ELECTROPHYSIOLOGY OF WORKING MEMORY: TASK MODALITY AND LOAD EFFECTS

by

Patricia Ross

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Abstract

Goldman-Rakic offers a conceptualization of working memory (WM) that emphasizes how prefrontal (PFC) and posterior cortical areas are linked in reverbatory circuits that keep information on-line. Goldman-Rakic argues that these WM circuits are modality-specific, with dorsal PFC and parietal activation for spatial processing, and ventral PFC and inferior temporal activation when non-spatial or pattern information is being processed. Cohen et al. (1997) demonstrated fMRI activation of the dorsolateral PFC as a function of load in an n-back WM task. We employed a similar task to test the modality-specific WM model, with a spatial condition (position being the matched criterion for letter stimuli presented either 1, 2 or 3 items earlier) and a verbal condition (specific letter to be matched). Electrophysiological measures were employed, including ERP and EEG spectral analysis, as well as EEG coherence, which can provide a functional measure of corticocortical communication. EEG was recorded from 9 frontal and 9 parietal coronal sites from an extended 10-20 system.

Support was not found for modality-specific WM systems. Instead, results suggest that there is a WM circuit that connects dorsal frontal with dorsal parietal areas which is activated during a WM task, regardless of the type of stimuli involved. Data also suggest that left dorsal frontal and parietal areas are sensitive to the level of difficulty of the WM task (0,1,2 and 3-back), as well as familiarity of task demands. Overall, results support a model of WM that conceptualizes a unitary WM system rather than a system composed of separate WM circuits for different modalities. More specifically, these data appear to favor the WM model of Petrides (1995) which suggests a ventral/dorsal distinction in frontal activation patterns is related to the executive processes being performed on the information.

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Introduction

Working memory (WM) is a system responsible for manipulating and temporarily storing information in support of ongoing cognitive activity (Baddeley, 1986). The concept of WM has become central to theories of executive function, and is considered critical for a wide range of cognitive operations, including reading (Daneman & Carpenter, 1980; Turner & Engle, 1989), language acquisition (Gathercole & Baddeley, 1989), problem solving (Kyllonen & Christan, 1990), mathematics (Hitch & McAuley, 1991; Swanson, Cooney & Brock, 1993), and reasoning (de Jong & Das-Smaal, 1995; Jurden, 1995), to name a few. Throughout the execution of such cognitive abilities, working memory allows for the temporary storage of information useful to the task being performed (Baddeley, 1995). .

Although the prefrontal cortex (PFC) is implicated in WM processes by several lines of research (e.g., Friedman & Goldman-Rakic, 1994; Petrides, Alivisatos, Evans & Meyer, 1993a, b), it is well accepted that this cortical area does not work in isolation but rather as part of a neural network that involves posterior regions as well. Technical limitations, as well as the expense, of methods currently used to study the neural substrates of cognitive activity (e.g., PET, fMRI, ERP) have made it difficult to investigate the functional associations between the various cortical regions activated during a WM task. As such, the present research proposes to employ electroencephalography (EEG) coherence measures to provide an alternative procedure to study brain activation involved in a WM task.

EEG coherence is a measure of the "shared activity" between spatially separated cortical generators (Thatcher, 1991). In other words, through computation of the correlation between two EEG signals for any given frequency band, coherence analysis indicates which

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particular brain areas are working together, whether in a resting state or a state of activation. It is postulated that the coherence between signals from two different brain regions should increase as these regions become more involved in related cognitive activity. EEG coherence analysis has been shown to be a useful technique, both for the validation of regionally specific cognitive activation tasks (e.g., Tremblay, Lacroix, Chaput, Fraile, Lamer & Albert, 1994) and in the assessment of deficits in cognitive function (e.g., Morrison-Stewart, Williamson, Corning, Kutcher & Merskey, 1991).

The experimental literature that will be reviewed reflects the contributions of neuroimaging and event-related potential studies of WM, as well as past applications and issues involving the use of EEG coherence analysis. First, however, models of working memory that will be investigated in this study are presented.

Models of Working Memory

The term 'working memory' is applied to the type of task-critical memory that is active for a short period of time, typically on the scale of seconds (Goldman-Rakic, 1995). It is important to bear in mind that the term has been used with different meanings in various areas of research (for a review see Baddeley, 1995). In the present context, the concept of WM has less to do with memory storage and retrieval processes, and more to do with the on-line mental representation of information and the ability to manipulate this information to generate and guide upcoming action (Welsh & Pennington, 1988). It is in this respect that WM is regarded as an essential element underlying executive abilities of the prefrontal cortex (Eslinger, 1996; Fuster, 1989; Roberts & Pennington, 1996).

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Both electrophysiological (Funahashi, Bruce & Goldman-Rakic, 1989; Gevins et al., 1996) and neuroimaging (Cohen et al., 1997; Jonides et al., 1993; Paulesu, Frith, Frackowiak, 1993; Petrides et al., 1993a, b) studies have provided evidence of the critical role of the prefrontal cortex in working memory processes. To date, it has been largely accepted that the PFC serves in the active maintenance of information across a delay period from stimulus presentation to response (Cohen et al., 1997; Courtney, Ungerleider, Keil, Haxby, 1997; Funahashi et al., 1989; Fuster & Alexander, 1971; Goldman-Rakic, 1995). Despite this relative consensus, however, there is considerable debate as to the precise role of this cortical area. Two schools of thought that have gained considerable attention in the literature consider the PFC to play either an executive role in governing WM processes (Baddeley & Hitch, 1974; Petrides et al.,1993a, b; Petrides, 1995), or a more specific role with individual PFC neurons serving to code modality-specific information and activate modality-specific WM circuits (Friedman & Goldman-Rakic, 1994; Wilson, Scalaidhe & Goldman-Rakic, 1993). Each of these theories will be reviewed in the following sections.

Executive Theories

Baddeley and Petrides are two key investigators who offer theories involving an executive role of the PFC in working memory. Whereas Baddeley offers a cognitive process approach, the theory of Petrides is derived from neuroanatomical investigations.

Baddeley's Theory of WM. Much investigation of working memory processes (e.g., D'Esposito et al., 1995; Fastenau, Conant & Lauer, 1998; Gevins et al., 1996) has been guided by the theoretical framework of Baddeley (Baddeley & Hitch, 1974; Baddeley, 1986). According to his tripartite model, WM is comprised of subordinate systems, the *phonological*

loop and the *visuo-spatial sketchpad*, that serve as 'slave systems' under a 'master' called the *central executive* (CE). Together these components allow for the temporary storage of task-relevant information, as well as for on-line computations and their results.

The phonological loop is considered a buffer that is responsible for maintaining acoustically coded information in WM (Baddeley, 1992, 1995). This component is hypothesized to involve two functionally linked processes, a phonological memory store along with processes for sub-vocal articulatory rehearsal. The memory store is involved in the initial registration of speech-based sound and is capable of holding information for a period of one to two seconds. The articulatory rehearsal processes function to refresh this verbal information so memory traces can be maintained for later processing. In addition, through sub-vocal naming, the rehearsal processes function to register visually presented material. Together, these components of the phonological slave system function to temporarily store verbal data while other cognitive tasks are being performed. For a more detailed review of the functioning of the phonological working memory system, see Torgeson (1996).

In an attempt to anatomically localize components of this slave system, Paulesu and colleagues (1993) measured regional cerebral blood flow while subjects performed a working memory task proposed to engage both components of the articulatory loop, along with tasks that purportedly engaged storage and rehearsal components separately. Results provided evidence for a multicomponent system, in which the two components are anatomically distinct. More specifically, increased activity in the left supramarginal gyrus was associated with the phonological store, whereas activity in Broca's area was associated with the subvocal rehearsal system.

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The second 'slave' system, the visuo-spatial sketchpad, is composed of a buffer responsible for the initial registration of visual and spatial material, along with a sketchpad postulated to be the mechanism by which such non-verbal information can be rehearsed. There is both a visual component of this system, concerned with factors such as color and shape, and a spatial component concerned with location (Baddeley, 1995). Neuroimaging studies have provided evidence that suggests the neuroanatomical correlates of the visuo-spatial sketchpad are anatomically dispersed, supporting the conceptualization of this buffer as involving distinct components. Jonides and colleagues (1993) found activation in the lateral prefrontal area, the premotor area and the parietal cortex in a task proposed to tap functioning of this slave system.

Finally, the CE is viewed as having a coordinative attentional function and is the component most clearly related to prefrontal tasks (Baddeley, 1992). It is considered a control system responsible for determining which information is made available for conscious processing. More specifically, the CE is hypothesized to perform the following supervisory functions: (1) link the slave systems with long term memory; (2) plan, select and modulate cognitive strategies, and finally, (3) integrate information from different sources, including but not limited to the two slave systems (Baddeley, 1992, 1995).

It is hypothesized that dual tasks, which involve simultaneous performance of some central process (e.g., discriminating between sounds) and the storage of information in one of the subsidiary systems (e.g., a series of numbers), provide one way to test the functioning of the CE. One important characteristic of the model is that the CE has a limited capacity so that as demands on the executive increase, processing space and cognitive energy available for the

subsidiary systems will decrease (Baddeley, 1995). This would account for decreased

performance during a dual task compared to tasks completed individually.

Although a fair amount of research has been completed investigating the two

subsidiary systems of the model, the CE remains a relatively unexplored construct (Baddeley

1992, 1995). A review of the WM literature evidences the lack of detailed understanding in

that descriptions of the CE are most often a simple reiteration of what Baddeley has already

offered. It appears that few investigators have attempted to broaden their delineation of the

CE. In speaking of the development of the WM model, Baddeley acknowledged this problem

in describing the CE as representing "an area of residual ignorance rather than a well-worked

out concept" (Baddeley, 1992, p. 12).

However, the number of investigations of the CE are increasing. For instance, the

cognitive capacities that underlie real-world tasks, such as the game of chess, have been

investigated with a focus on the role of this construct (for a review see Baddeley, 1992,

1993). Strategy selection, hypothesized as a function of the executive, was found to be

markedly affected during a chess game when the CE was loaded by having subjects generate

letters in a random fashion during the game. Such results exemplify the proposed limited

capacity of the executive.

A more developed area of CE research involves investigations of Alzheimer's Disease.

Alzheimer patients were reported to demonstrate minimal impairment in their performance of

single tasks, while demonstrating greater impairment, compared to young and elderly controls,

in dual-task conditions (Baddeley, Logie, Bressi, Della Sala & Spinnler, 1986). In addition, re-

testing Alzheimer patients after six months and a year found no change in performance on the

single tasks, with significantly increased impairment in the dual-task conditions (Baddeley, Bressi, Della Sala, Logie & Spinnler, 1991). Such results have led researchers to suggest that the CE might be central to the memory impairment seen in this population (Morris & Baddeley, 1988).

Despite the growing body of research on the CE, criticism remains (Parkin, 1998). One critique involves Baddeley's proposed homuncular approach to frontal lobe and CE functioning. More specifically, because different executive tasks involve coordination among different neural systems, Parkin argues that a single controlling process with a unitary anatomical location is not a realistic construct. Baddeley (1998) responds in agreement to this issue, replying that continued research on the CE is expected to result in a fractionation of the construct into subsystems. Further, Parkin argues that "the pervasive use of the term central executive resides in the absence of any good scientific proof that it exists" (p. 519). With this, Baddeley disagrees, providing arguments focusing on the usefulness of the construct in generating research and in providing insight into neuropsychological deficits of the frontal lobe in general and of Alzheimer's Disease specifically. Also, Baddeley points to the following neuroimaging study investigating the neural substrates of the CE.

D'Esposito and colleagues (1995) investigated the brain activation during performance of a dual-task in an attempt to study the CE of Baddeley's model. In this study, a semantic-judgement task (i.e., subjects were required to say which of a list of aurally presented words were the names of vegetables) and a spatial rotation task (i.e., subjects were required to match a feature of a geometric figure seen in different orientations) were performed by subjects, individually and simultaneously. Although neither task activated the prefrontal cortex when

performed alone, significant activation was noted bilaterally in the dorsolateral PFC during the

dual-task condition. Such results directly address the concerns raised about the localization of

a singular construct that is involved in cognitive control processes. Although there would be

little argument that the dorsolateral PFC would function in the context of a neural circuit

rather than alone, according to these functional neuroimaging results, this structure does

appear specific to performance of a dual-task.

Despite such preliminary neurological support for Baddeley's conceptualization of an

executive construct, further research is required to address the neural localization and

functioning of the CE. The present study aims toward this goal through an

electrophysiological exploration of the CE during working memory tasks that manipulate its

proposed limited capacity by increasing WM load, as well as during a dual-task condition

thought to specifically tap CE functioning.

Petrides' Conceptualization of WM. Whereas Baddeley focuses primarily on the

hypothetical constructs involved in working memory, Petrides has taken a neuroanatomical

approach in developing a model of the role of the prefrontal cortex in WM. More specifically,

Petrides (Petrides et al., 1993a, b; Petrides, 1995) provides a two-level distinction between the

functioning of the middle portions of the dorsolateral (areas 9 and 46) and the ventrolateral

(areas 45 and 47/12) frontal cortical regions (see Figure 1, Appendix A).

According to this model, the fundamental distinction between the activation of these

two frontal regions involves the nature of the executive processing that is being performed.

First, the ventrolateral frontal regions is where information is initially received and maintained

on-line. This ventral PFC region is also involved with the strategic encoding and retrieval of

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information held in posterior cortical regions and thus in selecting, comparing or deciding on short-term and long-term memory data. The dorsolateral PFC constitutes a second level of executive function that would only be involved if the task required some type of monitoring and/or manipulation of the temporary data. Petrides (1995) describes monitoring as involving "attention to the stimulus that is currently under consideration together with active consideration of several other stimuli whose current status is essential for the decision to be made" (p. 89). According to this conceptualization of WM, the two levels of mnemonic processing are likely required in many different tasks, and often simultaneously.

Evidence for this model comes from the work of Petrides and colleagues, primarily through use of the self-ordered WM task. This task involves the presentation of different arrangements of the same set of stimuli, with subjects required to select a different stimulus on each trial until all the stimuli are selected. For example, Petrides et al. (1993b) used a verbal self-ordered task that required participants to say aloud, in random order, the numbers from 1 to 10, without repeating any. Once all the numbers have been said once, they are asked to begin a new trial, again generating numbers randomly from 1 to 10 with no repetition. The 'monitoring' requirements of this task involve the participants continuously comparing the responses they have already made with those remaining to be carried out, while the 'manipulation' involves changing the status of each stimuli from 'one yet to be chosen,' to 'one not to be chosen again.' Evidence of dorsolateral PFC activation during tasks requiring such monitoring and manipulation processes has been provided by both animal lesion (Petrides, 1994, 1995) and PET studies (Petrides et al., 1993a, b).

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Petrides also designed tests to investigate the proposed functioning of the ventrolateral PFC, as well as the orbital frontal cortex. In an unpublished investigation (cited in Petrides, 1995), PET scans were taken while subjects were (1) observing familiar stimuli; (2) observing novel stimuli; and (3) making explicit recognition judgements between novel and familiar stimuli. He found that the orbitofrontal cortex had greater activity when the stimuli were novel compared to when they were familiar, suggesting this frontal area might be differentially sensitive to the relative familiarity of stimuli. Further, greater activation was found in the ventrolateral PFC when subjects were required to make decisions on the information being held in memory. Specifically, when decisions were required that also required the strategic retrieval of information from short- or long-term memory stores, the ventrolateral PFC was more apt to be involved (Buckner et al., 1995; Petrides, 1995).

Several neuroimaging studies have provided supportive evidence of this executive model. Owen, Evans and Petrides (1996) and Owens et al. (1999) completed a PET investigation of several different WM tasks, some of which required greater monitoring and/or manipulation of the information maintained on-line compared to the others. Results indicated that dorsal PFC activation was evident only for the WM tasks that required the additional processing. The tasks that did not require continued monitoring/manipulation of the information reportedly activated only ventral PFC regions. Salmon and colleagues (1996) found similar results in a PET investigation in a comparison of a WM task that required the updating of the information held on-line to a letter-span task that did not require such monitoring. Similar to the previous study, dorsal PFC activation was only evident in the WM task that required the additional processing. Finally, Zarahn, Aguirre and D'Esposito (1997)

found supporting data using event-related fMRI. Similar to other studies, dorsal PFC activity was evident when subjects performed a WM task that required the manipulation of a sequence of letters, while ventral PFC activation was evident when the requirement involved only the maintenance of the letter sequences on-line.

Although still presented by the researchers as providing evidence for Petrides' conceptualization of WM, the results of some studies find differential activation that is not entirely consistent. For example, D'Esposito, Postle, Ballard and Lease (1999) presented tasks with 'maintenance only' and 'maintenance plus manipulation' requirements. Contrary to predictions based on Petrides' model, dorsolateral PFC activation was evident during both tasks, although it did increase when manipulation of the stimuli was required. The investigators suggest that perhaps the dorsolateral region is involved in both maintenance and manipulation of data, although such activation was not evident in the above studies. It should be noted, however, that D'Esposito's tasks appear to emphasize the manipulation cognitive requirements, while the tasks of Petrides' emphasize the monitoring requirements.

In short, according to Petrides' model of PFC functioning and WM processes, it is the nature of the required executive processing, rather than the nature of the stimulus material, that is the critical factor determining whether the dorsolateral and the ventrolateral PFC are differentially activated. The ventrolateral frontal area is involved with the maintenance of information on-line, while the dorsolateral mediates the monitoring and manipulation of the temporary information. Thus, whether the information is of a spatial or a verbal nature, the same PFC areas will be involved accordingly. Evidence for Petrides' model is growing, although the results are not always entirely consistent.

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The models of Petrides and Baddeley can be viewed as similar in certain regards, although one presents a neuroanatomical approach and the other a cognitive process approach. In both, activation of the components of a WM system are seen as dependent upon the specific demands of the task at hand. Petrides' differentiation between the functions of the dorsolateral and the ventrolateral areas of the PFC might in fact be seen as the fractionation of the CE that Baddeley (1998) expects to document with continued exploration of his model. The current study will not attempt to differentiate between these two executive models, but rather collectively contrast them against modality-specific models of WM.

Modality-Specific WM Models

In contrast to the above models, modality-specific models propose that the cortical areas involved in subserving WM are dependent upon the type of information involved. For example, Goldman-Rakic and colleagues (Friedman & Goldman-Rakic, 1994; Wilson et al., 1993) offer a conceptualization of working memory that emphasizes how PFC and posterior cortical areas are modality-specific and linked in reverberatory circuits that work to keep information on-line. According to Goldman-Rakic (1995), "memory-guided behaviour obviously reflects the operation of a widely distributed system of brain structures and psychological functions, and understanding the prefrontal component is but one part of the grand design" (p. 477).

In order to investigate the neural substrates involved in WM, these researchers have employed single-cell recordings in nonhuman primates using various delayed-response paradigms (i.e., the animal must remember a cue stimulus over a delay period and then make a behavioural response based on the cue). Such investigations have revealed that prefrontal

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neurons that code visuospatial aspects of stimuli are located in separate areas from those that code categorical features of stimuli (for an overview see Beardsley, 1997). First, Wilson and colleagues (1993) recorded neuronal activity from monkeys during performance of oculomotor delayed-response tasks in which spatial or pattern information had to be remembered. Results indicate that neurons in the inferior convexity of the PFC were especially responsive to pattern-delayed-response trials. In contrast, Funahashi et al. (1989) found activity of dorsolateral prefrontal neurons to be related to spatial information in delayed-response tasks. Based on several investigations, researchers have concluded that individual prefrontal neurons that code the location of targets rarely, if ever, code object qualities, or vice versa (Courtney, Ungerleider, Keil & Haxby, 1996; Fuster & Jervey, 1982; Goldman-Rakic, 1995; Wilson et al., 1993).

Further investigation has shown that the pattern-specific inferior prefrontal neurons project to inferotemporal (IT) neurons, which have also been found to be activated during the delay period in memory tasks (Fuster, Bauer & Jervey, 1985; Miller & Desimone, 1994). Miller, Desimone and colleagues have intensively studied the activity of IT neurons in memory tasks involving non-spatial stimuli such as shapes, faces and complex patterns (Desimone, Albright, Gross & Bruce, 1984; Miller, Li & Desimone, 1991). Investigations have revealed that activity in prefrontal cells during the delay of a WM task was maintained throughout the trial, even when other test stimuli intervened. In contrast, activity in the IT cells during the delay period was disrupted by intervening stimuli (Miller, Erickson & Desimone, 1996). This led to the suggestion that inferior prefrontal neurons prime IT neurons, and that together they represent two nodes in a WM neural network specific to pattern information.

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To explore the components of the WM neural network involving spatial information, Friedman & Goldman-Rakic (1994) trained monkeys to perform spatial alternation tasks or visual-pattern-discrimination memory tasks. Comparing the two groups, monkeys that had performed the spatial WM tasks showed significant metabolic activation (using the C-2-Deoxyglucose (2DG) method) in the principal sulcus region of the PFC, as well as in regions of the inferior parietal cortex. These findings support previous results, which found spatial PFC memory centers to be densely connected to the parietal cortex (Cavada & Goldman-Rakic, 1989).

The accumulation of the above findings suggests that there are prefrontal areas that are specialized for the processing of object ("what") and spatial ("where") visual information and that these specialized areas are linked in different cortical reverberatory circuits. More specifically, dorsal PFC areas appear to recruit parietal regions in WM tasks involving spatial information, whereas ventral PFC regions activate inferior temporal neurons when non-spatial or pattern information is key in a WM task. In this regard, working memory cortical substrates are considered functionally heterogeneous.

