activation studies points to a critical role for the right frontal lobe. Feeling and understanding the continuity of experience appear to depend on the unique convergence of personal affective state, of abstract knowledge of the affect of others or even the self in hypothetical circumstances (theory of mind), and of retrieval of the memory of personal experience (autonoetic consciousness) that occurs in the right frontal lobe.

In *Galatica 2.2* by Richard Powers, the narrator suggests that there may be no better definition of consciousness than the ability to remember a past experience and the powerful feelings that accompanied it, while aware that the feeling is not accessible in the present and will not be in the future. The right frontal lobe may be essential for this capacity of mental juggling.

Some future research directions

Because we have frontal lobes we can imagine important areas of future research.

1. Although logistically difficult and experimentally messy, continued study of patients with disparate focal frontal lesions should continue as a primary tool to clarify and characterize dissociable supervisory processes. One particularly important avenue may be the differentiation of the anterior attentional processes.

2. There should be a renewed emphasis on the neuropsychiatry of the frontal lobes: e.g., depression, socialization, and personality. A potentially exciting approach would be to have parallel studies of patients with focal lesions and those with psychiatric disorders.

3. Comparison of patients with focal lesions in various brain regions with experiments of supervisory processes should gradually explain the network interactions between various anterior and posterior regions.

4. The frontal regions involved in supervisory and self-awareness processes are supported by numerous subcortical loops that consistently involve the thalamus, the striatum, and the cerebellum. Both lesion studies and activation imaging studies will be required to explain the roles of these structures in “frontal” tasks. Could the

closed striatal-thalamus loop be required for maintaining patterns of neural activity during a task (working memory), while the cerebellar-thalamic loop erases (inhibits) active neural patterns to allow supervisory processes to reengage as new inputs? The facilitory and inhibitory pathways must overlap in frontal cortex but might diverge elsewhere. Can we define this divergence?

5. If supervisory and self-awareness processes are distributed in numerous networks within the frontal lobes, can patients recover or retrain damaged elements of these processes when lesions are small or incomplete? Does extent of white matter damage constrain the capacity to recovery or to "reconnect" in both the anatomical and the Hebbian sense?

6. Can we extract measures of supervisory activity and self-awareness that are clinically useful for diagnosis, for prognosis, or for specifying treatment?

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