Considering the theories of Baddeley (1986) and Petrides (1995), Goldman-Rakic (1999) points out that neuroimaging studies with humans have not been able to establish a particular PFC area that mediates the metacognitive processes emphasized in the executive models. Based on her research, she therefore argues that "metacognitive phenomena are constructed from domain-specific networks" (p. 653).

It should be noted that not all single-cell studies have supported Goldman-Rakic's model of modality-specific working memory circuits. Arguing that separation of object and

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spatial information rarely occurs in the real world as it does in experimental designs, Rao, Rainer and Miller (1997) propose that evidence of modality-specific neurons might reflect an artificial behavioural segregation. To investigate, they completed single-cell recordings of PFC neurons while nonhuman primates solved delayed-choice tasks that required them to remember information about *both* the appearance and the spatial location of objects. Results were somewhat consistent with previous findings in that the activity of some neurons responded to either object or spatial cues, but not both. In contrast, however, over half of the neurons investigated were active during different epochs of the same behavioral trial, appearing to be responsive to both object and spatial information. Both the specialized ('what' cells and 'where' cells) and the non-specialized WM neurons were found to be equally distributed between the dorsolateral PFC and the ventrolateral PFC, thereby contradicting the results of Goldman-Rakic and colleagues.

Modality-Specific WM in Humans. Neuroimaging studies have investigated functionally heterogeneous WM systems in humans. Although some results have been supportive of different neural structures being activated when different types of information are presented in a WM task, there are conflicting results, both within the neuroimaging literature, as well as between this body of research and that involving single-cell recordings with nonhuman primates.

Jonides and colleagues (Jonides et al., 1993; Koeppe et al., 1993, cited in Smith & Jonides, 1995) performed a series of PET studies of regional cerebral blood flow in normal adults completing working memory tasks. With one group of subjects (Jonides et al., 1993), PET measurements were taken while participants performed a spatial WM task in which a

target location had to be remembered. Several areas of statistically significant activation were reported, including right prefrontal (area 47), right posterior parietal (area 40), right occipital (area 19) and right premotor cortex (area 6). Despite results that indicate predominately right hemisphere activation, the researchers caution about localizing the relevant processes to only this hemisphere because there was also increased activation (although not statistically significant) in the homologous left hemisphere regions. Nevertheless, such results do indicate that performance of a spatial WM task is mediated more directly by the right, rather than the left, hemisphere.

Koeppe and colleagues (1993, cited in Smith & Jonides, 1995) present data on another group of subjects who completed an object WM task that required they remember unfamiliar geometric figures. The pattern of cortical activation as measured by PET revealed significant activation in the left inferior prefrontal gyrus (area 6), left parietal lobe (area 40), left inferior temporal gyrus (area 37) and the anterior cingulate areas (area 32).

Together, the results of these PET studies support previous findings that the PFC is involved in governing working memory, with activation in the object task in a region superior and posterior to that found for the spatial task (i.e., area 6 versus area 47). Although this result is opposite to the findings of Wilson et al. (1993) who report inferior PFC activation with an object WM task, Smith and Jonides describe their results as consistent given that dissociable areas of activation for the two types of WM tasks were evident, even if not entirely the same, in human and non-human primates. Results also suggest that different posterior areas are involved in mediating WM processes, again dependent on the type of stimuli presented in the task. First, the neural network activated during the spatial WM task

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involved the parietal cortex, a result similar to the findings of Friedman and Goldman-Rakic (1994). The object WM task activated the inferior temporal lobes, an outcome similar to that found by Wilson et al. (1993). However, unlike the single-cell-recording animal research, the object WM task also activated the parietal lobes, which is similar to the PET activation found during the spatial WM task. Also, the PET studies found the spatial tasks to recruit processes largely in the right hemisphere, and the object task to more strongly recruit processes in the left hemisphere.

The possibility of modality-specific working memory systems has also been explored using other neuroimaging techniques. For instance, Manoach and colleagues (1997) investigated the neural networks involved in a non-spatial WM task using functional magnetic resonance imaging (fMRI). The Sternberg Item Recognition Paradigm (Sternberg, 1966) was employed which requires participants to memorize a set of target digits and then identify whether single probe digits later presented were part of the memorized set. A 'high WM load' of five target digits and a 'low WM load' of two target digits were presented in order to examine the effect of WM load on cortical activation.

Several regions in the frontal and parietal lobes displayed significant levels of activation, including the dorsolateral PFC, supplementary motor area, lateral premotor and primary motor cortex, as well as the intraparietal sulcus. Given that the stimuli were of a non-spatial nature, it would have been expected, based on the results of animal research (e.g., Wilson et al., 1993), that inferior prefrontal areas, as opposed to dorsal prefrontal areas, and also that temporal cortex, rather than the parietal cortex, would have shown activation. However, this result of parietal activation during an object WM task is similar to the PET

study of Koeppe et al. (1993) who found parietal activation during both spatial and object WM tasks, although Koeppe also found additional temporal activation during the object task that was not evident in the fMRI results.

Another interesting finding of Manoach et al.'s (1997) study is that the dorsolateral PFC was preferentially activated in the right hemisphere. Again, given the results of the PET studies of Jonides and colleagues, such activation would not be expected because the task was non-spatial in nature.

It is clear that although the results of neuroimaging studies with human subjects coincide in some respects with the non-human neuronal recording research, there are some contrasting results as well. First, the human research reports significantly stronger activation in a specific hemisphere (although the hemisphere activated for spatial and non-spatial tasks is different according to PET and fMRI studies). In contrast, no evidence of preferential activation of a given hemisphere has been reported in the primate research. With respect to the cortical regions activated, two studies report more dorsal prefrontal activation during an object WM task (Koeppe et al., 1993; Manoach et al., 1997), while another indicates inferior prefrontal activation during a spatial WM task (Jonides et al., 1993). This pattern of activation is opposite to that reported by Goldman-Rakic and colleagues (i.e., Friedman & Goldman-Rakic, 1994; Wilson et al., 1993). Furthermore, the PET studies suggest that both the temporal and the parietal regions are involved with object WM tasks, whereas the results of the fMRI study suggest only the parietal area is activated during such tasks. These results are also in contrast to many animal studies (i.e., Fuster et al., 1985; Miller & Desimone, 1994; Miller et al., 1991), which report that inferotemporal neurons are involved only with non-

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spatial stimuli.

These contrasting results might be at least partially explained by consideration of methodological issues. First, it must be noted that all visual tasks inherently consist of both spatial and object information to varying degrees. The contrasting results of parietal and temporal activation during performance of certain object WM tasks may reflect this because different tasks and stimuli are used across studies. For instance, Manoach et al. (1997) employed numbers as stimuli, which although non-spatial in nature, differ from pattern stimuli. However, it is noted that Koeppe et al. (1993) used unfamiliar geometric shapes as stimuli, similar to the pattern stimuli of Wilson et al. (1993), and yet also reported prefrontal activation that was more dorsal compared to the activation during the spatial WM task.

A second issue is that the control tasks administered may not always be successful in subtracting out additional cognitive processes required to perform the WM tasks (D'Esposito, Zarahn & Aguirre, 1999). Typically, a WM task is presented in which a delay period is inserted between the "perceptual processes" of the task and the "choice" processes of the task, with the processes of interest being those that are occurring within this delay period. The subtraction task presented usually involves the same perceptual and choice processes, with the period of delay removed. D'Esposito et al. argue that this paradigm might fail to meet the assumptions of cognitive subtraction if the insertion of the delay period affects the other non-working-memory processes involved in the task. If this occurs, the resulting artifacts could lead to the association of specific cortical activity to the proposed WM processes involved during the delay period. D'Esposito concludes that there are "empirical grounds for adopting a healthy doubt regarding the inferences drawn from imaging studies that have relied on

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cognitive subtraction" (p. 162).

The present research proposes to deal with several of these methodological issues. First, in contrast to the neuroimaging studies that have investigated modality-specific WM by comparing activation patterns in different subjects, the present study proposes such a comparison within subjects. Also, two versions of a single WM task (i.e., n-back task) were administered that differed only in their requirement to attend to either the spatial location or the specific letter as the stimuli to match; the visual presentation and required response were entirely the same.

The 'n-back' is a sequential-letter memory task that has been employed in several investigations and is reported to reliably produce activation of cortical regions believed to subserve the processes of WM (e.g., Braver et al., 1997; Cohen et al., 1994; Cohen et al., 1997; D'Esposito et al., 1998a; Gevins et al., 1996, Smith et al., 1996). Some studies have found evidence of differential cortical activation patterns for the two tasks (e.g., Smith et al., 1996), while others have not (e.g., D'Esposito et al., 1998a). Although using a task that differs only in the type of information to be maintained on-line is seen as an improvement over studies comparing tasks that differed on several dimensions, this approach is not without its disadvantages. First, if subjects maintain on-line the verbal aspect of the stimuli for both tasks (i.e., letter presented), there is the potential of a lessening of a modality-specific pattern of cortical activation. However, given that the stimuli are presented quickly and there is continuous monitoring and manipulation of each stimuli required, it is believed that subjects would not be able to perform the spatial-back tasks successfully unless they attended to the stimulus attribute (i.e., spatial position) instructed to. Consequently, although keeping the

perceptual and response requirements of the tasks identical is disadvantageous in some respects, making a spatial task with different, non-verbal stimuli would introduce potential confounds as the tasks could then not be completely equated. It seems there is no 'perfect' method to investigating modality-specific WM that would both completely equate the tasks on all other cognitive requirements, as well as keep all attributes of each stimuli within one-modality only. As such, we have chosen to equate the tasks in all respects except for the type of information to be maintained on-line, while acknowledging the potential disadvantage associated.

Electrophysiology

Two strategies can be followed in electrophysiological studies of cognitive processes: (1) event-related potentials (ERPs) which are time-locked to a specific stimulus, and (2) the analysis of the spontaneous EEG while the cognitive process is being tapped. Although most studies focus on one or the other of these methods, the current study will employ both. First, a brief explanation of event-related potentials will be provided, followed by a review of ERP investigations of working memory. Next, EEG methodology and literature will be reviewed.

Event Related Potentials

Event-related potentials are small fluctuations in the electrical activity of the brain that are time-locked to a specific event, such as the onset of a stimulus (Picton, 1988). ERPs consist of successive positive and negative deflections that are produced by synchronous activation of neurons in cortical or subcortical generators, with each deflection reflecting contributions from groups of neuroanatomical structures that are either structurally or functionally related (Woods, 1990). In other words, the latencies and scalp topographies of

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the deflections reflect the timing and spatial configuration of activated brain areas (i.e., the passage of information through the nervous system). In this way, the fractionation of the ERP waveform into constituent components allows for investigation of relatively specific aspects of information processing.

In general, the earlier components (e.g., N100, P200) are thought to reflect automatic aspects of processing a stimulus. In contrast, later components (e.g., P300) reflect controlled aspects of processing, such as the subject's cognitive strategy (Picton & Hillyard, 1988). Shiffrin and Schneider (1977) distinguish between the two types of processes as follows: (1) *Automatic processes* are those that function continuously and independently of intention; whereas (2) *Controlled processes* depend on the subject's intent, can be easily monitored by introspection, and can interfere with other simultaneous controlled processes.

More specifically, the N100 has been associated with early detection and analysis of stimulus features, with 'attended' stimuli associated with a more negative (greater amplitude) N100 compared to 'unattended' stimuli (Naatenen & Picton, 1987). This effect has been considered by some as an early filtering process that reduces the processing of irrelevant information, and by others in terms of additional attentional resources being provided to process critical information (for further discussion see Ray, 1990b). Next, the early positive component (P200) is also associated with early selection processes and its amplitude can be similarly enhanced in 'attend' conditions (Naatenen, 1990). In contrast, the later N200 and P300 are considered probability-sensitive components that reflect perceptual processing (Rugg et al., 1988). More specifically, the N200 is considered a sign of effortful stimulus processing, with its latency a reflection of the duration of stimulus categorization processes

(Rugg et al., 1988), whereas the P300 is considered an index of active decision processes (Donchin & Coles, 1988; Mecklinger & Ullsperger, 1993; Snyder, Hillyard & Galambos, 1980).

It is important to note that each ERP component has been found to be differentially sensitive to experimental manipulations. Largely due to its robustness and easy elicitation in relatively simple experimental paradigms, the centro-parietal maximal P300 has been the most thoroughly investigated. The amplitude of this late component has been shown to be affected by a combination of the probability, task relevance and informational value of the eliciting event (Hoffman, 1990; Picton & Hillyard, 1988; Regan, 1989). Kramer and Spinks (1991) summarize the effects of variable manipulations on the P300 as indexing changes in amplitude related to the amount of attention directed toward a particular stimulus feature.

The latency of the P300 component is considered to reflect stimulus evaluation time (Hoffman, 1990; McCarthy & Donchin, 1981; Rugg et al., 1988). To exemplify, Magliero, Bashore, Coles & Donchin (1984) found P300 latency lengthened systematically as noise set size was increased and therefore the time required to identify the target increased. In contrast, manipulations that affected response selection and execution (e.g., target vs. non-target) did not increase P300 latency.

Some researchers suggest that increased P300 latencies are directly related to the level of task difficulty (Grillon, Courchesne, Ameli, Elmasian & Braff, 1990). In other words, as the level of task difficulty increases, the time to process the stimuli also increases. However, others have argued that increased P300 latencies are a passive reflection of increases in the latency of the earlier components, i.e., reflecting the effects of automatic processing (Goodin,

Starr, Chippendale & Squires, 1983; Ritter, Simson, Vaughan & Friedman, 1979). The latter studies have demonstrated that as task difficulty increases, the latencies for both early (i.e., N200, P200) and late (P300) components also increases.

In contrast to analyzing well-studied ERP components, such as the P300, investigators can instead consider how the waveform at particular intervals of time relates to various independent variables (e.g., Schuboltz & Friederici, 1997). One such approach involves a measurement of the area under the waveform (Dywan, Segalowitz & Webster, 1998). An area analysis provides an advantage to considering a specific ERP component in that the amplitude of the wave can be analyzed without limiting the focus to a single time point. For example, the effect of a manipulation that lengthens the P300 component might be better understood if the entire area under the waveform was considered, compared to the single peak around 300 ms. Analysis of both the amplitude and latency of the P300, as well as the area under the waveform from 300 ms to 1500 ms will be conducted in the present study.

Rugg (1995) outlines several benefits of ERP investigations in memory research. First, ERP's have a high temporal resolution and therefore are well-suited to address the time-course of brain activity associated with cognitive processes. Second, ERPs can serve as "covert" measures of processing in that they often illuminate differences in processing that are not detected by behavioural measures. Finally, comparison of the scalp distributions of ERP waveforms might suggest different patterns of neural activity between experimental conditions, thereby providing support for functionally distinct processes. Given these benefits, researchers have employed this electrophysiological technique to the study of working memory.

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Event-Related Potential Working Memory Studies. Initial investigations of

working memory have focused on a slow wave component that appears to be specific to WM

operations (Mecklinger et al., 1996; Ruchkin, Johnson, Grafman, Canoune & Ritter, 1992;

Schuboltz & Friederici, 1997). This component is reported to arise over much of the scalp but

appears primarily in the frontal areas (Chao & Knight, 1997) and is of a long duration (i.e., up

to 4 seconds). According to Ruchkin and colleagues (1992), ERP analysis has revealed a

number of topographically and functionally distinct slow wave components that overlap to

varying degrees, which suggests that both discrete and cascading information processes are

involved with WM tasks.

The results of several ERP studies add to the body of converging evidence regarding

domain-specific cognitive subsystems by noting that the processing of stimuli reflecting

different information content is associated with distinct event-related activity. For instance,

slow waves have been reported to be largest over the left hemisphere during phonological

memory operations (Barrett & Rugg, 1990; Rugg, 1984a, b), but largest over the right

hemisphere during visual- feature memory operations (Barrett & Rugg, 1989; Barrett, Rugg

& Perrett, 1988). Furthermore, Uhl et al. (1990) found that slow waves were largest over the

parietal scalp when subjects imagined a diagram of a map but largest over temporal and

occipital regions when they imagined faces and colours.

More specifically in terms of working memory and domain-specific subsystems,

Schuboltz and Friederici (1997) had subjects perform WM tasks requiring judgement as to

whether two stimuli were the same or different with regard to either temporal duration or

spatial location. The ERP waveforms showed significant topographical differences between

the auditory and the visual modality, and three distinct processing phases were noted. Specifically, from stimulus onset to around 500 ms ("modality-specific encoding" phase), the waveforms elicited by the spatial task were significantly more negative in frontal areas, whereas the temporal task elicited waveforms that were significantly more positive in the centroparietal area. Next, from 500 to 2000 ms after stimulus onset ("information-specific encoding" phase), the spatial WM task generated a parieto-occipital negative slow wave, while the duration judgement task yielded a negative slow wave with a fronto-lateral focus. Finally, a large centroparietal-focused positivity was found from 1200 to 5500 ms ("inhibitory accompanied retention of information" phase) for the duration judgement task, which was not demonstrated with the spatial task. Instead, this latter task demonstrated a slight, nonsignificant, slow negative shift. In short, the different waveforms produced by the spatial and duration judgement tasks support the conceptualization of modality-specific WM systems.

The results of Ruchkin and colleagues (1992) also provide some support for the presence of specialized brain systems for maintaining information of different content on-line during a working memory task. In their study, the ERP components elicited during a visuo-spatial (involving two-dimensional patterns) WM task were compared to those elicited during a phonological (pronounceable non-words) WM task. Both similarities and differences were noted in the waveforms associated with the two tasks.

With regard to the activity involved in the processing of the visuo-spatial task, the waveform morphology was relatively simple, involving a large parietal-maximal, negative slow wave immediately following the P300, which continued until the end of the recording epoch. According to these researchers, the timing of the P300 and the onset of the slow negative

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wave suggests that encoding and beginning of rehearsal processes were more rapid in the visuo-spatial task. Furthermore, although the ERP activity recorded during the early (before stimulus offset) and middle intervals was clearly lateralized over the right parieto-temporal areas, by the late (retention) interval maximal activity shifted to the mid-line during the visuo-spatial task.

With regard to the ERP activity recorded during the phonological WM task, the morphology of the wave was comparatively more complex, with four different slow waves elicited. First, between 600 and 1500 ms, a negative slow wave localized to occipital and left posterior temporal scalp (regions purported to be involved in phonological input mechanisms) was evident. Next, between 1000 and 3000 ms there was a parietal slow wave, whose duration and amplitude were both directly related to the number of syllables processed. Lastly, from about 3000 ms to the end of the recording, there was a left frontal negative slow wave, as well as a bilaterally symmetrical centro-parietal negative slow wave.

According to these researchers, these latter two negative waves are likely associated with rehearsal processes and are consistent with Baddeley's (1986) conceptualization of a phonological rehearsal loop involved with WM operations (i.e., frontal regions are concerned with the phonological output buffer, whereas parietal regions are involved with phonological and lexical activation as well as perceptual discrimination). Furthermore, given the timing and topography of a negative slow wave in the left frontal areas apparent 1000 ms after stimulus onset in both WM tasks, the researchers suggest that the wave reflects functioning of the central executive of Baddeley's model. However, these interpretations are presented as conjectural since relevant experimental manipulations were not conducted.

It is, in fact, relatively rare that ERP investigations are designed specifically to test psychological models of cognitive processes. As a result, it is difficult to directly assess models, such as those presented by Baddeley, Petrides and Goldman-Rakic, using existing ERP research. The current study, however, is designed with this aim.

As with the single-cell recording studies previously reviewed, it is important to note that not all ERP investigations of WM support the existence of modality-specific neural networks. For example, Gevins et al. (1996) present an ERP study that employed 115 channels and two WM tasks which were described as identical in their perceptuomotor requirements but different in the type of information to be kept on-line. More specifically, n-back WM tasks were employed, one that required the participant to match the specific letter, and another that required the spatial position of the letter to be matched. Results indicated both task-specific and task-independent ERP components. With regard to task differences, the central P200 potential was larger in the spatial tasks compared to the verbal tasks. In addition, the non-matching stimuli elicited a frontal, positive P300 peak that was larger in the spatial WM task. In contrast, the slow wave components, most closely identified with WM processes, did not show modality-specific task differences. Regardless of the information to be maintained on-line, a P450 potential was noted over the left frontal cortex, followed by a sustained potential over the superior parietal cortex. The common distribution of this slow wave for both spatial and verbal WM suggests that it was not produced by modality-specific storage of representations, but rather more general processes related to the maintenance of information on-line.

Similar to the single-cell-recording animal research and the neuroimaging studies, the results of ERP investigations continue to provide conflicting results regarding the existence of modality-specific WM systems. In addition to improving the experimental paradigm by systematically increasing WM load and comparing within subjects, as already discussed, the current study aims to employ both ERP and EEG technologies to directly investigate both executive and modality-specific WM models. In this way, results can be compared to previous research that has employed similar tasks, and can also be used to provide an alternative method of investigation (EEG coherence) into the neural substrates of WM.

Electroencephalography Techniques

As previously discussed, EEG provides another electrophysiological method of investigating cognitive processes. EEG is a record of the spontaneous electrical activity in the brain as recorded from the surface of the scalp. Information flow through the central nervous system is primarily conducted through postsynaptic potentials (PSPs), which can be either excitatory or inhibitory in nature. Scalp-recorded EEG is considered a reflection of the average of these potential differences (Petsche & Rappelsberger, 1992; Ray, 1990a). Specifically, it is the graded synaptic and dendritic potentials, rather than the all-or-nothing action potentials, that summate and reflect the strength of the stimulus. In describing the physiological basis of the EEG, Elul (1972) describes "synaptic functional units" that are composed of thousands of synapses. Within each functional unit, the synapses share the same presynaptic input, resulting in the depolarization or hyperpolarization of an immense number of neurons as a unit. It is the activity within these functional units that is recorded by surface electrodes.

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It is argued that only the vertically oriented pyramidal cells contribute to the EEG

signal (Lutzenberger, Elbert & Rockstroh, 1987; Martin, 1985). Given that their dendrites run

perpendicular to the surface of the cortex, the potential generated on the dendrites is picked

up with little attenuation. In contrast, due to their geometry, basket and stellate cells do not

contribute significantly to the EEG signal. Another important characteristic of the pyramidal

cell that pertains to its contribution to the EEG signal is its characteristic dendritic

organization. Because the apical dendrites of the pyramidal cell cross several layers of the

cortex, input from many different sources can be derived. In addition, pyramidal dendrites

contain booster zones that amplify synaptic currents, thereby enabling input from distant

synaptic sites (for a more thorough review see Martin, 1985). As such, potentials of pyramidal

cells can temporally and spatially summate to produce a signal that can be picked up by

surface electrodes.

Petsche and Rappelsberger (1992) emphasize the importance of the synchronization of

the pyramidal cell activity underlying the electrode. They argue that without synchronization

of the potentials, EEG would not be recordable at the scalp because the bone and its

underlying tissue act as low-pass filters. Cooper, Winter, Crow and Walter (1965) have

demonstrated that cortical areas of several cm^2 must be involved in the same wave pattern to

become detectable at the scalp.

EEG Analysis. Traditionally, the EEG was analyzed by visually inspecting pen-

deflection patterns, without the use of quantitative data. This obviously placed limitations on

the use of the EEG in the investigation of cognitive processes. However, since EEG

methodology has become refined by the use of computer-based analytic techniques, two

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signal-processing procedures have become increasingly employed in human EEG research. The first and more commonly used approach is referred to as *power spectral analysis*, and the second approach, used somewhat less frequently, is *coherence analysis*.

Power spectral analysis involves the spectral decomposition of the complex EEG signal into its component frequencies through techniques such as Fast-Fourier Transformation (FFT; Ray, 1990a). According to Shaw (1984), the EEG signal can be regarded as "the sum of many components of different frequencies summating to produce the resultant complex pattern of fluctuation" (p. 258). Fourier analysis transforms this summated EEG signal, as expressed in terms of time, into quantified frequency spectra. The major frequency bands include delta (0.5 to 3.5 Hz), theta (4-7.5 Hz), alpha (8-12.5 Hz) and beta (13 to 30 Hz). The relations between brain function and EEG measures have commonly been investigated by comparing regional changes in the amount of EEG activity within these particular frequency bands and at particular scalp regions (Ray, 1990a).

The delta and theta bands are referred to as slow-wave activity. Delta activity is most commonly associated with stage 4 sleep in adults and is a predominant frequency of the newborn during the first two years of life. Theta activity, on the other hand, is predominant in children between one and six years of age and, similar to delta, decreases with age. Theta has been associated with a variety of psychological processes, including hypnagogic imagery, rapid-eye-movement sleep, problem solving, hypnosis and meditation (for a review of slow-wave activity, see Ray, 1990a).

The alpha bandwidth has received widespread attention in EEG investigations of cognitive processes (e.g., Duffy, Bartels & Burchfield, 1981; Rappelsberger & Petsche, 1988).

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Alpha activity, which is recorded best over parietal and occipital areas, is associated with a state of relaxed wakefulness (Martin, 1985). Therefore, a reduction in alpha (referred to as alpha blocking) is typically thought to represent cognitive activity and information processing (Ray, 1990a). However, Petsche and colleagues (Petsche, Lindner, Rappelsberger & Gruber, 1988) caution against this practice, reporting a consistent lack of expected effects in the alpha bandwidth in their investigations of different cognitive processes. Instead, these researchers found more task-dependent effects in the theta and beta bandwidths. Although not as frequently investigated as activity in the alpha band, beta activity is thought to directly represent cortical activation and mental activity (Ray, 1990a), and is best recorded over the frontal regions (Martin, 1985).

Whereas the traditional method considers the power spectral density for each channel, coherence analysis gives the covariance of spectral energies between any given pair of channels at a particular frequency (Ray, 1990a). In short, coherence provides a measure of the degree of "phase synchrony" or "shared activity" between spatially separated cortical generators (Thatcher, 1994). Mathematically speaking, coherence is analogous to a cross-correlation in the frequency domain (Thatcher, 1992). Because coherence reflects the number and strength of connections between distant cortical areas, such measures may be more sensitive to the relations between the EEG and mental activity than traditional measures of EEG amplitude (Thatcher et al., 1987, p. 264).

Thatcher, Krause & Hrybyk (1986) present a two-compartment model of the neurophysiological foundation of EEG coherence measures. The model is based on the two types of cells contained within the neocortex: (1) long-axoned pyramidal or Golgi type I cells

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that have apical dendrites that receive input primarily from long-distance intracortical connections, and (2) short-axoned Golgi type II cells, which have basal dendrites that receive input primarily from the axon collaterals from neighbouring pyramidal cells. These two systems are said to reflect different network properties. First, the Golgi type II cells are involved with local interactions in the order of millimeters to a few centimeters, whereas the Golgi type I cells are involved in long distance feedback or loop systems that are in the order of several centimeters. It is these latter cells that compose the majority of white matter fibres.

According to this model, short axonal connections (Golgi II cells) will contribute highly to EEG coherence for short electrode distances (e.g., local coherence between frontal electrodes). In contrast, at long electrode separations (e.g., frontal-posterior electrode pairings) the contribution of short axonal connections to coherence would be minimal and the main contributor would be the long axonal connections (Golgi I cells). As such, both short and long distance axonal systems can be reflected in EEG coherence (Thatcher et al., 1987).

According to Thatcher et al. (1986), an increase in coherence could theoretically be a result of (1) two cortical areas directly coupled, (2) a third cortical or subcortical source related to both, or (3) a cascade of regions functionally interrelated at the recorded areas. As these factors are reflected in EEG coherence values, coherence can provide a measure of both the functional and structural organization of electrocortical brain activity.

To explain further, if one brain area becomes either active or inactive, the correlation between the EEG from that area with another area will change, resulting in either increases or decreases in coherence values across electrode pairs. In addition, if a subcortical structure that is driving two separate cortical areas changes its role, a change in the coherence across

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electrode pairs would be evident. Such activity is still reflective of communication between cortical structures however, even though this communication is achieved indirectly through reciprocal cortical/subcortical connections. It is important to note that volume conduction must be considered when discussing EEG coherence changes. That is, there must be differentiation in the changes in coherence values between electrodes (i.e., coherence does not increase or decrease between all electrode pairs at any given recording epoch) for specificity in the communication between the cortical areas underlying the electrodes to be assumed.

EEG coherence analysis has been successfully applied in studying cognitive processes in adult populations (e.g., Morrison-Stewart et al., 1991; Petsche et al., 1988; Petsche, Lacroix, Lindner, Rappelsberger & Schmidt-Henrick, 1992; Rappelsberger & Petsche, 1988). For instance, Tremblay and colleagues (1994) used coherence to investigate cortical activation during a maze task thought to primarily involve frontal lobe functioning. Increases in coherence were evident within the prefrontal regions, between parietal and central electrodes paired with frontal electrodes, and in the posterior temporal, parietal and occipital regions. These findings support the use of EEG coherence measures in the study of executive functions, such as working memory, as is undertaken in the current study.

EEG measures may be more informative than other techniques used in recent WM research in several ways. First, in comparison to brain imaging techniques, electrophysiological methods offer a better temporal resolution with which to investigate the time-course of brain activity associated with cognitive processes. It is acknowledged that ERPs are reputed to provide an even better temporal resolution than the EEG, and are therefore most commonly employed in cognitive research. Finally as was briefly discussed, in

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contrast to PET, fMRI, ERP and traditional EEG spectral analysis, which only provide information about activation, coherence measures are sensitive to the existence and magnitude of corticocortical connections (Thatcher, 1991; 1997). As such, it seems evident that EEG coherence would provide the best test of Goldman-Rakic's reverberatory WM circuits.

Technical Issues. Although it is argued that EEG coherence might provide a useful technique for investigating the neural substrates of WM, there are limitations to this technology that must be considered. The first issue focuses on the spatial resolution of the EEG. Shaw (1984) criticizes research that interprets the EEG as representing a one-to-one relation between structure and function. In his opinion, such interpretations are misleading because scalp recorded EEG signals have a low resolution in relation to the complexity of the brain because the skull acts as a low-pass filter, which results in a blurred electrical signal. As Bullock et al. (1995) describe, "there is a large cone of brain tissue "seen" by each electrode that prevents resolution of the finer structure of activity" (p. 162). Given this factor, coherence values can be artificially high over many centimeters of the scalp because neighbouring pairs of electrodes are not necessarily independent in terms of the signal being picked up.

Bullock and colleagues (1995) investigated local differentiation through subdural and depth recordings with epileptic patients via electrodes placed five to ten mm apart. Using such methods, significant differentiation in activity could be made between electrode loci in the millimeter domain. However, because such fine discriminations cannot be made using scalp EEG recordings, differentiation between the finer structure of cortical activity is prevented.

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Given this problem of signal blurring, our hypotheses will focus on 'trends' of coherence value changes, rather than on individual electrode differences. For example, examining changes in activation between dorsal and ventral prefrontal areas will not take the form of comparing electrode f7 (left most ventral) to electrode f1 (left most dorsal). Instead, increases or decreases in gradients from the more ventral few electrodes (e.g., f7, f5) to the more dorsal few electrodes (e.g., f1, f3) will be considered.

A second issue to consider is that of the recording reference to be used (Fein, Raz, Brown & Merrin, 1988). Recording EEG involves measuring the electrical difference between two electrode sites - the reference electrode and each "active" site of interest (Ray, 1990a). There are several choices of reference methods used in psychophysiological research, and there is considerable debate as to which should be employed.

The procedure of using one electrode as the reference is referred to as monopolar or common reference recording (Ray, 1990a). The reference electrode is placed at a location theoretically considered inactive (i.e., not reflecting a source of EEG signals), such as the ear. However, this site is not necessarily inactive as the ears may pick up surrounding signals, such as temporal-lobe activity, therefore contaminating the recorded EEG. As French and Beaumont (1984) explain, this is a particular problem when measuring coherence as the activity at the reference site will contribute to both electrode loci being analyzed and therefore artificially influence the correlational value obtained. Only if the reference signal is low can a change in coherence be considered a change in the relations between the two signals of interest. However, as mentioned, one cannot be sure that the reference potential is negligible.

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Given this problem, there are other possible reference methods that might be employed. For instance, average referencing involves mathematically averaging all electrodes and then using this unweighted averaged value as the reference to which each individual electrode is compared (Ray, 1990a). By subtracting activity picked up at the ear and therefore removing common variance, activity at each scalp site is further differentiated, resulting in a more distinct signal. As expected, the advantage offered by this method is particularly important when considering coherence analysis because common variance could result in increased coherence values that are really artifact. Although such mathematical methods of exaggerating differences between electrode sites might seem artificial, it must be remembered that the EEG measures relative, not absolute, activity from cell assemblies.

In the current study, additional electrodes were placed in the frontal and parietal/temporal areas in order to address the above two technical issues. Recent investigations (e.g., Gevins, Leong, Smith, Le and Du, 1995) have advocated using an increased number of electrodes in order to increase the spatial localization ability of the EEG.

Research Plan

Both the executive and the modality-specific models account for working memory. The first emphasizes the prefrontal cortex and executive processes, such as attentional scheduling (Baddeley, 1986; Baddeley & Hitch, 1974) or the monitoring/manipulation of on-line material (Petrides et al.,1993a, b; Petrides, 1995). The latter model emphasizes frontal-posterior coordination and modality-specific cortical systems (Friedman & Goldman-Rakic, 1994; Wilson et al., 1993). As was summarized, supporting evidence from a variety of sources can be cited for each of the models. However, at the time of initiating this study, no one had

compared the neural activation patterns in the same subjects in tasks derived from the models, thus checking whether they reflect similar processes. Also, there are some contrasting results that require further investigation.

Working Memory Tasks

The *'n-back test'* has reliably produced activation of cortical regions that are believed to be involved in working memory (e.g., Cohen et al., 1997; Cohen et al., 1994; Smith, Jonides & Koeppe, 1996). This sequential-letter memory task requires participants to indicate whether a presented letter matches the one seen n-trials earlier in a series. There is also a 0-back condition in which participants must indicate the occurrence of a previously specified target.

Some investigations have used a single n-back task, either the 2- or the 3-back, to assess WM, with the 0-back task presented as a control (e.g., D'Esposito et al., 1998a; Gevins et al., 1996; Smith & Jonides, 1997). Others have employed the task in an incremental fashion, with the 0-, 1-, 2- and 3-back tasks representing a varying load on WM systems (e.g., Cohen et al., 1997). In addition, some investigations have employed a single version of the task in that only one type of stimulus, such as letters, is required to be matched (e.g., Cohen et al., 1997), whereas others have used two versions, with one requiring verbal (i.e., letter) stimuli and the other requiring spatial stimuli (i.e., position) to be matched (e.g., D'Esposito et al., 1998a; Gevins et al., 1996; Smith & Jonides, 1997). To our knowledge, however, the current study is the only one to include both of these methods, namely presenting two types of stimuli to assess modality-specific WM, as well as incrementally varying the WM load across four levels of task difficulty.

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In terms of WM load, the 0- and 1-back conditions do not introduce conflicting stimuli between the presentation of the target and its match, and therefore reflect minimal demands on working memory in comparison to the 2- and 3-back conditions. It is believed that this approach of incrementally increasing the separation between the stimuli to be remembered will provide a clearer picture of the effects of increasing working memory load compared to simply presenting a 0- and 2- or 3-back task as is common in the literature.

In terms of the investigation of modality-specific WM, the two conditions the n-back task will be presented in are as follows: (1) *spatial working memory task* - the participant is required to match the spatial position of a letter with a spatial position that had occurred 'n' trials earlier, regardless of what the letter was (or press a key whenever a letter appeared in the top, center space for the 0-back condition); and (2) *verbal working memory task* - the participant is required to match the letter with a letter that had occurred 'n' trials previously, regardless of the spatial location (or press a key whenever the letter 'B' appeared for the 0-back condition). Varying the n-back WM task to focus on either verbal or spatial stimuli is aimed at testing the modality-specific WM model of Goldman-Rakic. The requirement in each of the tasks to continuously monitor the stimuli and upgrade their temporal position in the series is aimed at testing the executive model of Petrides. It should be noted that although the n-back tasks using letters do not directly replicate the work of Goldman-Rakic in which pattern stimuli were employed, use of the n-back will allow for the replication of neuroimaging studies that found evidence for modality-specific WM.

Finally, because the letters are presented in a continuous manner, the n-back requires that subjects not only keep information on-line but also perform computations on each

stimulus with respect to its constantly changing temporal position (i.e., how many spaces back each letter appeared). According to Petrides' executive model, the monitoring and manipulation of stimuli in a WM task is mediated by the dorsolateral PFC (Petrides et al., 1993b).

Auditory Oddball Task

The auditory oddball task involves a standard two-tone discrimination paradigm that is commonly used to elicit the P300 component in ERP research. As previously discussed, the P300 wave is a parietocentral positive wave that is considered an index of information processing (Picton, 1992). The procedure involves the presentation of auditory stimuli (low tones and high tones) with one type occurring less frequently than the other. The subject is required to press a button on a computer keyboard whenever the infrequent (high tone) or target stimulus is presented.

Dual-task

The dual-task will involve the standard auditory oddball task, along with the 0-back tasks. The auditory oddball and the verbal 0-back task will be administered simultaneously, followed by simultaneous administration of the auditory oddball and the spatial 0-back test. It is hypothesized that this dual-task will allow us to tap the central executive of Baddeley's (1986) WM model.

Hypotheses and Predictions

The electrophysiological data that will be recorded during administration of the above tasks will be presented using different approaches of EEG analysis, namely (1) power spectral analysis, and (2) EEG coherence (frontal-posterior coherence, central-frontal/central-posterior

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coherence and local frontal and local posterior coherence). In addition, different approaches of ERP analysis, namely analysis of the (1) P300 component and (2) area under the curve will also be considered. Within each of these methods, the following predictions are made regarding how the data could provide support for the models of interest.

Power Spectral Analysis. Support for modality-specific WM circuits might be found in a spectral analysis of the verbal and spatial n-back tasks. Specifically, supporting data would be evident from dorsal frontal and parietal sites showing greater cortical activation during the spatial WM task, and ventral frontal and temporal sites showing greater cortical activation during the verbal WM task. This increased cortical activation could be evident in two ways. First, since beta is associated with cognitive activity, the above results should be found within the beta bandwidth. Further, because a reduction of alpha is also associated with cognitive activity, reciprocal results should be found within the alpha bandwidth, with lower amounts of alpha representing increased cortical activation.

Given that the n-back task requires continuous monitoring of the stimuli, as well as manipulation of the on-line information in terms of the constantly changing position of each stimulus, the WM model offered by Petrides would predict dorsal frontal areas would be predominantly activated during all conditions of this task. Therefore, to support the executive model of Petrides (Petrides et al., 1993 a, b; 1995), increased beta activity and decreased alpha activity would be expected in the dorsal frontal electrode sites.

EEG Coherence During WM Tasks. The coherence analysis is thought to be the best non-invasive test of the modality-specific WM circuits proposed by Goldman-Rakic and colleagues, because high coherence values have been interpreted as evidence of a structural

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and functional connection between cortical areas underlying the recording electrodes. Considering the results of the neuroimaging (Manoach et al., 1997) and ERP studies (Cohen et al., 1997; Gevins et al., 1996), as well as primate studies of modality-specific WM systems (e.g., Goldman-Rakic & Chaffee, 1994), the following hypotheses are made. First, it is predicted that coherence values between the more dorsal frontal electrodes and parietal electrodes will increase during the spatial n-back tests. In contrast, during performance of the verbal n-back tests it is predicted that coherence values between the more ventral frontal electrodes and temporal electrodes will increase. Support for Petrides' view would be that for both verbal and spatial tasks, the dorsal frontal-to-posterior coherence should be higher than the ventral frontal-to-posterior coherence values.

ERP Analysis of WM Tasks. It is expected in the current study that P300 latency will increase in the specific areas thought to be subserving WM as the memory requirements increase from the 0- to the 3-back condition. Modality-specific WM models would predict that the increased latencies would be evident in the dorsal frontal and dorsal posterior areas for the spatial task, and in the ventral frontal and ventral posterior areas for the verbal task. In contrast, the executive model of Petrides would predict that the increased P300 latencies would be evident in the dorsal frontal areas for both tasks.

A slow wave component should also be evident in the ERP data associated with these WM tasks. To support modality-specific WM systems, it would be expected that larger components would be evident in the more dorsal frontal and parietal electrodes during the spatial-back tasks, and larger slow wave components in the ventral frontal and temporal electrodes during the verbal-back tasks. Again, larger slow wave components would be

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evident in dorsal frontal areas for both tasks according to the WM model of Petrides.

Dual-task Condition. There are several possible ways the dorsolateral PFC (central executive) activation expected during a dual-task might be evident in the current study. First, increases in frontal-parietal coherence might be noted, indicating communication between the CE and posterior attentional systems. Second, a decrease in local coherence in frontal leads might be found given that the dorsal frontal areas would be performing a different task compared to the ventral frontal areas. Finally, considering spectral analysis of the data, a decrease in alpha with a concomitant increase in beta in the dorsal frontal areas might be noted to indicate activation as well.

Summary of Predictions. To summarize, the following predictions are offered with regard to the models of interest. With regard to the modality-specific WM models, dorsal frontal and dorsal posterior activation would be expected for the spatial tasks, and ventral frontal and ventral posterior activation for the verbal task. This pattern of cognitive activity would be evident in the following:

(1) *Power Spectral Analysis*: Dorsal frontal and parietal sites would show greater cortical activation (i.e., increased beta, decreased alpha) during the spatial WM task, whereas ventral frontal and temporal sites would show greater cortical activation during the verbal WM task.

(2) *EEG Coherence:* Coherence values between the more dorsal frontal electrodes and parietal electrodes would increase during the spatial n-back tests, whereas during performance of the verbal n-back tests coherence values between the more ventral frontal electrodes and temporal electrodes would increase during the spatial n-back tests.

(3) *P300 Analysis:* The P300 elicited during the n-back tasks would display increased

latencies as the memory requirements increase from the 0- to the 3-back condition, with the increases evident in dorsal frontal/dorsal posterior areas for the spatial task, and in ventral frontal/ventral posterior areas for the verbal task.

(4) *Area under the curve:* Larger slow wave components would be found in the more dorsal frontal and parietal electrodes during the spatial-back tasks, and larger slow wave components found in the ventral frontal and temporal electrodes during the verbal-back tasks.

With regard to the executive models, the neuroanatomical approach of Petrides (Petrides et al.,1993 a, b; Petrides, 1995) allows for specific predictions to be made. Specifically, the two n-back tasks should produce similar patterns of cortical activity, with dorsal frontal activation evident in the following ways:

(5) *Power Spectral Analysis*: Dorsal frontal sites would show greater cortical activation (i.e., increased beta, decreased alpha) during both WM tasks.

(6) *P300 Analysis:* The P300 elicited at dorsal frontal sites during both n-back tasks would display increased latencies as the memory requirements increase from the 0 to the 3 back condition.

(7) *Area under the curve:* The waveforms elicited during the two WM tasks would be similar, with larger slow wave components specific to WM evident in the more dorsal frontal electrodes.

In terms of the executive model of Baddeley, the following predictions are made with regard to the dual-task:

(8) *Power Spectral Analysis*: A decrease in alpha with a concomitant increase in beta in the more dorsal frontal electrodes would be expected to indicate activation of the CE.

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(9) *Frontal-Posterior Coherence:* Increases in frontal-parietal coherence might be noted, indicating communication between the CE and posterior attentional systems.

(10) *Local Coherence:* A decrease in local coherence in frontal leads might be found given that the dorsal frontal areas would be performing a different task compared to that being performed by ventral frontal areas.

Method

Participants

Participants in this study were recruited from a first year psychology course and received course credit for their participation. A total of 24 individuals participated, however the data from only 17 could be used in the final analysis because of technical difficulties with the EEG recording or excessive artifacts due to eye blinking or other movements.

Procedure

Electrophysiological Recording

Electroencephalograph recordings were obtained from all participants. Electrode caps were used to position the electrodes. Each cap was designed to include the typical midline (fz, cz, pz), frontal (f3/f4, f7/f8), central (c3/c4, t3/t4) and posterior (p3/p4, t5/t6) sites, as well as four additional frontal (f1/f2, f5/f6) and four additional posterior (p1/p2, p5/p6) sites (see Appendix B, Figure 1). The electrode cap was designed according to the International 10/20 system of electrode placement, which labels leads positioned on the left hemisphere with odd numbers and leads positioned on the right hemisphere with even numbers. The alphabetical portion of the site designations refers to the cortical region where the electrodes are positioned, with F referring to the frontal lobe, C to central cortical areas, P to the parietal lobe and T to the temporal lobes. EEG was recorded to the left ear and off-line rereferencing done to averaged ears. Electrooculogram (EOG) activity was constantly monitored with bipolar electrodes placed at the outer cantus and supraorbital ridge of the eyes. Electrode resistance was set below 5 k Ohms. EEG data were filtered between 0.2 Hz and 30 Hz. The sampling rate was 256 points per second. The time constant was set for .67 seconds.

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To select EEG data for ERP quantitative analysis, artifact-free EEG was manually selected, as were the individual peaks for each individual. Also, trials for which behavioural performance was inaccurate were eliminated. To select EEG data for the spectral and coherence analysis, a computer program was developed to select the first 90 artifact-free epochs for analysis. For completion of the spectral analysis, Fast Fourier Transformation (FFT) was then computed for each condition and the following measures obtained for each monopolar lead: (1) absolute power in each of four frequency bands: delta (0.5-3.5), theta (3.5 - 7.5), alpha (7.5 - 12.5), beta (12.5-30.5); and (2) relative power was computed for each band as a percentage of total EEG activity. Because power is not normally distributed, scores were converted to amplitude first. Coherence values were computed for all pairwise combinations of the frontal, central and posterior leads.

Tasks

Working Memory. [1] The 'n-back task' required participants to press the space bar on a computer keyboard to indicate whether a presented letter matches the one seen 3, 2 or 1 items earlier in a series. There was also a zero-back condition in which participants were instructed to indicate when they saw a previously specified target. The 0- and 1-back conditions did not introduce conflicting stimuli between the presentation of the target and its

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[1] An additional working memory task, the Sternberg Procedure, was also administered. This task required participants to indicate whether a target was among a set of letters previously presented. Working memory load was manipulated through the presentation of set sizes of either one, three or five, to which the one target needed to be compared. These various set sizes were presented in a randomized, interspersed manner in order to prevent the confounds of effort that may have resulted if each set size was presented in a blocked fashion. In order to obtain enough artifact-free data for analysis, 100 items of each set size were presented for a total of 300 trials. The results of this task were not analyzed for this thesis.

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match, and therefore are believed to reflect minimal demands on WM in comparison to the 2- and 3-back conditions. A benefit of the n-back task is that it required that the information be updated on a trial-to-trial basis. Similar to the delayed-response paradigms used by Goldman-Rakic in the non-human primates, the correct response is guided by a mental representation of a prior stimulus rather than solely by the present stimulus itself. In addition, the correct response on any given trial cannot be predicted from the preceding trial.

The n-back task was tested in 2 separate conditions: (1) *spatial working memory* - participants were required to match the position with one that had occurred 'n' trials earlier, regardless of what the letter was; the 0-back in this condition involved pressing a key whenever a letter appeared in the top, center space; (2) *verbal working memory* - participants were required to match the letter with one that had occurred 'n' trials previously, regardless of spatial location; 0-back in this condition involved pressing a key whenever the letter 'B' appeared. Varying the n-back WM task to focus on either verbal or spatial stimuli is aimed at testing the modality-specific WM model. See Appendix C for task instructions.

In order to obtain adequate amounts of artifact-free EEG data, 180 trials (in order to accommodate the dual-task condition) of each 0-back condition were presented, with the target (either the letter 'B' or the top center space) occurring for 20% of those trials. In terms of the 1, 2 and 3 verbal- and spatial-back conditions, 100 individual trials were presented for each, again with 20% of those trials being targets. In both the verbal- and spatial-back conditions, 12 capital letters of the alphabet were presented (B, C, F, H, K, M, P, T, W, X, Y, Z) on a computer screen that had been divided into nine equal spaces. The specific letters were chosen to replicate Gevins et al. (1996). Letter name and position were counterbalanced

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across conditions so that each letter and position occurred with equal probability. Stimuli were presented at randomized ISI rates of between 1.5 and 2.0 seconds, with each appearing for a duration of 250 ms. The verbal and spatial n-back tasks were each presented as a block of four tasks. Although the block of verbal and the block of spatial tasks were alternated among participants, given that the tasks were incremental within each block, the order remained the same (i.e., 0-back, 1-back, 2-back, 3-back).

Auditory Oddball Task. The auditory oddball task involved a standard two-tone discrimination paradigm that is commonly used to elicit the P3 component in ERP research. The procedure involved the presentation of auditory stimuli (low tones and high tones) with one occurring less frequently than the other. There were 160 frequent non-target (low tone - 800 Hz) stimuli presented, along with 41 rare-target (high tone - 1500 Hz) stimuli presented. All oddball stimuli were presented at an inter-stimulus interval that randomly varied between 1200 and 1800 ms. The subject was required to press a button on a computer keyboard whenever the target (high tone) stimulus was presented.

Dual Task. The dual tasks involved the standard auditory oddball task, along with the 0-back tasks. The auditory oddball and the verbal 0-back were administered simultaneously, followed by simultaneous administration of the auditory oddball and the spatial 0-back task.

Statistical Analysis

Before the statistical analyses are described, it is important to note that given the large number of variables included in this study, only the leads and electrode pairs that were relevant to our hypotheses were included in the analyses. However, given this concern regarding Type I error, results were interpreted in terms of patterns of consistent effects

rather than with respect to each individual result.

Behavioural Analysis. Behavioural reaction times as well as total correct responses, omission errors and commission errors were analyzed for each task. Repeated measures analysis of variance was conducted for each of these behavioural measures of the n-back tasks, with level of difficulty (0, 1, 2 and 3 back) and task (verbal vs. spatial) as the within-subject variables. Repeated measures analysis of variance was also conducted for each of these behavioural measures with the dual tasks, with task as the within-subject variable.

Coherence and Spectral Analysis. Both the coherence and spectral data were analyzed separately for each of the verbal and the spatial n-back tasks in a repeated measures analysis of variance with *(1)* level of difficulty (0, 1, 2 and 3-back), *(2)* ventral-dorsal sites, *(3)* task (verbal vs. spatial) and *(4)* hemisphere (left vs. right) as the within-subject variables.

Dual task analysis was completed for each of four data sets, *(1)* verbal dual task vs. 0-verbal back, *(2)* spatial dual task vs. 0-spatial back, *(3)* verbal dual task vs. tone, and *(4)* spatial dual task vs. tone. Again, a repeated measures analysis of variance was used with *(1)* task (dual vs. single), *(2)* ventral-dorsal sites, and *(3)* hemisphere as the within-subject variables.

The dependent variables for the spectral analysis involved individual frontal (f1/f2, f3/f4, f5/f6, f7/f8) and posterior (p1/p2, p3/p4, p5/p6, t5/t6) electrodes. The dependent variables for the coherence analysis involved each frontal site paired with each posterior site (f1-p1/f2-p2, f1-p3/f2-p4, f1-p5/f2-p6, f1-t5/f2-t6, f3-p1/f4-p2, f3-p3/f4-p4, f3-p5/f4-p6, f3-t5/f4-t6, f5-p1/f6-p2, f5-p3/f6-p4, f5-p5/f6-p6, f5-t5/f6-t6, f7-p1/f8-p2, f7-p3/f8-p4, f7-p5/f8-p6, f7-t5/f8-t6). This pattern of testing is considerably reduced from the "all possible

combinations"approach often found in the literature and again, in this study results were interpreted in terms of patterns of consistent effects. In terms of the spectral analysis, both absolute and relative values were analyzed statistically, and only those FFT results that were significant in both analyses were interpreted.

ERP Analysis. The latency and amplitudes of the P300 component for individual frontal (f1/f2, f3/f4, f5/f6, f7/f8) and posterior (p1/p2, p3/p4, p5/p6, t5/t6) sites were analyzed separately for each of the verbal and the spatial n-back tasks in a repeated measures analysis of variance with *(1)* level of difficulty (0, 1, 2 and 3-back), *(2)* ventral-dorsal sites, *(3)* task (verbal vs. spatial) and *(4)* hemisphere (left vs. right) as the within-subject variables. Analysis of the ERP components occurring after 300 ms considered the area under the wave at the following times: *(1)* 300 - 600 ms, *(2)* 600 - 900 ms, *(3)* 900 - 1200 ms, and *(4)* 1200 - 1500 ms. A similar analysis of variance was completed on these data.

RESULTS

The results will be presented in the following order: (1) effects of increasing WM load (LOAD effects); (2) effects of task type, namely the comparison of the spatial to the verbal task (TASK effects); (3) hemispheric effects, and finally, (4) dual task results. The reader is referred to Appendix B for diagrams of the electrode sites and coherence pairings to understand the placement of the various electrodes being described. The grouped averaged ERP waveforms to the verbal and spatial n-back tasks at each level of difficulty are presented in Appendix D. The figures containing graphical representation of the data are contained in Appendix F. Also, note that electrode pairs denoting similar placement on either hemisphere are separated by a slash (e.g., f1/f2, f3/f4), whereas electrode pairs being represented as paired for coherence values are separated by a dash (e.g., f1-p1, f3-p1). To aid in the understanding of the results, each section of findings will be preceded by the relevant predictions previously offered.

Load Effects

Behavioural Data - Load Effects

__Predictions__

Significant effects concerning the level of task difficulty are expected. As the number of intervening stimuli between the target and the match increases, more information is required to be maintained on-line, presumably making the task increasingly difficult. Thus, load effects are predicted between the 0-, 1-, 2- and 3-back tasks.

__Results__

Analysis of the behavioural data for the n-back tasks found a LOAD main effect for

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the total number of items correct [$F_{(3,48)}$ = 1474.43, p <.001], commission errors [$F_{(3,48)}$ = 31.29, p<.001], omission errors [$F_{(3,48)}$ = 1511.92, p <.001], and reaction time [$F_{(3,48)}$ = 25.35, p<.001]. Post hoc analysis of the total number of items correct reveals that each level of difficulty differs significantly from the others, with a consistent decrease in number correct as the task difficulty increases. Similar results were found for the omission errors, with all levels significantly different and the errors increasing as the level of difficulty increases. In terms of commission errors, further analysis revealed that the 0-back and the 1-back tasks, which had the same mean number of errors, were significantly different from the 2- and the 3-back tasks, and that the two higher difficulty levels were also significantly different from each other. Finally, further analysis of the reaction time data found all levels to significantly differ from each other, with the exception of the 1-back and 2-back tasks. The reader is referred to Table 1 for these behavioural data.

Spectral Analysis - Load Effects

Predictions

In terms of spectral analysis, we would expect a LOAD main effect in both frontal and posterior areas. Specifically, as the level of task difficulty increases, there will be concomitant increases in the beta band and decreases in the alpha band, reflecting increased cortical activation.

Results

The results of the spectral analysis were not entirely consistent with the predictions made. Although frontal sites were only sensitive to WM load in the beta bandwidth, posterior sites were only sensitive to load in the alpha bandwidth.

A significant *frontal* LOAD main effect [F(3, 45)=7.63, p<.001] was evident when the verbal and spatial tasks were analyzed together. Specifically, the beta values decrease as the levels of difficulty increase (0-back = 16.06; 1-back = 15.06; 2-back = 14.96; 3-back = 14.50). Post hoc analysis revealed that the 0-back had significantly higher beta values than the 3-back.

A similar pattern of results in terms of overall significance in the beta bandwidth was noted when the two tasks were analyzed separately. The spatial back tasks had a significant LOAD main effect [F(4, 67)=2.68, p=.036], with post hoc analysis finding that the 0-back test had significantly greater amounts of beta than the 1-back and 3-back tests but not the 2-back. A LOAD main effect was also found for the verbal task analysis [F(3, 45)=5.35, . p=.003], with the 0-back having significantly greater beta than the 2-back and the 3-back but not the 1-back, and the 1-back having significantly more beta than the 2-back.

A significant LOAD x VENTRAL-DORSAL SITE interaction was also found in the beta bandwidth [F(9,135)=4.68, p<.001] at the *frontal* sites. At the most ventral sites, there are similar amounts of beta evident for all four levels of task difficulty. However, as we move dorsally from f7/f8 to f5/f6, we find an increase in beta across all levels, with the greatest increase associated with the 0-back. Beta then decreases for all task levels as we continue to move dorsally, with the 0-back continuing to show higher amounts of beta (see Figure 1, Appendix F).

With respect to the analysis of the *posterior* sites, a LOAD main effect [F(3, 45)= 5.80, p=.002] was evident in the alpha bandwidth when the verbal and spatial tasks were analyzed together. Post hoc analysis revealed that the 0- and 2-back tests had greater

amounts of alpha as compared to the 3-back (0-back = 7.39, 1-back = 7.22, 2-back = 7.34, 3-back = 7.03).

A similar pattern of results in terms of overall significance in the alpha bandwidth was noted when the spatial tasks were analyzed separately. A significant LOAD main effect [$F_{(3, 45)}$= 5.09, p=.008] was evident, with post hoc analysis finding the 3-back task had significantly less alpha as compared to the 0-, 1-, and 2-back tasks. Consideration of the verbal back tasks separately did not find a significant load effect [$F_{(3, 45)}$= .94, p=.407].

Coherence Analysis - Load Effects

Predictions

The results of neuroimaging studies have reported both frontal and posterior regions to be sensitive to the level of WM load. Given these results, we would expect changes in both local frontal and local posterior coherence, as well as in frontal-posterior coherence as the level of task difficulty increases.

Results

Frontal-Posterior Coherence. No significant main effects of LOAD, FRONTAL or HEMISPHERE were found, but a significant 3-way interaction was evident [$F_{(9, 144)}$ = 2.51, p=.034] indicating a LOAD x FRONTAL interaction in the left hemisphere analysis of beta coherence. According to further analysis of the left hemisphere data, the mean coherence values at each frontal electrode fluctuate as a function of WM load, i.e., whether the stimuli to be remembered were 0, 1, 2 or 3 back. As is evident in Figure 2, Appendix F, the interaction was due to a marginally significant difference between 0- and 1-back ($F_{(1,16)}$ = 4.33, p = .054) and a significant difference between 1- and 2-back conditions ($F_{(1,16)}$ = 4.49, p = .05).

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There was no significant difference between 2- and 3-back conditions. Further, additional analyses indicate no Load x Frontal Site interaction, indicating that the additional WM load was not associated with increases at specific locations. Nor was there any interaction with Task.

As mentioned, only the left hemisphere was sensitive to WM load. Right hemisphere analysis did not reveal a sensitivity of frontal sites to level of difficulty.

Central-Frontal / Posterior Coherence. No significant LOAD effects were found in the frontal-central or central-posterior coherence analysis of the beta or alpha bandwidths. This suggests that the frontal-posterior coherence effects are not due to general volume conduction but to long fibre pathway communication.

Local Coherence. A significant LOAD main effect [F(3, 48)= 3.66, p=.025] was found in the *frontal* analysis of the beta bandwidth. Post hoc analysis revealed that the more difficult levels of the WM tasks had higher mean local beta coherence values (2-back = .71; 3-back = .71) as compared to the less difficult levels (0-back = .68; 1-back = .66). Contrary to predictions made, posterior local coherence values were not sensitive to the effects of WM load.

ERP Analysis - Load Effects

Predictions

It is expected that the P300 amplitude will decrease and the P300 latency will increase with increasing task difficulty/complexity for both WM tasks. With regard to the area-under-the- curve analysis, an increased area should be found as the WM load increases.

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Results

P300 Component. A LOAD main effect was found in the P300 amplitude analysis for *frontal* sites [F(3, 48)= 6.10, p=.004]. Further analysis revealed the 0-back task was associated with a significantly lower P300 amplitude as compared to both the 2- and the 3-back tasks (0-back = 4.68, 1-back = 5.82, 2-back = 7.16, 3-back = 6.58). Analysis of P300 amplitude for *posterior* sites found LOAD to approach significance [F(3, 48)= 2.86, p=.057] when both tasks were included in the analysis, with the pattern of results the same as with the frontal sites (0-back = 9.35, 1-back = 9.59, 2-back = 12.06, 3-back = 11.01). When the *posterior* P300 amplitude for the spatial task was analyzed separately, a LOAD main effect was found [F(3, 48)= 4.55, p=.014], with the 1-back task showing lower amplitude than the 3-back. When the posterior P300 amplitude for the verbal tasks were assessed separately, LOAD was not significant [F(3, 48)= 1.91, p=.157].

A VENTRAL-DORSAL SITE main effect was evident for both *frontal* [F(3, 48)= 24.48, p<.001] and *posterior* [F(3, 48)= 40.48, p<.001] sites for the P300 amplitude analysis, and for *posterior* sites for the P300 latency [F(3, 48)= 18.58, p<.001] analysis. Further analysis indicated an increase in P300 amplitude as we move from ventral to dorsal sites. In the *frontal* regions, the most ventral sites (f7/f8) showed significantly lower amplitudes than the other sites. In the *posterior* regions, the two most ventral sites (t5/t6, p5/p6) significantly differed from each other, and showed significantly lower amplitudes than the two dorsal sites. In either analysis, the P300 amplitude at dorsal sites did not differ from each other (see Figure 3, Appendix F).

With regard to the VENTRAL-DORSAL SITE main effect for the P300 latency at

posterior sites, a steady decrease was noted as we move dorsally. The most ventral site (t5/t6

= 351.72) had a significantly longer P300 latency than the two dorsal sites (p3/p4 =342.25,

p1/p2 = 341.28) (see Figure 4, Appendix F).

A LOAD x VENTRAL-DORSAL SITE interaction was found at the *frontal* sites in

the P300 amplitude analysis [$F_{(9, 144)}$= 3.74, p<.001 and at the *posterior* sites in the latency

analysis [$F_{(9, 144)}$= 2.64, p=.007]. As is evident in Figure 5, Appendix F, in terms of the

frontal amplitudes, the 0- and 1-back tasks show similar amplitudes for the f5/f6, f3/f4 and

f1/f2 sites, with the most ventral sites (f7/f8) showing a much lower amplitude. As we move

to the 2-back, greater amplitude increases are found for the two most dorsal sites (f1/f2, f3/f4)

as compared to the increases in amplitude at the two most ventral sites. VENTRAL-DORSAL

SITE differences are again noted as task difficulty increases to the 3-back, with a decrease

noted in the amplitudes for the two dorsal sites but no amplitude change noted for the ventral

sites. In terms of the *posterior* latency interaction, latencies are similar across sites for the 0-

back, but decrease from ventral to dorsal sites within each of the other levels of task difficulty

(see Table 2).

A TASK x LOAD interaction was also found in the *posterior* P300 latency analysis

[$F_{(3, 48)}$= 2.99, p=.04]. The latencies for the verbal task were greater across collapsed levels

of difficulty, with the greater differences compared to the spatial task in the 0- and 2-back (see

Figure 6, Appendix F).

Area-Under-the-Curve Analysis. An analysis of the area under the curve was

completed at four different time intervals, namely 300-600 ms (Time 1), 600-900 ms (Time 2),

900-1200 ms (Time 3) and 1200-1500 ms (Time 4). The data do provide some support for our hypotheses in that ERP components at both frontal and posterior sites were found to be sensitive to WM load. However, the results did not reveal the expected incremental increase in the area under the waveforms.

Frontal Electrodes. The results regarding the area analysis at the *frontal* electrode sites can be summarized by considering two overall findings. First, differences noted between verbal and spatial waveforms 300 to 900 ms after presentation of the stimulus seem to be related to the level of task difficulty rather than simply the type of information to be remembered. A LOAD main effect [F(3, 48)= 4.50, p=.01] was found at Time 2 which suggests the waveform is most sensitive to WM load from 600 to 900 ms (see Table 3). A significant LOAD x TASK interaction at Time 1 [F(3, 48)= 4.41, p=.018] provides further evidence that the waveform is sensitive to WM load. From 300 to 600 ms, there was increased differentiation between the spatial and the non-spatial tasks at the higher levels of task difficulty, i.e., 2- and 3-back (see Figure 7, Appendix F), however the results are difficult to interpret. This first time interval is especially important to consider given that it contains the P300.

The second main finding of the analysis of *frontal* electrodes involves topographical waveform differences that suggest the waveforms found at dorsal frontal sites (f3/f4, f1/f2) are more sensitive to WM load and related task differences. Evidence for this finding is derived from the following significant results: (1) VENTRAL-DORSAL SITE main effect; (2) LOAD x VENTRAL-DORSAL SITE interaction; (3) TASK x VENTRAL-DORSAL SITE; and (4) LOAD x TASK x VENTRAL-DORSAL SITE interaction.

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First, a significant VENTRAL-DORSAL SITE main effect was found at the *frontal* sites at Time 1 [$F(3, 48)= 4.85$, $p=.027$], Time 2 [$F(3, 48)= 8.07$, $p=.005$] and Time 4 [$F(3, 48)=17.17$, $p<.001$]. These effects are particularly strong from 300 to 900 ms (Time 1 and Time 2) after presentation of the stimulus after which time they diminish to non-significance (Time 3). However, even up to 1500 ms, there remains a differentiation among the waves elicited at ventral and dorsal frontal sites. The analysis of Time 1 (300-600 ms) and Time 4 (1200 - 1500 ms) reveals an increase in the area under the curve as we move from ventral to dorsal frontal sites, with the dorsal sites showing the largest waveform. However, the data for Time 2 (600-900 ms) are not as straightforward and are difficult to interpret (see Table 4).

A significant LOAD x VENTRAL-DORSAL SITE interaction evident at Time 1 [$F(9, 144)= 3.04$, $p=.038$] and Time 2 [$F(9, 144)= 6.18$, $p<.001$] expands on the suggested sensitivity of the waveform in that dorsal sites seem particularly affected by the level of task difficulty. Figure 8 (Appendix F) shows an increased differentiation of the waveform at the dorsal (f3/f4, f1/f2) compared to the ventral (f7/f8, f5/f6) sites across the levels of WM load.

A significant LOAD x TASK x VENTRAL-DORSAL SITE interaction [$F(9, 144)= 4.439$, $p=.004$] was also found at the *frontal* sites at Time 1, which suggests that the wave components across the levels of difficulty at the dorsal sites are different across tasks. More specifically in the spatial tasks, the 0-back and 2-back tasks show similar values, whereas the 1-back and the 3-back tasks also show similar values, with the differences being greatest at dorsal sites (see Figure 9, Appendix F). The verbal tasks do not show this same pattern across the levels of difficulty, however they do show more differentiation due to WM load at dorsal sites (see Figure 10, Appendix F).

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In short, the results are difficult to interpret as they are somewhat inconsistent in terms of significance at different time intervals and there is not a straightforward incremental increase in the area under the curve with WM load. Nevertheless, there is no ventral-dorsal site by task interaction, suggesting that despite difficult interpretation of the findings, there is clearly no support for a modality-specific WM model. Further, sensitivity of the waveform elicited at the frontal sites to level of task difficulty is a consistent finding. In addition to this load sensitivity being strongest from 300 to 900 ms, the data also suggest that it is the dorsal frontal sites that are most sensitive. Further, although task differences in the waveforms were noted, they are highly correlated with level of task difficulty.

Posterior Electrodes. Analysis of the area under the curve at *posterior* sites reveals similar results, with some key exceptions. First, as with the frontal electrode sites, there is consistent evidence that the posterior waveform is also sensitive to level of task difficulty. However, in the posterior areas, this sensitivity remains pronounced for a much longer period. As with analysis of the frontal sites, a LOAD main effect [$F(3, 48)= 9.21$, $p<.001$] was found at Time 2 (see Table 5). In contrast however, a significant LOAD main effect [$F(3, 48)= 4.27$, $p=.017$] was also found at Time 3 for posterior areas, suggesting a longer time interval during which the waveform is influenced by WM load (see Table 5).

Another similarity between the frontal and posterior waveforms involves task differences. This is suggested by a significant TASK main effect [$F(1, 16)= 8.353$, $p=.011$] for the *posterior* area under the curve at Time 2 (600 to 900 ms), with the area analysis suggesting that the verbal task (area $= 1.20$) has a much greater area compared to the spatial task (area $= .09$). Further, a TASK x VENTRAL-DORSAL SITE interaction [$F(3, 48)= 6.05$,

p=.019] was also found at Time 2 for the *posterior* sites. These results suggest that the

waveform area is larger for the verbal task, especially at dorsal sites (see Figure 11, Appendix

F). This finding seems consistent with the increased P300 latency of the verbal task that is

suggesting it is a more difficult task and also with results suggesting the dorsal parietal areas

are more activated during both WM tasks.

Also with regard to task differences, a significant LOAD x TASK interaction was

found at the *posterior* sites at Time 1 [$F_{(3, 48)}= 6.41$, p=.004] and Time 2 [$F_{(3, 48)}= 4.67$,

p=.012]. Further analysis of the results suggested that from 300 to 600 ms there was increased

differentiation between the spatial and the non-spatial tasks at the higher levels of task

difficulty (i.e., 3-back), whereas from 600 to 900 ms there appears to be more differentiation

between the posterior waveforms elicited by the 0- and 2-back verbal and spatial tasks (see

Table 6).

Furthermore, with regard to topographical waveform differences a significant

VENTRAL-DORSAL main effect was evident at the *posterior* sites at Time 1 [$F_{(3, 48)}=$

42.47, p<.001], Time 2 [$F_{(3, 48)}= 10.75$, p=.002] and Time 4 [$F_{(3, 48)}=9.63$, p=.005]

suggesting that the waveform, as was found in the frontal analysis, is sensitive to

topographical placement from 300 to 900 ms, and again from 1200 to 1500 ms. These data

suggest the waveform elicited at the dorsal posterior sites has a greater area compared to

those elicited at ventral posterior sites (see Table 7). However, in contrast to the frontal

electrodes, the sensitivity of the dorsal electrodes to the level of task difficulty (LOAD x

VENTRAL-DORSAL SITE interaction at Time 2 [$F_{(9, 144)}= 5.18$, p=.003] and Time 3 [$F_{(9,}$

$_{144)}= 4.64$, p=.006]) becomes pronounced later in the posterior areas (600 ms compared to

300 ms) and lasts for a longer time (1200 ms compared to 900 ms).

Finally, a significant LOAD x TASK x VENTRAL-DORSAL SITE interaction was also found at the *posterior* sites at Time 1 [$F_{(9, 144)}= 4.37$, $p=.006$] and Time 2 [$F_{(9, 144)}= 4.74$, $p=.011$], which suggests that the patterns of differentiation across the levels of difficulty at the posterior sites are different across tasks. More specifically, at Time 1 the verbal 1-back and 2-back tasks show similar values at both ventral and dorsal sites (see Figure 12, Appendix F). The spatial tasks do not show this pattern across the levels of difficulty, with the 1- and 3-back tasks instead showing similar patterns across ventral and dorsal sites (see Figure 13, Appendix F). At Time 2, this pattern changes and we find that the verbal task now shows the 0- and 3-back have similar waveforms, although in the spatial tasks, the 1- and 3-back have similar components, and the 0- and 2-back also show similar components (see Figure 14 and Figure 15, Appendix F). It is difficult to interpret precisely what these differences mean, however they do provide evidence that the two tasks are not producing similar waveforms at the various levels of task difficulty.

Again, despite some inconsistencies in terms of significant effects at the different time intervals, there remain consistent findings that clearly suggest some similarities and differences in terms of frontal and posterior area under the curve. Results suggest that the area under the curve is sensitive to WM load and that the task effects noted seem specifically related to level of task difficulty. Also, both the frontal and posterior dorsal electrodes are more sensitive to the WM load, regardless of the type of stimuli presented. An interesting difference, however, between the frontal and posterior electrodes is that the sensitivity to WM load seems to become more pronounced later, and remain longer, in the posterior areas.

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Task Effects

Behavioural Data - Task Effects

Predictions

The verbal and spatial tasks only differed in the instruction to attend to either the letter or the space the letter appeared in as the stimulus to match. Given that the perceptual and response requirements were entirely the same, any differences between the tasks would be due to higher-order processing.

Results

A TASK main effect was found for both the commission errors [$F(1,16) = 11.42$, $p=.004$] and reaction time [$F(1,16) = 21.63$, $p <.001$] analyses. Further analysis found that the spatial- back task had significantly more commission errors ($M=1.81$) compared to the non-spatial task ($M=1.22$). Although this difference in commission errors is significant, it is not thought that a difference of 0.6 errors is meaningful in terms of behavioural performance. In terms of reaction times, the spatial task had a shorter mean reaction time ($M=536.05$) as compared to the non-spatial task ($M=593.08$), demonstrating that participants took longer to complete the verbal task.

Further, a significant LOAD x TASK interaction was found for the reaction time [$F(3, 48) = 5.73$, $p =.004$] analysis. The two tasks differed significantly from each other at all levels of difficulty except for the 1-back, during which the reaction time was found to be quite similar (see Table 8). Not only do these data suggest an increase in reaction time as the WM load increases, but the 0-, 2- and 3-back data suggest the verbal task may have been more difficult overall given the increased reaction times.

In contrast to the reaction time data that suggest the two tasks differ in terms of level of difficulty, when we consider the percentage of total items correct, along with the percentage of omission errors, we find the values quite similar for each task across the levels of difficulty (see Table 9). From these results, it is thought that the verbal and spatial tasks are equated in terms of behavioural performance, however perhaps not in the processing effort required to obtain the similar accuracy level since the reaction time is greater in the verbal task.

Spectral Analysis - Task Effects

Predictions

Support for modality-specific WM circuits might be found in a spectral analysis of the data. In this case, a VENTRAL-DORSAL SITE by TASK interaction would be required for both frontal and posterior analyses. More specifically, it would be expected that dorsal frontal and dorsal posterior sites would show greater cortical activation during the spatial WM task, whereas ventral frontal and ventral posterior sites would show greater cortical activation during the verbal WM task. Cortical activation should be evident as an increase in beta, as well as a decrease in alpha in the expected areas.

Results

Task differences evident in the FFT spectral analysis were found to be supportive of modality-specific coding in posterior areas but not in frontal areas.

First, a TASK main effect for the *posterior* sites was noted for the beta band $[F(1,15)=5.42, p=.034]$. Further analysis revealed that the verbal-back tasks show a greater amount of beta (M=14.27) compared to the spatial tasks (M=13.87). A similar effect was also

found for the alpha band [F(1,15)=6.06, p=.026]. However, the reverse pattern was found, in that the verbal tasks had lower amounts of alpha (M=7.03) as compared to the spatial tasks (M=7.45). This reciprocal finding (increased beta, decreased alpha) has been associated with mental activation and suggests the verbal tasks involve greater cognitive resources as compared to the spatial tasks.

With regard to the analyses of the *frontal* sites, a VENTRAL-DORSAL SITE x TASK interaction was found in the alpha bandwidth [F(3,45)=4.18, p=.034]. These results reveal that the dorsal sites differentiate the tasks more than the ventral sites, with the verbal task showing lower alpha, presumably indicating greater activation. (see Figure 16, Appendix F).

In terms of the analyses of the *posterior* sites, a VENTRAL-DORSAL SITE x TASK interaction was found in both the beta [F(3,45)=5.40, p=.003] and the alpha [F(3,45)=5.63, p=.002] bandwidths. The results conform to the predictions made regarding modality-specific coding. For the verbal task, beta activity is lowest at the dorsal sites and greatest at the ventral sites. For the spatial task, beta activity shows the reverse pattern, now being greatest at the dorsal sites and lowest at the ventral sites (see Figure 17, Appendix F).

With regard to the *posterior* alpha VENTRAL-DORSAL SITE x TASK interaction, both the verbal and spatial-back tasks increase in alpha as we move from ventral to dorsal sites, with a greater increase noted in the spatial-back tasks. See Table 10 for spatial/verbal alpha values.

Coherence Analysis - Task Effects

Predictions

It is thought that the coherence analysis would be the strongest non-invasive test of the modality-specific WM circuits proposed by Goldman-Rakic and colleagues, because high coherence values have been interpreted as evidence of a structural and functional connection between cortical areas underlying the recording electrodes. Given this, it is predicted that in an analysis of frontal-posterior coherence, correlations between the more dorsal frontal electrodes and parietal electrodes will increase during the spatial n-back tasks, without similar increases between frontal-central, central-parietal or central-temporal coherences. In contrast, during performance of the verbal n-back tasks, it is predicted that coherence values between the more ventral frontal electrodes and inferior temporal electrodes will increase, again without concomitant increases between frontal-central, central-parietal or central-temporal coherences. Again, the reader is referred to the diagrams in Appendix B which depict the ventral and dorsal coherence pairings to help in understanding the following results.

In terms of local coherence, it would be expected that in both frontal and posterior areas, significant task differences would be noted, as one area would be engaged in the task while the other wouldn't. The more dorsal electrodes should reveal higher coherence values compared to the ventral electrodes during the spatial task, with the opposite pattern noted for the verbal tasks.

Results

Frontal-Posterior Coherence. The proposed findings that would support the existence of modality-specific WM circuits were not found in the coherence analysis. Verbal

and spatial n-back tasks demonstrated similar patterns of cortical connections.

A significant FRONTAL x POSTERIOR interaction was found when both hemispheres were analyzed together, across both the beta [$F(9,144) = 171.2$, $p < .001$], and alpha bandwidths [$F(9,144) = 191.57$, $p < .001$]. Dorsal frontal-dorsal posterior electrode pairings (*f1-p1, f1-p3, f3-p1, f3-p3* for left-side sites and analogous pairings for right-side sites, see Figure 2, Appendix B) had higher coherence values compared to dorsal frontal-ventral posterior electrode pairings (see Table 11 for dorsal frontal coherence values; see Figure 3, Appendix B for electrode pairings). Ventral frontal electrodes did not show this differentiation when paired with dorsal posterior (see Figure 4, Appendix B) compared to when paired with ventral posterior electrodes (see Figure 5, Appendix B), with little difference between ventral frontal electrode pairs across the four posterior sites noted (see Table 12 for ventral frontal coherence values). These findings were significant across both the alpha and beta bands when the two hemispheres were analyzed separately, when verbal and spatial tasks were analyzed together, as well as when the two types of tasks were analyzed separately (all $p < .001$).

Central-Frontal / Posterior Coherence. Again, verbal and spatial n-back tasks demonstrated similar patterns of cortical connections, with the predicted TASK X SITE interaction not evident. Results are similar to the frontal-posterior coherence analyses in reflecting a pattern of greater coherence between dorsal sites (see Figure 6, Appendix B for electrode pairings). Specifically, a significant FRONTAL x CENTRAL interaction was found across the beta [$F(3, 48) = 117.15$, $p < .001$] and alpha bandwidths [$F(3, 48) = 289.89$, $p < .001$]. Further, a significant CENTRAL x POSTERIOR interaction was found, again across

both the beta [$F_{(3, 48)} = 256.36$, $p < .001$], and alpha bandwidths [$F_{(3, 48)} = 515.79$, $p < .001$].

When we consider the beta bandwidth, we find that for both *dorsal* frontal-*dorsal* central (i.e., *f1-c3, f3-c3* and analogous right hemisphere pairings, Figure 6, Appendix B), and *dorsal* central-*dorsal* posterior (i.e., *p1-c3, p3-c3*, Figure 10, Appendix B) electrode pairings, higher coherence values were evident compared to *dorsal* frontal-*ventral* central (i.e., *f1-t3, f3-t3*, Figure 7, Appendix B) and *dorsal* central-*ventral* posterior (i.e., *p1-t3, p3-t3*, Figure 11, Appendix B) electrodes pairings. *Ventral* central electrodes (*t3/t4*) did not show this differentiation when paired with either *dorsal* frontal or *dorsal* posterior versus *ventral* frontal or *ventral* posterior electrodes. In other words, as is graphically depicted in Figure 18 (central-frontal pairings) and Figure 19 (central-posterior pairings; Appendix F), there is little difference between ventral central (t3/t4) electrode pairs across the four frontal and four posterior sites, compared to the differences noted between the dorsal central (c3/c4) electrode pairs. This pattern of results is reflective of the results involving frontal-posterior coherence.

When we consider the alpha bandwidth, we find that the *dorsal* frontal-*dorsal* central (i.e., *f1-c3, f3-c3*, Figure 6, Appendix B) and the *dorsal* central-*dorsal* posterior (i.e., *p1-c3, p3-c3*, Figure 10, Appendix B) electrode pairings have higher coherence values compared to *dorsal* frontal-*ventral* central (i.e., *f1-t3, f3-t3*, Figure 7, Appendix B) electrodes pairings. However, in contrast to the beta analysis, ventral electrodes also showed some differentiation in their pairings with *ventral* central-*dorsal* frontal (i.e., *t3-f1, t3-f3*, Figure 7, Appendix B) and *ventral*-central-*dorsal* posterior pairings (i.e., *t3-p1, t3-p3*, Figure 12, Appendix B) showing similar coherence values, and *ventral* central-*ventral* frontal (i.e., *t3-f5, t3-f7*, Figure

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9, Appendix B) and *ventral* central-*ventral* posterior pairings (i.e., *t3-p5, t3-t5*, Figure 13, Appendix B) showing higher alpha values compared to the *ventral* central-*dorsal* frontal and ventral central-dorsal posterior pairings (see Appendix F, Figure 20 for frontal-central pairings and Figure 21 for central-posterior pairings). Again, the results of the alpha bandwidth are similar to those reported for the frontal-posterior coherence values and does not reflect overall increases in volume conduction as there is differentiation between ventral and dorsal pairings.

Local Coherence. Local coherence results did not reveal the expected task effects in either frontal or posterior areas, in neither the alpha nor beta bandwidths. However, frontal sites did show a VENTRAL-DORSAL SITE main effect in both the alpha [$F(2, 32) = 37.20$, $p < .001$] and the beta [$F(2, 32) = 68.57$, $p < .001$] bandwidths. In both, a post hoc analysis revealed the most dorsal electrode pairing (*f1-f3, f2-f4*) showed higher amounts of coherence compared to the ventral pairings (see Figure 22, Appendix F).

ERP Analysis - Task Effects

Predictions

P300 Component. Again, to provide evidence for modality-specific WM systems, differences in P300 amplitude and latency, in terms of a VENTRAL-DORSAL SITE by TASK interaction, should be found in frontal and posterior sites according to which cortical areas are proposed to be activated during each task (i.e., dorsal areas with spatial task and ventral areas with verbal task).

Area Under the Curve Analysis. With regard to the ERP analyses, to support modality-specific WM circuits, we would expect topographical and waveform differences

between the spatial and verbal tasks. As mentioned, the area-under-the-curve analysis was completed at four different time intervals, namely 300-600 ms (Time 1), 600-900 ms (Time 2), 900-1200 ms (Time 3) and 1200-1500 ms (Time 4). In order to provide support for modality-specific working memory circuits, larger area under the curve values in the more dorsal frontal electrodes should be elicited during the spatial WM task. In contrast, the verbal task will elicit larger waveforms in the more ventral frontal electrodes.

Results

P300 Component. Although some significant task effects were found in the analysis of the P300 amplitude, the results were not supportive of modality-specific WM systems. Instead, the effects were specific to the 3-back task, with the significant findings being lost when the 3-back data were not included in the analysis. However, for the sake of completeness, the results are included.

First, P300 amplitude analysis showed a significant TASK x LOAD interaction at the *posterior* sites [$F(3, 48)$= 3.34, p=.032]. As described, further analysis revealed the significant difference to involve the 3-back task specifically. In the spatial task, there was an increase in P300 amplitude from the 2-back to the 3-back, but with the verbal task, there was a large decrease from the 2-back to the 3-back, with the P300 amplitude being similar to the amplitude for the verbal 0-back.

A significant TASK x LOAD x VENTRAL-DORSAL SITE interaction was found in the P300 amplitude analysis of the *frontal* sites [$F(9,144)$= 3.30, p=.001]. With the spatial task, all four electrode sites show slight decreases in P300 amplitude from the 2-back to the 3-back. In the verbal task, however, a similar decrease in amplitude from the 2-back to the 3-

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back is only noted for the two most dorsal sites (f1/f2, f3/f4), not for the ventral sites.

Further, a significant TASK x LOAD x HEMISPHERE interaction was also found in the P300 amplitude analysis of the *frontal* sites [$F_{(3, 48)}$= 8.98, p<.001]. Specifically, right hemisphere amplitudes are similar for the two tasks, however in the left hemisphere, the verbal task shows a decreased P300 amplitude for the most difficult 3-back task only.

With regard to the analysis of the P300 latency, a TASK main effect was found in the analysis of the P300 latency of both *frontal* [$F_{(1, 16)}$= 6.74 , p=.019] and *posterior* [$F_{(1, 16)}$= 7.41, p=.015] sites. In both, the verbal task was found to have greater latencies (Frontal = 352, Posterior =356) as compared to the spatial task (Frontal = 330, Posterior =335). Such findings suggest a greater difficulty level of the verbal task overall, however they provide no support for modality-specific WM systems. Unlike the other TASK effects, this significant result was not specific to the 3-back task.

Area Under the Curve. As with previous results, analysis of the area under the curve did not reveal supporting evidence for modality-specific WM systems. A TASK main effect was found for only the Time 2 interval in the analysis of the *posterior* sites [$F_{(1, 16)}$= 8.35, p=.011]. Further, although a VENTRAL-DORSAL main effect was consistently found in the analysis of both *frontal* and *posterior* sites, there was not the significant interaction with task that was required to support the hypotheses (see the previous section concerning the LOAD effects for a more thorough description of these results). Given these results, it is concluded that the area-under-the-curve analysis does not provide supporting evidence for modality-specific WM circuits. Instead, the area results are similar to those regarding the P300 component, which suggest that the level of task difficulty might be more effective in

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explaining waveform differences between tasks than the type of stimuli presented.

Hemispheric Effects

Predictions

No specific hemisphere effects were expected based on the WM models presented. In addition, results appear to be mixed regarding laterality in frontal and posterior activation patterns during WM tasks according to the neuroimaging studies, while animal single-cell recording studies do not report significant differences. Since the human literature does consistently consider hemisphere effects, the results are included despite their lack of importance to the models being investigated.

Results

Spectral Analysis

A significant HEMISPHERE x VENTRAL-DORSAL SITE interaction was found in both the alpha [$F(3, 45)= 22.28$, $p<.001$] and beta [$F(3, 45)= 3.89$, $p=.048$] bandwidths for the *frontal* sites. More specifically, both analyses reveal higher levels at the f6 electrode site in the right hemisphere. These results, however, are thought to be spurious because the significance is lost when the analysis is completed on the relative, rather than the absolute data. These results might be related to eye movement artifacts given the location of the sites yielding increased power.

A significant HEMISPHERE x VENTRAL-DORSAL SITE interaction was also found in both the alpha [$F(3, 45)= 20.91$, $p<.001$] and beta [$F(3, 45)= 23.47$, $p<.001$] bandwidths for the *posterior* sites. These results are consistent for absolute and relative alpha and beta and are also consistent with the coherence results. Specifically, the data suggest

greater activation within both bandwidths in the left hemisphere, with the activation levels in both hemispheres more similar at dorsal sites than at ventral sites (see Table 13).

There were no significant HEMISPHERE x TASK interactions.

Coherence Analysis

Frontal-Posterior Coherence. A HEMISPHERE main effect was found for both the alpha [$F_{(1, 16)}$= 60.62, $p<.001$] and beta bandwidths [$F_{(1, 16)}$= 24.82, $p<.001$]. The left hemisphere was found to have greater amounts of coherence in both bandwidths (*mean alpha values*: left = .48, right = .42; *mean beta values*: left = .42, right = .36).

A significant FRONTAL x HEMISPHERE interaction was also found for both the alpha [$F_{(3, 48)}$= 32.83, $p<.001$] and beta bandwidths [$F_{(3, 48)}$= 14.05, $p<.001$]. Within both bands, the dorsal sites show higher coherence across both hemispheres, with the left hemisphere showing greater coherence values across all the sites (see Table 14).

Further, a significant POSTERIOR x HEMISPHERE interaction was found for both the alpha [$F_{(3, 48)}$= 4.59, $p=.019$] and beta bandwidths [$F_{(3, 48)}$= 3.29, $p=.05$]. Results were similar to the frontal interaction in that dorsal sites again showed higher levels of coherence across both hemispheres, with the left hemisphere showing greater coherence values across all posterior sites (see Table 15).

Finally, a significant 3-way interaction was found between FRONTAL x POSTERIOR x HEMISPHERE [$F_{(9, 144)}$= 3.26, $p=.018$] in the beta bandwidth. More specifically, dorsal electrode pairings (i.e., *f1-p1, f1-p3, f3-p1, f3-p3* for the left hemisphere and analogous pairings for the right, Figure 2, Appendix B) show more beta coherence in both hemispheres compared to ventral electrode pairings (i.e., *f5-p5, f5-t5, f7-p5, f7-t5* for the left hemisphere,

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see Figure 5, Appendix B). However, also noted is that the left hemisphere shows higher coherence values across both dorsal and ventral sites as compared to the right hemisphere in which the ventral sites show lower values (see Appendix F, Figures 23 and 24).

Local Coherence. Hemispheric effects were found for the coherence between the frontal electrodes (i.e., *f1-f3, f3-f5, f5-f7*) in both the alpha [F(1, 16)= 42.21, p<.001] and the beta [F(1, 16)= 21.67, p<.001]. Within both bandwidths, the left hemisphere (alpha = .902, beta = .739) showed greater coherence as compared to the right hemisphere (alpha = .775, beta = .641). However, no hemispheric effects were found in the coherence between posterior sites.

Further, a frontal VENTRAL-DORSAL SITE x HEMISPHERE interaction was found to be significant, again within both the alpha [F(2, 32)= 31.35, p<.001] and the beta [F(2, 32)= 16.33, p<.001] bandwidths. In both, hemispheric differentiation was greater in the left ventral frontal electrode pairings as compared to the right. Coherence values for dorsal frontal electrode pairs were in fact quite similar. Also, similar to previous findings, left hemisphere coherence was found to be greater across all frontal sites (see Table 16).

Finally, a significant LOAD x HEMISPHERE interaction was found for the frontal coherence in the beta bandwidth [F(3, 48)= 2.91, p=.047]. Again, greater left hemisphere activation was evident, with this hemisphere being more sensitive to the level of WM load. This sensitivity is noted to work in a step-wise fashion in that the greatest increase is between the 1- and 2-back tasks, with the two easier tasks showing similar values and the two more difficult tasks showing similar values (see Figure 25, Appendix F). As such an increase in local coherence is associated with higher levels of task difficulty.

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P300 Effects. Similar to previous results regarding analysis of the P300, although

significant hemispheric effects were found, they seem to be specific to the 3-back task. A

significant TASK x LOAD x HEMISPHERE interaction was found [F(3, 48)= 8.98, p<.001]

in the analysis of the frontal sites. However, the significant findings were lost when the 3-back

data were not included in the analysis.

In contrast, analysis of the P300 amplitude at posterior sites was more straightforward,

showing a significant LOAD x HEMISPHERE effect [F(3, 48)= 3.84, p=.022]. P300

amplitudes in the left hemisphere were greater at the lower levels of WM load (i.e., 0- and 1-

back). As the task difficulties increase, the hemispheric differences are lost (see Figure 26,

Appendix F).

No significant hemispheric effects were found in the analysis of the P300 latency.

Dual Task

Spectral Analysis

Predictions

Support for the functioning of the central executive and its purported location in the

dorsolateral PFC area, as is suggested by the fMRI results of D'Esposito et al. (1995), could

be evidenced by a decrease in alpha with a concomitant increase in beta in the more dorsal

frontal electrodes.

Results

Spectral analysis of the theta, alpha and beta bandwidths did not reveal any significant

effects that were task-specific, thereby providing no support for the functioning of the CE

during a dual-task condition. These findings were consistent when we compared the dual task to the verbal 0-back, the dual task to the spatial 0-back, as well as each of the dual tasks to the condition of the tone task performed separately.

Coherence Analysis

Predictions

With regard to coherence analysis, there are several ways that the dorsolateral PFC (central executive) activation expected during a dual-task condition might be evident. First, increases in frontal-posterior coherence might be noted, indicating communication between the CE and posterior attentional systems. Second, a decrease in local coherence in frontal leads might be found during the dual-task condition given that the dorsolateral PFC area would be performing a different task as compared to other frontal areas.

Results

Frontal-Posterior Coherence. Analysis of the coherence between frontal and posterior sites did not support the hypothesized functioning of the CE, as the significant main effects and interactions were not specific to task in any of the bandwidths. Again, similar results were found across all dual-task conditions.

Local Coherence. The local coherence analysis of the frontal sites did not support the hypothesized functioning of the CE in the dorsal areas as no significant effects with task were found in the alpha, beta or theta bandwidth. Significant task effects were also not found in the local coherence analysis of the posterior sites. The significant main effects and interactions that were apparent in the dual-task analyses will not be discussed because they were not specific to task effects and therefore bear no relevance to the dual-task condition specifically. As above, similar results were found across all four dual-task comparisons.

Discussion

There are several strengths of the current research which should be outlined. First, although functional imaging methods, such as PET and fMRI, have a high spatial resolution, their low temporal resolution results in a fairly static picture of the neural substrates of working memory. In contrast, the higher temporal resolution of electrophysiological methods allows for a picture of subsecond changes in cortical activity during cognitive processes. Further, the use of additional electrodes, as well as of averaging techniques to reduce common variance, allows for increased spatial resolution of the EEG methodology. Finally, because EEG coherence provides a measure of both the functional and structural organization of electrocortical brain activity, it should prove to be more informative than neuroimaging techniques that are limited to outlining areas of activation only. This advantage is of particular importance when investigating a model that focuses on neural networks that involve frontal and posterior communication.

The study at hand also attempted to deal with some of the methodological shortcomings of previous neuroimaging and ERP studies that may have, at least in part, influenced the findings. First, many previous neuroimaging studies compared brain activation during different WM tasks and across subject groups. Because all visual tasks inherently consist of both spatial and object information to varying degrees, it is difficult to directly compare the results. The present study instead compares spatial and object WM in tasks with the same visual presentation, only differing in the requirement to attend to the spatial location or to the specific letter. In this way, a more direct comparison of brain activation during the two tasks could be achieved. Secondly, our task comparisons were within subjects, rather

than between subjects, allowing a more statistically powerful comparison.

The current study also employed an additive-factors approach in that WM load increased across tasks without any other aspect of the task being altered. This method of increasing task difficulty presents an advantage compared to neuroimaging studies in which the technique of administering control tasks to subtract out cognitive processes not specific to WM has been questioned about its effectiveness (D'Esposito et al., 1999).

One major aim of the current study was to investigate the conceptualization of WM as being separable into modality-specific cortical components. As reviewed, although there is evidence for this conceptualization from animal single-cell recording research, neuroimaging and ERP studies, the results have not been entirely consistent. Although the current study does provide evidence of modality-specific coding in posterior cortical areas, frontal regions did not show differential task activation patterns. Overall, the current study, therefore, adds to the body of research that does not support the existence of modality-specific working memory circuits. Instead, a picture emerged that is more consistent with working memory as an executive process, closely related to attentional functions, and involving dorsal frontal structures regardless of the type of information to be remembered. Before the results that are specific to the WM models are discussed, the tasks used to test working memory will be reviewed.

n-Back WM Task

Consideration of the behavioural data suggests that the participants performed the n-back tasks as expected. As the number of intervening stimuli between the target and the match increased, significant increases in errors and reaction time were evident, as was a decrease in

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the total number of items correctly identified. In other words, as the WM load increased, performance levels decreased and reaction times were slower. As such, the data suggest that the n-back tasks in this study were successful, from a behavioural perspective, at challenging the WM systems by increasing WM load.

With regard to the electrophysiological data, dorsal frontal and dorsal parietal cortical areas were noted to be sensitive to WM load. This finding is consistent with previous studies of cortical activation during working memory tasks (e.g., Braver et al., 1995; Braver et al., 1997; Cohen et al., 1997; Manoach et al., 1997). The results of Barch et al. (1997) are important to consider at this point. This fMRI investigation was designed to address the possibility that increased PFC activation with WM load was reflective of more general processes associated with task difficulty and mental effort, rather than specific to working memory. A task was presented in which WM load and task difficulty were independently manipulated. Consistent with other studies, dorsolateral PFC activation was associated with the WM task, increasing as the memory load increased. In contrast, however, when task difficulty was increased without a concomitant increase in WM load, dorsolateral PFC activation was not affected. As such, the sensitivity of the dorsal PFC to increased WM load, as was evident in the current study, can be considered specific to the cognitive process of working memory, rather than to other processes that might be affected by increases in task difficulty.

With regard to the comparison of the spatial and verbal n-back tasks, it should be reiterated that only the instruction as to whether to attend to the specific letter, or the space the letter appeared in, differed between the two tasks - all other perceptual and response

requirements were entirely the same. In terms of behavioural data, overall accuracy rates did not discriminate between the verbal and spatial tasks at any level of WM load. In fact, percentages correct were remarkably similar. Performance levels across the two tasks are important to consider given the concern that subjects might attend to the verbal aspect of the stimuli in the spatial-back tasks, rather than the spatial position as instructed. Given that subjects were required to perform the n-back rapidly and continuously, it is believed that accuracy on the spatial tasks would have decreased had subjects maintained the verbal stimulus attributes on-line instead of, or in addition to, the spatial attributes. Given the similar accuracy levels across tasks, we conclude that subjects did attend to the stimulus attribute they were instructed to. Also, as will be discussed more thoroughly in the results of the spectral analysis, posterior activation patterns suggest modality-specific coding of the stimulus attributes, suggesting that the verbal and spatial stimulus attributes were coded as required for each task.

Although the tasks were equated in terms of accuracy, reaction time and electrophysiological data suggest that the verbal task required more cognitive resources to obtain this level. First, significantly greater average response times were evident in the verbal task. Also, the P300 latencies, reported to be directly related to task difficulty (Grillon et al., 1990), were increased at both frontal and posterior sites for the verbal tasks. Spectral analysis also showed consistently higher levels of beta and lower levels of alpha activity for the verbal task. Given these data, it appears that the verbal task was more difficult overall in that greater cognitive resources were required to obtain performance accuracy levels similar to the spatial task.

There are several possible reasons that might account for the increased difficulty when the stimuli to be attended to involved letters rather than the space the letter was in. First, although the number of possibilities was the same for both tasks (i.e., nine letters and nine spaces), participants were not specifically advised of this. The division of the computer screen into a 3 X 3 grid (without visible lines) was quite apparent. However, it was likely less apparent that only nine out of 26 letters were being used. Consequently, the increased task difficulty may be associated with participants perceiving a larger set size to keep on-line during the task. In addition, discrimination of letter stimuli might have required an extra step of decoding that was not required when discriminating spatial stimulus features. However, these reasons are presented only as conjectures. It is difficult to account for task difficulty differences when perceptual and response characteristics were kept constant.

Further, although only the 0- and 3-back tasks were presented in their study, the ERP data of Gevins et al. (1996) suggested that the spatial task was more difficult than the verbal task. It might be that presenting the task in an increasing level of difficulty rather than simply one difficult and one easy task (i.e., 3- vs. 0-back) resulted in the development of different strategies to complete the tasks in the current study compared to those developed by Gevins' subjects. Unfortunately, participants were not debriefed regarding strategies employed, leaving us unable to further speculate in this regard. Another possible reason for the differences in task difficulty might be that Gevins presented the stimuli in a circular grid, rather than a square grid as in the current study. A circular grid decreases the distance between spatial positions and also makes the spatial positions more central on the computer screen. Due to divisions in our visual system, central vision is less sensitive to movement information

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but more sensitive to details, which might account for Gevins' centrally presented spatial task being more difficulty than the verbal task. The opposite arrangement was used in the current study, with more peripherally presented stimuli (due to the use of a 3 x 3 square grid). With such a presentation, the visual system would be more sensitive to the peripherally presented spatial positions compared to the peripherally presented details.

These data highlight the importance of employing tasks that differ on as few attributes as is possible while still differing in modality. Another conclusion is that behavioural data do not necessarily represent valid measures with which to equate task difficulty. Also, these data emphasize the importance of an additive factors approach that increases task difficulty in an incremental fashion so that trends of change can be considered in data interpretation.

In short, there is evidence that the n-back tasks presented in this study were effective in tapping WM processes. Overall, frontal activation was noted for both the verbal and spatial tasks, which is consistent with the accepted role of the PFC as critical in governing WM processes (e.g., Cohen et al., 1997; Funahashi et al., 1989; Gevins et al., 1996; Jonides et al., 1993; Paulesu et al., 1993). In addition, the sensitivity of the frontal regions to the effects of increasing WM load are consistent with previous research (e.g., Barch et al., 1997; Braver et al., 1997).

Of particular interest in this study was whether manipulating the type of information held on-line would result in different patterns of electrophysiological activation, thus supporting modality-specific WM models (e.g., Friedman & Goldman-Rakic, 1994; Wilson et al., 1993). As mentioned, behavioural performance and power spectral results (discussed more thoroughly in the next section), suggest that verbal and spatial stimulus attributes were

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maintained on-line as instructed for each task. To review, according to the modality-specific

model outlined by the work of Goldman-Rakic and colleagues, spatial WM tasks were

predicted to be represented by neural circuits involving dorsal frontal and dorsal posterior

(parietal) regions, whereas verbal WM tasks were predicted to be represented by ventral

frontal and ventral posterior (inferior temporal) regions. The data of this study do not support

this ventral/dorsal division in frontal cortical regions dependent upon the type of stimuli

presented, although there was some support for modality-specific coding in posterior regions.

Because the different electrophysiological methods employed in this study highlight

somewhat different aspects of the data and raise different issues, the main findings within the

spectral, coherence and ERP analyses will be presented separately with a specific focus on the

lack of evidence for modality-specific WM systems. Following this, a discussion will be

offered regarding how the current results coincide with studies that also fail to support this

conception of WM. Finally, consideration will be given to how the present data seem to most

closely support the executive models of working memory, namely those of Petrides (1995)

and Baddeley (1986).

Spectral Analysis Results

Support regarding predictions for modality-specific WM systems was evident in the

spectral analysis of the posterior sites, but not the frontal sites. First, with respect to posterior

sites, beta activity was lowest at the dorsal sites and greatest at the ventral sites for the verbal

task, and greatest at the dorsal sites and lowest at the ventral sites for the spatial tasks. This

differential activation supports the predications made regarding modality-specific coding. Also

we should note that there is more beta overall at the posterior sites for the verbal task, which

is consistent with other electrophysiological data suggesting this task required greater processing effort overall.

These beta results speak to the concern of using letter stimuli rather than pattern stimuli, as is employed in the single-cell recording research of Goldman-Rakic (e.g., Wilson et al., 1993). This task differentiation suggests that our letter stimuli in the verbal n-back were treated like a pattern task, as we had hoped, as the ventral posterior areas involved in coding the non-spatial stimuli in the single-cell recordings (e.g., Miller et al., 1991) are also activated in our study with letters. It can therefore be concluded that although we did not find evidence of modality-specific activation patterns in frontal areas, it is not because the stimuli in the tasks were not coded differently in terms of their modality.

This is an important finding since there was no evidence of modality-specific coding of information in frontal areas. In the spectral analysis of the alpha activity at frontal sites, dorsal regions were found to differentiate the tasks more than the ventral sites. This does not support the predictions made regarding ventral/dorsal activation patterns dependent on the type of stimuli maintained on-line. Also, the verbal task showed lower amounts of alpha activity overall, presumably indicating greater activation.

When we consider the beta bandwidth, the results are more supportive of frontal sites being sensitive to level of difficulty rather than type of information. However, these results concerning the beta bandwidth were not entirely as expected. Since beta is commonly thought to be associated with cortical activation, it was predicted that beta would increase with increasing WM load. However, the opposite pattern was found, with beta decreasing as WM load increased.

As previously discussed, an inverse relation between alpha and beta (reduction in alpha with an increase in beta) has been typically associated with mental activation. Although this pattern was evident in the posterior regions, it was not for the beta activity at the frontal sites. Additionally, although the beta bandwidth was sensitive to the effects of WM load (decreased beta with increased WM load) in the frontal sites, only the alpha bandwidth was sensitive to load (decreased alpha with increased WM load) in the posterior sites.

It might be that these data demonstrate differences in what alpha and beta activity represent regarding cognitive activation patterns in frontal and posterior sites. Alternatively, there might be other explanations that were not considered in our predictions. For example, the pattern of a decrease in frontal beta activity with WM load might be reflective of familiarity of task demands and strategy selection, and therefore reflective of functioning of Baddeley's (1986) CE construct (this idea will be more fully explored in the discussion of the executive models). However, both of these explanations are post hoc and require further investigation to completely understand.

Coherence Analysis Results

Although neuroimaging and ERP electrophysiological methods are cited as providing evidence for modality-specific WM systems (e.g., Ruchkin et al., 1992; Smith & Jonides, 1997), it is argued that investigation using EEG coherence would provide the best test of this model. As previously discussed, by computing the correlation between two EEG signals for any given frequency band, coherence measures can provide insight into structural and functional connections underlying the electrodes (Thatcher et al., 1986; Thatcher, 1992). In contrast, other techniques only provide a picture of activation, without the ability to consider

the possible shared activity between cortical areas that is outlined in the modality-specific model.

However, consistent with the other electrophysiological results of this study, there was no evidence of modality-specific WM systems in the analysis of EEG coherence. The principal coherence findings in this study can be summarized as follows: (1) A lack of effect of task, with verbal and spatial tasks demonstrating similar patterns of cortical connections; (2) Left frontal coherence pairings fluctuating as a function of task familiarity and level of difficulty; and (3) Dorsal frontal electrodes consistently showing higher levels of posterior communication, particularly when paired with dorsal-parietal electrodes. These data suggest a dorsal frontal and parietal circuit that is activated during a WM task, regardless of task type.

More specifically, investigation of local coherence in the frontal regions found dorsal paired sites (i.e., f1-f3) to show higher levels of coherence in the beta bandwidth for both n-back tasks. Additionally, contrary to predictions based on the model of Goldman-Rakic that only the spatial WM tasks would show increased coherence across the dorsal frontal and parietal sites, results suggest that both verbal and spatial tasks activate this dorsal circuit. Dorsal frontal electrodes consistently showed higher levels of posterior communication in both the alpha and beta bandwidths, particularly when paired with dorsal-parietal electrodes. As such, similar to the spectral data, coherence results suggest the existence of a dorsal frontal-parietal circuit that is specific to working memory, regardless of the type of information being maintained on-line.

When interpreting the correlational value of two sites in a coherence analysis, consideration must be provided to the spatial distance between the two electrode sites of

interest: two spatially closer electrodes might have higher coherence values compared to more distant electrodes because of volume conduction. However, this does not appear to account for the significant increase in coherence between the dorsal frontal and posterior pairings. The ventral frontal-dorsal posterior electrode pairs (see Figure 4, Appendix A) are more than 4 cm separated compared to the ventral frontal-ventral posterior electrode pairs (see Figure 5, Appendix A). However, there is no significant difference between the ventral-dorsal and ventral-ventral coherence values. When we consider the dorsal frontal electrode pairings, there is less than 2 cm difference between the dorsal frontal-dorsal posterior (see Figure 2, Appendix A) and the dorsal frontal-ventral posterior (see Figure 3, Appendix A) electrode pairings, yet the coherence values are significantly different. As such, it seems that the result of increased coherence between dorsal electrodes is indicative of functional connectivity during WM tasks.

Overall, similar to the spectral analysis of the frontal sites, coherence results seem more supportive of the conceptualization of WM as being closely related to attentional functions, as is suggested by the executive WM models. This is suggested by the sensitivity of frontal sites to the level of WM load (discussed further under "Executive Models of WM").

ERP Results

Similar to the EEG results, ERP data did not provide support for modality-specific WM systems. Before these results are discussed, differences between the present and previous ERP investigations of WM should be highlighted. First, it is important to note that earlier ERP studies were not designed to specifically test the WM models presented in this study. Consequently, key features that were included in the present investigation to directly compare

the two models were not included in previous studies, limiting the utility of previous studies for theory evaluation.

One might consider that the shorter time constant we used might account for our lack of negative slow waves, the shorter time constant forcing the signal to return to baseline more quickly than in the Ruchkin et al. (1992) study. However, our time constant of 1 second was more than adequate to produce second-long slow wave components in other paradigms presented in our lab. More likely, the research paradigm employed might also account for a slow wave not being associated with our WM task. For instance, Ruchkin et al. (1992) employed a WM task that involved the presentation of a stimulus set, followed by the presentation of a probe. After a decision was made regarding each probe, the contents of WM could be "emptied" to prepare for the next stimulus set. The n-back task, in contrast, does not allow for the emptying of WM contents even after a response has been made as the temporal position of the previous stimulus must be maintained and manipulated on each trial. Gevins et al. (1996) also did not find evidence of a slow wave associated with the n-back task. In short, the specific task requirements (and possibly the time constant) might account for the absence of the slow wave in our WM task. However, this will have to be investigated more thoroughly before definitive answers can be provided.

The principal ERP findings in this study can be summarized as follows: (1) There was a remarkable lack of effect of task on site: spatial versus object stimulus manipulation did not differentially affect activation at dorsal versus ventral sites; (2) ERP components were found to be sensitive to level of task difficulty, which seems to account for significant task effects; (3) ERP components were also found to be sensitive to site, in that dorsal sites in both frontal

and posterior cortical areas seem to be involved with WM regardless of the type of information to be remembered.

The task-related effects in the P300 analysis were found to not support modality-specific WM systems, but instead appeared related to the level of WM load as the two tasks did not follow the same pattern across levels of difficulty. Considering the spatial n-back tasks and P300 amplitude, the levels of WM load behaved as predicted in that the 0- and 1-back conditions, believed to reflect minimal demands on WM because there are no interfering stimuli, showed similar P300 amplitudes. In contrast, the 2- and the 3-back conditions, predicted to reflect more heavy demands on WM, also showed similar P300 amplitudes that were greater in amplitude compared to the easier tasks. This expected pattern was not evident in the verbal task. In this case, the 1-back did not seem to reflect minimal WM demands as the P300 amplitudes were more similar to the 2- and 3-back rather than to the 0-back task. In other words, whereas the spatial 1-back task might not be reflecting much demand on WM structures, the verbal 1-back task does seem to tap WM processes.

A closer analysis of the ERP data found that many of the task differences were specific to the verbal 3-back task. Whereas the spatial 3-back consistently followed the pattern of results established by the lower levels of the task, the verbal 3-back often presented a completely unexpected and nonsensical pattern compared to easier test levels. Because the verbal task was overall found to be more difficult (i.e., increased P300 latency, greater response time, higher commission errors), it might be that participants were not employing the same strategies during the 3-back that were previously effective. If this study had considered only the 3-back tasks this effect would not have been evident and results might have been

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interpreted as reflecting modality-specific WM systems. This demonstrates the utility of incrementally increasing WM load in that such an approach allows for close investigation of the pattern of results, which can assist in the interpretation of the findings.

As mentioned, ERP results consistently indicate that both frontal and posterior dorsal electrode sites were more activated during the WM tasks, regardless of the type of information to be remembered. Furthermore, although ventral sites were not affected by task difficulty, the dorsal frontal and posterior electrodes were sensitive to the effects of WM load, both in terms of increased P300 amplitudes and increased area under the curve. The area-under-the-curve analysis suggests an important difference between frontal and posterior sensitivities to task difficulty in that the frontal sites were most sensitive 300 to 900 ms after stimulus presentation, whereas the sensitivity at the posterior sites became pronounced later (600 ms) and remained for a longer period of time (1200 ms to 1500 ms). However, as previously noted, the data were not entirely consistent across time intervals, making interpretation difficult.

Overall, there was no support for the hypotheses concerning distinct ERP patterns for the processing of spatial and verbal features of a given stimulus. Differences that were observed between tasks probably involved the level of task difficulty. As mentioned, the lack of supportive findings for the WM model of Goldman-Rakic can be added to an already growing body of literature that argues against modality-specific WM. It is to this discussion we now turn.

Modality-Specific WM Models

As is evident, although the various electrophysiological results highlight somewhat

different issues, overall the findings are consistent in their lack of support for the modality-specific WM systems proposed by Goldman-Rakic and colleagues (Friedman & Goldman-Rakic, 1994; Wilson et al., 1993). Instead, results consistently suggest the existence of a cortical circuit connecting dorsal PFC and parietal areas, which appears to be active during WM tasks regardless of the type of information processed. As such, this study is consistent with a growing body of research that demonstrates contrasting evidence for the conceptualization of modality-specific WM.

With regard to the frontal components of the WM circuit, not all investigations have revealed a ventral/dorsal distinction for different types of information being maintained on-line. As previously reviewed, Rao and colleagues (1997) argue that separating object and spatial attributes in an experimental task is not representative of real-world tasks. In an attempt to investigate a more realistic presentation of stimuli, nonhuman primates were presented with WM tasks which required attention to both object and spatial WM. Single-cell recording results indicated that although some PFC neurons were in fact specific to the coding of one type of stimulus, more than half of the recorded neurons were activated in response to both types of stimuli. These latter nonspecific neurons first conveyed object information and then conveyed spatial information, as the task required. Thus, the researchers argue that the presentation of tasks in which only one type of information needs to be analyzed might result in an artificial segregation of neuronal firing.

D'Esposito and colleagues (1998a) also present a lack of evidence towards a ventral/dorsal dissociation in frontal activation during a WM task that is dependent on the type of information being maintained. First, they completed an fMRI investigation of WM

using 0- and 2-back verbal and spatial tasks. Results revealed that both 2-back tasks were associated with significant activation in the right dorsal PFC (area 46), along with supplementary, lateral premotor cortex, and posterior parietal areas. In an additional effort to study modality-specific WM, these researchers conducted an analysis of all the functional neuroimaging studies done to investigate WM systems, plotting the results of each onto a standardized brain. Results of this plotting were 'intermixed', with both spatial and non-spatial working memory tasks activating ventral and dorsal prefrontal areas, including the inferior frontal gyrus (area 47), middle frontal gyrus (areas 9/36), and superior frontal gyrus (areas 8/6). As such, neither the experimental nor the meta-analytic approach of these researchers was found to support the conceptualization of WM as modality-specific.

Research regarding the posterior components of the WM circuit also does not consistently support a ventral/dorsal distinction in activation for spatial and non-spatial tasks. Across most neuroimaging studies, parietal activation is noted during a WM task, regardless of the type of information involved, with additional temporal activation noted during non-spatial tasks only (e.g., D'Esposito et al., 1998a; Manoach et al., 1997; Smith & Jonides, 1995). This is in contrast to the model proposing distinct parietal activation for spatial tasks and distinct temporal activation for non-spatial tasks (Friedman & Goldman-Rakic, 1994; Wilson et al., 1993). This pattern of results is more suggestive of a dorsal posterior WM system that is activated regardless of the type of stimuli to be remembered, along with an additional ventral region that is specific to non-spatial information.

The ERP investigation of modality-specific WM systems completed by Gevins and colleagues (1996) is also suggestive of a dorsal frontal-parietal working memory circuit. In

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this study, the waveforms elicited by a verbal and spatial 3-back task were topographically similar and suggestive of a dorsal WM network that is activated regardless of the type of information maintained on-line. Similar to the results of the current study, the differences in task difficulty between the spatial and verbal tasks seemed to account for the task differences that were evident in the waveforms.

Taken together, this accumulating body of unsupportive findings regarding modality-specific WM systems presents a definite challenge to this model. Considering the work of Goldman-Rakic and colleagues (e.g., Friedman & Goldman-Rakic, 1994; Wilson et al., 1993), it might be that either there is not complete homology between human and nonhuman primates in prefrontal cortical organization, or that the functional WM divisions do not actually exist and that the model is erroneous in its predictions. It is important to note that the current study was a replication of the neuroimaging and ERP studies that assessed modality-specific WM using n-back tasks. The series of studies performed by Goldman-Rakic and colleagues involved patterns as objects, not letters. Although such methodological differences might account for the findings not being consistent with the animal research supporting modality-specific WM systems, they would not account for the lack of consistency with the human research using n-back tasks that supports this model. As such, although these results do not precisely replicate Goldman Rakic's animal research, it is believed they do directly assess the issue of modality-specific WM.

Executive Models of WM

To review briefly, two executive models were considered in the present study. First, a conceptual model presented by Baddeley (1986; 1995) that proposes a tripartite WM system

composed of two slave components and an executive component. This central executive is hypothesized as a control system and as being closely associated with attentional requirements. A second executive model, namely that of Petrides (Petrides et al., 1993a, b; Petrides, 1995) involves a neuroanatomical approach, which suggests that activation of the PFC in a WM task is dependent upon the nature of the processing that is being performed, rather than the type of information involved. As previously stated, the results of the current study seem to favour these executive models.

Baddeley's WM Model

In addition to the WM tasks investigated in this study, a dual task that involved subjects performing a 0-back task and an auditory-oddball task simultaneously was considered to investigate the functioning of the CE. This direct investigation of Baddeley's model did not provide evidence for the existence of this construct. With regard to behavioural data, both in terms of reaction time and correct responses, results suggest that the dual tasks presented in this study were effective in reducing attentional resources in that both reaction time and errors increased. However, there were no significant task differences noted in any of the electrophysiological analyses. This lack of supporting data is in contrast to the results of D'Esposito et al. (1995) who found significant bilateral activation in the dorsolateral PFC when two tasks were performed simultaneously but not when the tasks were performed individually.

There are several possible reasons for the lack of supportive findings in the current study. First, it might be that the dual task presented in this study was simply not difficult enough to present a challenge to the CE. Before performing the dual task, participants had

performed all the spatial and verbal n-back tasks, allowing for much practice. As such, later

dual-task performance involving the 0-back tasks might not have been very difficult, even

though behavioural performance was affected. Alternatively, given the contrast with the fMRI

results, it might be that EEG analysis is not sensitive enough to detect increased functioning of

the CE during a dual task.

It is interesting that although our data do not provide evidence that the CE was

activated during a dual task, the data from the n-back tasks might provide some support for

the functioning of the central executive as explained by Baddeley's (1986) WM model.

Proposed functions of the CE include the allocation of attentional resources, as well as

involvement in the planning and selection of cognitive strategies (Baddeley, 1986; 1995).

Since the 0-back was the first task presented for each of the two groups of WM task types,

greater attentional resources and the planning of cognitive strategies were likely required

while the subject became accustomed to the stimuli to be judged (i.e., letter or location). This

is supported by both higher coherence values, as well as higher levels of frontal beta in the

spectral analysis, suggesting increased cognitive activity for the 0-back condition. As a

subject progressed to the 1-back, fewer attentional resources would be required because of

familiarization with the task, thereby reducing demand on the CE and resulting in a decrease in

frontal coherence and a decrease in the amount of beta activity. Given the considerable

increase in difficulty of the 2-back task, increased attentional resources and new cognitive

strategies (as selected by the CE) would be required, supported by an increase in coherence

values during this task. Finally, there was no significant coherence change from the 2- to the

3-back conditions, both of which represent high WM demands and perhaps employ similar

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strategies.

These results are thought to be consistent with the proposed functioning of the central executive. When new cognitive strategies are required to complete the task at hand (i.e., 0- and 2-back conditions in the present study), the CE is tapped and increasing activity is noted at dorsal frontal sites. When the subject was able to employ strategies used on the previous trial (i.e., during the 1- and 3-back conditions), no increase in frontal activity was found.

The present results are both similar to and different from the fMRI results of D'Esposito and colleagues (1995).These researchers argue that an increase in prefrontal activation should not occur as task difficulty increases because activation of the CE is not simply due to a nonspecific increase in mental effort. However, this would not be the case if increased task difficulty required the participant to change their cognitive strategy, as described above. The CE should not be considered as a digital mechanism that is either turned on or off, but rather as an area that increases or decreases its functioning as changes in attentional resources or changes in cognitive strategies are required. D'Esposito, Aguirre, Ballard and Zarahn (1998b) address a similar issue in their conclusions that the PFC supports processes in addition to WM.

It should be noted that this interpretation of the data is highly conjectural. Further investigation, perhaps alternating the order of the n-back tasks, is required to more thoroughly investigate this post hoc explanation. It should be acknowledged that it is somewhat difficult to interpret electrophysiological data as providing evidence for a conceptual model that does not make specific neuroanatomical predictions. In addition, although the proposed explanation involving strategy selection and task difficulty level as accounting for the current pattern of

results does seem to intuitively fit Baddeley's description of CE functioning, the dual task specifically presented to tap the CE did not provide the expected results. Given the contrasting findings with the results of D'Esposito et al. (1995), who did find evidence of dorsolateral PFC activation specific to a dual task, it is difficult to assess the support of the current results for the model presented by Baddeley. In contrast, the executive model of Petrides, which does allow for specific neuroanatomical predictions, seems to provide the best explanation of the current data.

Petrides' Executive WM Model

The trend of activation of dorsal frontal areas during the n-back task in the current study is consistent with the two-level model proposed by Petrides (Petrides et al., 1993a, b, 1995). According to his model, information is initially received in ventral PFC areas and comparisons of information held in WM are made. Tasks that require the monitoring of events within WM or manipulation of the information are then subserved by the dorsolateral PFC. The n-back is proposed as such a task in that attention must be given to the stimulus (i.e., either letter or space) that is currently under consideration, as well as to several other stimuli whose current position in the continuously changing series is essential for the decision of a match to be made. Because each stimulus had to be judged and kept on-line for a certain period of time (i.e., monitoring requirements), as well as the temporal position changed on each trial (i.e., manipulation), dorsolateral PFC activation during both tasks was expected. In contrast, because the current stimulus was not matched with information stored in either short- or long-term memory, no such information needs to be retrieved and therefore ventral areas not predominately involved in mediating responses.

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There are several results that are consistent with these predictions. First, ERP analysis found the amplitude of the P300 at dorsal sites to be more sensitive to WM load compared to the P300 amplitude at the ventral sites. Also, in the power spectral analysis, the lack of task differentiation at the ventral sites is consistent with Petrides' model since the ventral sites were not expected to be activated during the n-back. However, at the dorsal frontal sites, where activation was expected, lower levels of alpha were evident for the verbal task that is suggested by other data to have required more cognitive processes than the spatial task. Finally, the coherence analysis suggests functional connectivity between the dorsal frontal and dorsal posterior sites, regardless of the type of information maintained on-line.

Overall, this study therefore adds to the growing body of knowledge that seems to better support the executive model of Petrides, compared to the modality-specific WM model of Goldman-Rakic. For instance, the meta-analysis of D'Esposito and colleagues (1998a) provides interesting support for Petrides' two-stage model of WM. In addition to plotting the results of the WM studies according to the type of stimulus to assess the modality-specific WM model, the researchers also divided the tasks according to the type of processes involved (i.e., 'maintenance only' or 'maintenance plus additional processing') to test the executive or "process" model. Delayed-response tasks that required the maintenance of information across a delay period with no distractions and therefore no additional manipulation of the material were grouped together, whereas tasks that required either reshuffling of the information or the processing of intervening stimuli during the maintenance of stored information (e.g., self-ordered tasks, n-back tasks) were grouped together. In contrast to the plotting of the verbal/spatial task divisions, results of the maintenance/maintenance-plus processing analysis

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did find a ventral/dorsal distinction in the brain areas activated. As expected based on the

model of Petrides, most maintenance-only studies (12 out of the 18 analyzed) found only

ventral PFC areas activated, whereas most of the maintenance-plus processing studies (16 out

of 17) found dorsal PFC areas activated. D'Esposito et al. describe some methodological

concerns, such as increased interstimulus intervals and statistical issues evident in the studies

that did not support this ventral/dorsal distinction, which may account for the contrasting

findings.

It is apparent that the literature is beginning to favour a WM model that suggests

frontal ventral/dorsal activation is dependent upon the executive processes being carried out

on the information, compared to the type of information involved (D'Esposito et al., 1998a;

1999; Owen et al., 1999). The current study adds to this body of research. The

electrophysiological data consistently demonstrated no evidence of a ventral/dorsal distinction

in activation patterns that was specific to the verbal and spatial tasks. Instead, dorsal

activation was noted that was similar for both tasks, and dorsal sites were also found to be

more sensitive to the effects of WM load. However, the task manipulation in this study

focused upon comparing verbal and spatial information in WM, however did not compare

'maintenance only' and 'maintenance plus manipulation' cognitive requirements. Therefore, the

current results can be presented only as consistent, and not as directly supportive, of Petrides'

executive model.

Lateralization

Although the WM models do not make specific predictions regarding lateralization of

WM processes, the literature consistently deals with hemispheric findings. With regard to the

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results of the current study, no hemispheric task differences were noted that were directly related to the type of information being maintained on-line. Instead, the hemispheric differences seemed more related to a ventral/dorsal activation pattern. More specifically, at ventral sites the hemispheric distinction was greater compared to that at the dorsal sites, where the electrophysiological activity in the two hemispheres was more similar. This pattern was evident at both frontal and posterior electrode sites. In addition, left-hemisphere activity seemed to be greater across all electrophysiological measures and to be more sensitive to the effects of WM load. At low levels of task difficulty, greater activation of the left hemisphere was evident regardless of the type of information being analyzed. However, as the WM load increased, the activation patterns became more similar across both hemispheres.

The meta-analysis of D'Esposito et al. (1998a) suggests that hemispheric specialization varied with whether the task activated dorsal or ventral PFC areas. Specifically, when dorsal PFC areas (areas 9/46) were activated, either bilateral or right hemisphere activity was found, regardless of whether verbal or spatial information was being maintained in WM. In contrast, when ventral PFC areas (areas 44, 45, 47) were activated, lateralization dependent on the type of information was found, with spatial stimuli associated more with right hemisphere activity and non-spatial stimuli with activity on the left side.

The current study partially concurs with the results of the WM meta-analysis in that when dorsal activation was evident, the cortical activity was more similar across the hemispheres. However, in contrast to the meta-analysis, ventral lateralization did not appear to be dependent on the type of information, but rather was strongest in the left hemisphere regardless of task type. It might be that the identification of the letter was a prepotent,

automatic response in both task conditions, thereby activating the left hemisphere. It is difficult to discern the meaning of the contradictions regarding lateralization in WM tasks. At this time, the WM models have not focused specifically on this issue and results across studies remain contradictory. However, the current study, along with the meta-analysis of D'Esposito and colleagues (1998a) does seem to suggest that dorsal sites are activated bilaterally, whereas ventral activation is more lateralized. However, the precise determinants of this lateralization remain unknown.

Overall Summary

The current study was designed with the primary intention of investigating modality-specific WM circuits, as well as to consider executive WM models, using electrophysiological methods to investigate the neural substrates of WM. Taken together, the key findings of this study are as follows: (1) Similar patterns of cortical activation were demonstrated regardless of the type of information to be remembered; (2) A dorsal frontal and parietal circuit seems to be activated during WM tasks; and (3) Task familiarity and level of difficulty appear to account for significant task effects. Overall, these results are supportive of a WM system that is closely related to the executive processes being performed on the information and attentional demands, compared to a system composed of modality-specific components.

A secondary purpose of the current study was to develop EEG coherence as a methodology to examine the neural substrates of WM. Given the consistency of the data across the three electrophysiological analyses, as well as the sensitivity of coherence measures to WM load, it is believed that this metric could be useful to study paradigmatic issues as was presented in this study. This is the first known attempt to use this methodology to assess

functional relations between frontal and posterior areas during a WM task. It is well accepted that cortical regions, such as the PFC, do not work in isolation but rather as part of a neural network involving posterior brain regions. Consequently, it is believed that a measure sensitive to the existence of corticocortical connections, such as EEG coherence, would be beneficial in investigating a cognitive construct such as WM.

Criticisms of the Current Study

It must be acknowledged that the current study was exploratory in nature, both with regard to the methodology employed, as well as to the investigation of several WM models. The tasks employed were focused upon comparing verbal and spatial information in working memory, in an attempt to investigate modality-specific cortical circuits. Although the n-back task does provide for consideration of the model presented by Petrides in that manipulation and constant monitoring of the stimuli is required, there was no task presented that did not require such additional processing. Therefore, although the current data are consistent with the model of Petrides in that expected dorsal frontal activation was evident, further investigation would be required to adequately assess this model.

In terms of the exploratory nature of the electrophysiological measures, there were several aspects of the data that were difficult to interpret, such as the area-under-the-curve ERP analysis. As such, trends in the results that were consistent across methodologies were predominantly considered in the overall interpretation of the findings.

One specific criticism of the current study involves the practice trials provided to the participants. In comparison to other studies such as Gevins et al. (1996), subjects of this investigation were given relatively few practice trials to become accustomed to the demands

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of the task. This was mostly because of the significant time requirements through which many participants found difficult to sustain attention. However, increased practice trials might have resulted in clearer ERP data for the seemingly difficult 3-back task.

The current analysis also defined the alpha and beta bandwidths broadly. There has been some suggestion in the literature that there is functional independence of frequency bands within these broadly defined bands (e.g., Petsche, Kaplan, von Stein & Filz, 1997). Therefore, it might prove useful to examine more narrowly defined frequency ranges such as a low and high alpha bandwidth and a low and high beta bandwidth. In this way, the activity in the bandwidth most associated with the cognitive activity could be more closely examined and perhaps produce more informative results.

Additionally, there is some question as to whether the recording epoch of one second used in this study is the most effective for the investigation of cognitive processes given that much can happen cognitively within this time frame. Although long epochs, such as 2 or even 4 seconds are common in the literature on EEG coherence, 1/2 second or 1/4 second epochs might be more sensitive to cortical processing. However, this necessarily implies a reduction in frequency resolution. This trade-off between time resolution and frequency resolution is an empirical one that has not yet been investigated.

Future Research

The consistency between the results of the EEG coherence analysis and the other electrophysiological analyses supports the use of this measure to assess the functional relations between cortical regions activated during a WM task. Consequently, further research of the neural substrates involved in WM processes could serve to greatly increase knowledge

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in this area of study, as well as of other cognitive processes.

It is evident that there is a developing body of research, including the present findings, that does not support the existence of modality-specific WM circuits in humans. It cannot be completely ruled out that within the dorsal frontal and parietal WM circuit proposed, there is some differentiation among individual neurons activation that is dependent on the modality of the stimulus material. However, it seems that the investigation of the cortical activation during WM tasks will likely be more fruitful if the tasks are considered by the nature of their required executive processing rather than by the nature of the stimulus material. A benefit of considering the executive model proposed by Petrides is that specific predictions can be made regarding the frontal activation that would be elicited by WM tasks that differ in their processing requirements.

Given the apparent utility of EEG coherence measures in examining the neural substrates of WM, further research is indicated with a specific focus on investigating the model outlined by Petrides (1995). As has been undertaken in several neuroimaging studies (e.g., Owen et al., 1996; Salmon et al., 1996; Zarahn et al., 1997), tasks designed that specifically differ as to whether additional processing and manipulation of the data is required or not can be investigated employing the methods of the current study. As such, the communication between the frontal and the posterior components might be better investigated.

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APPENDIX A

BRAIN MAP

Figure 1. Schematic drawing of the human brain to illustrate the location of the dorsolateral and ventrolateral frontal regions (Petrides, 1995).

B

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9/46

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10   47/12

RE 2. Schematic diagrams of the lateral surface of the macaque monkey (A) and the
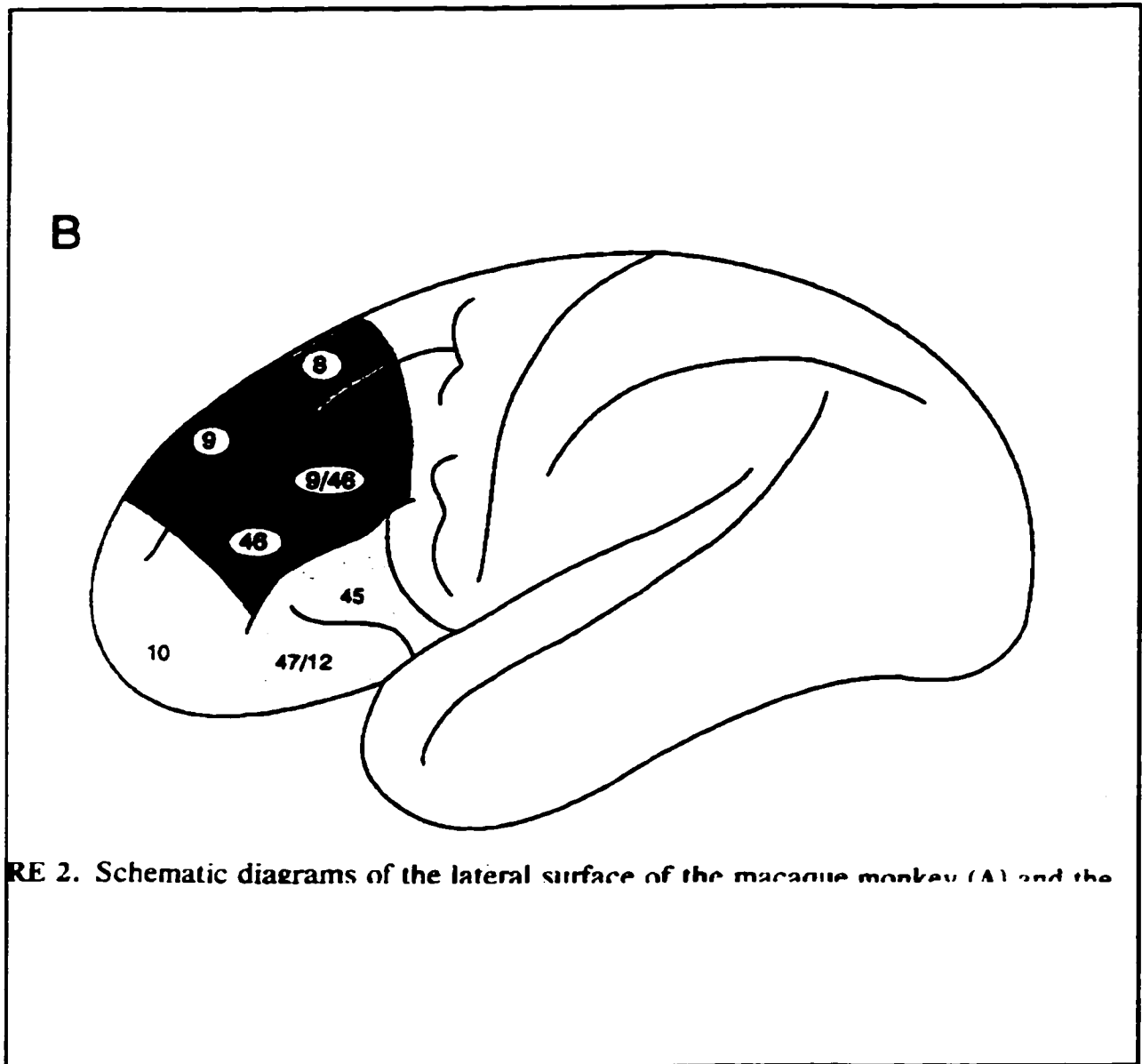
APPENDIX B

EEG MONTAGE AND COHERENCE PAIRINGS

FIGURE 1. EEG ELECTRODE PLACEMENT ACCORDING TO THE EXTENDED 10/20 SYSTEM
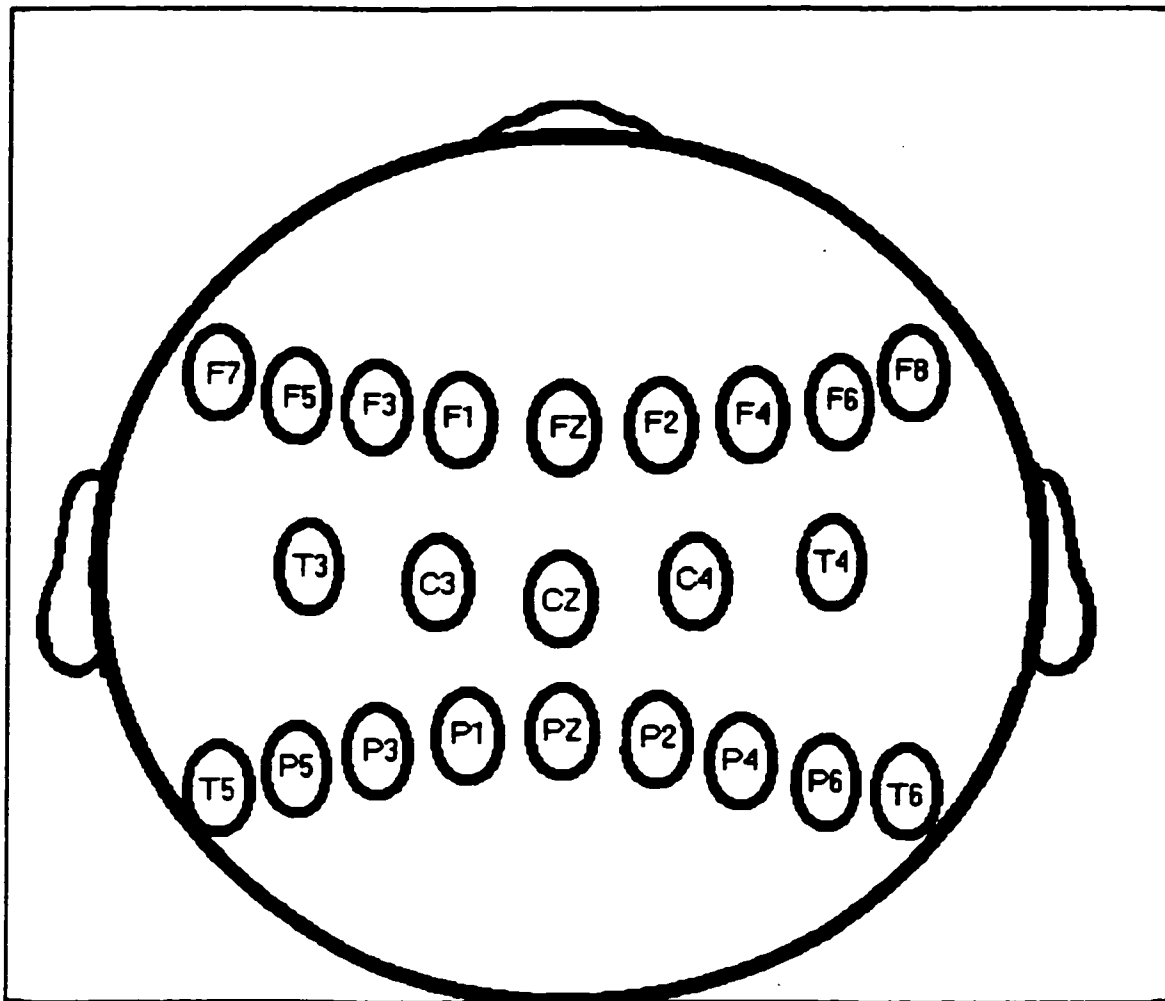
FIGURE 2. DORSAL FRONTAL - DORSAL POSTERIOR COHERENCE PAIRINGS.
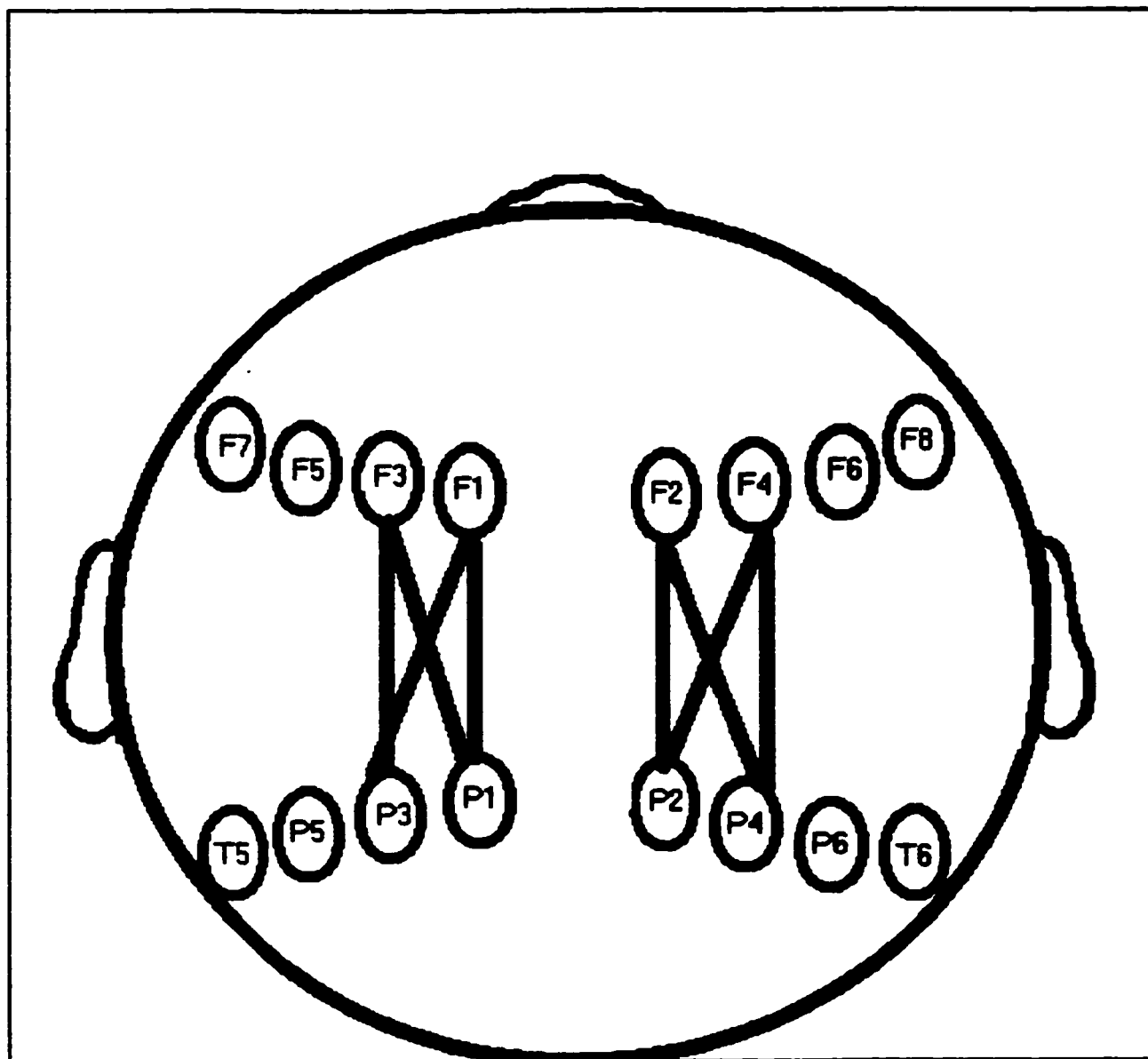
ELECTRODE DISTANCE:
    F1-P1 = 14.1 cm
    F1-P3 = 14.0 cm

FIGURE 3. DORSAL FRONTAL - VENTRAL POSTERIOR COHERENCE PAIRINGS.
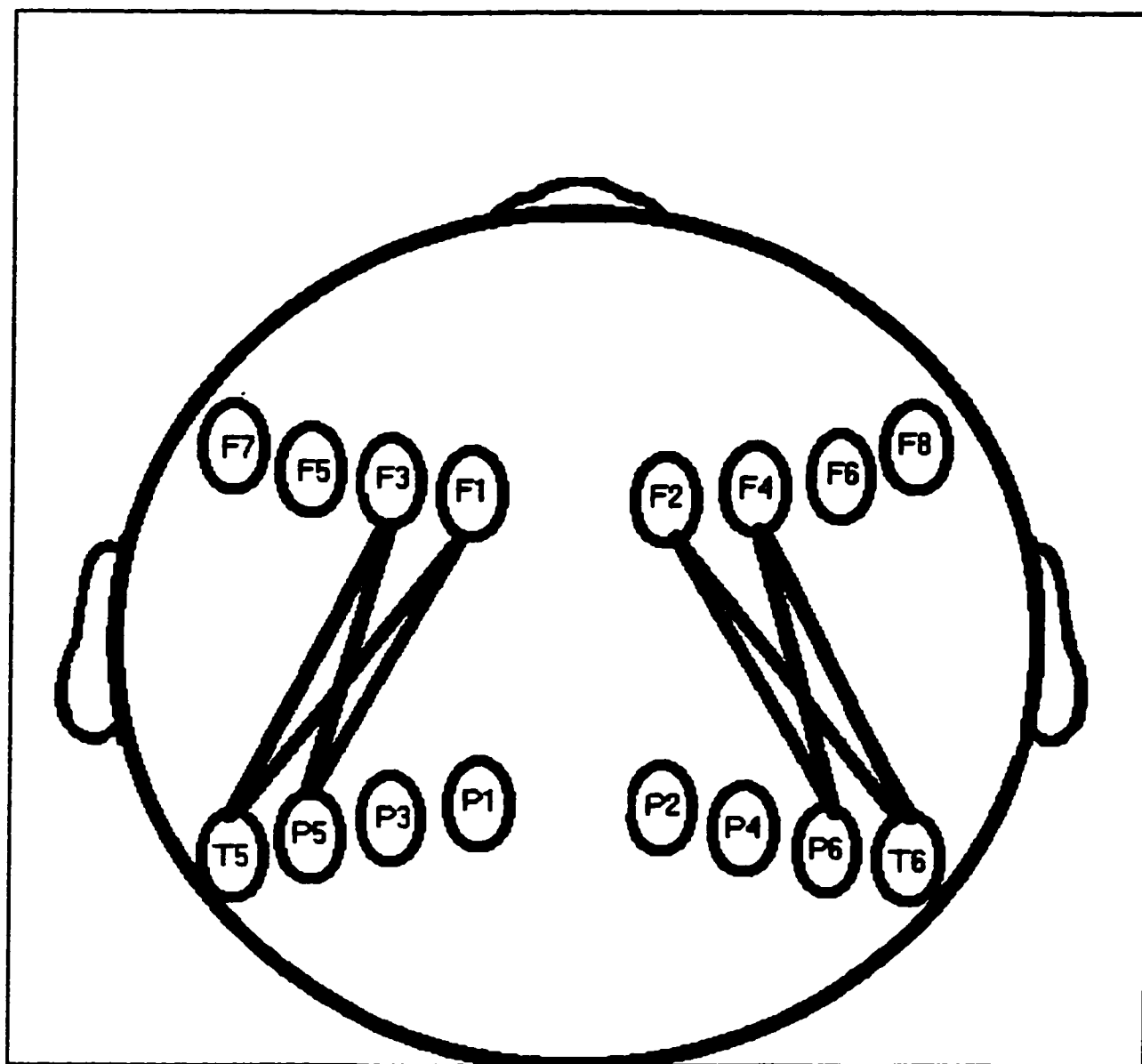
ELECTRODE DISTANCE:
    F1-P5 = 14.8 cm
    F1-T5 = 15.4 cm

FIGURE 4. VENTRAL FRONTAL - DORSAL POSTERIOR COHERENCE PAIRINGS.
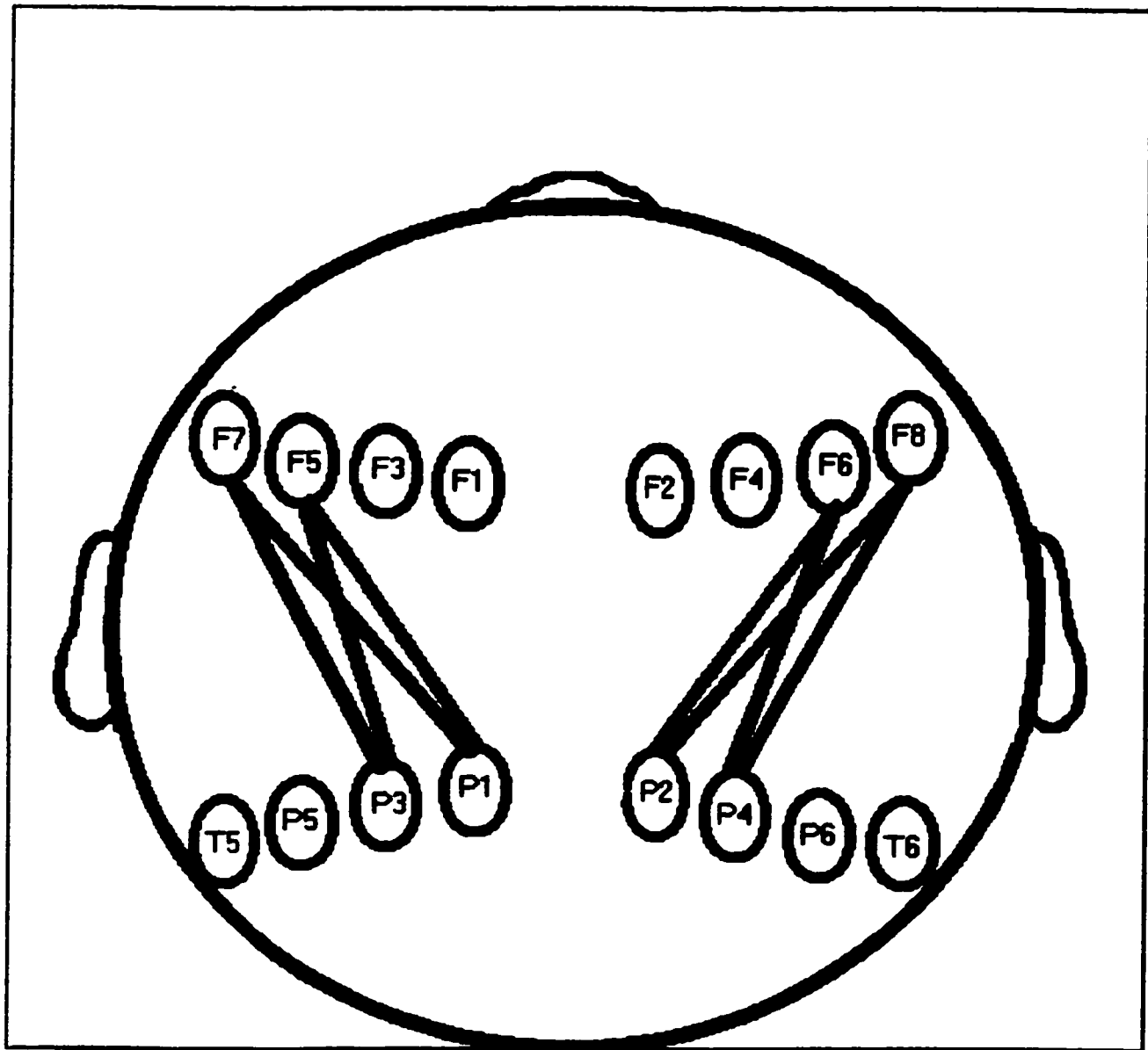
ELECTRODE DISTANCE:
    F7-P1 = 16.6 cm
    F7-P3 = 14.6 cm

FIGURE 5. VENTRAL FRONTAL - VENTRAL POSTERIOR COHERENCE PAIRINGS.
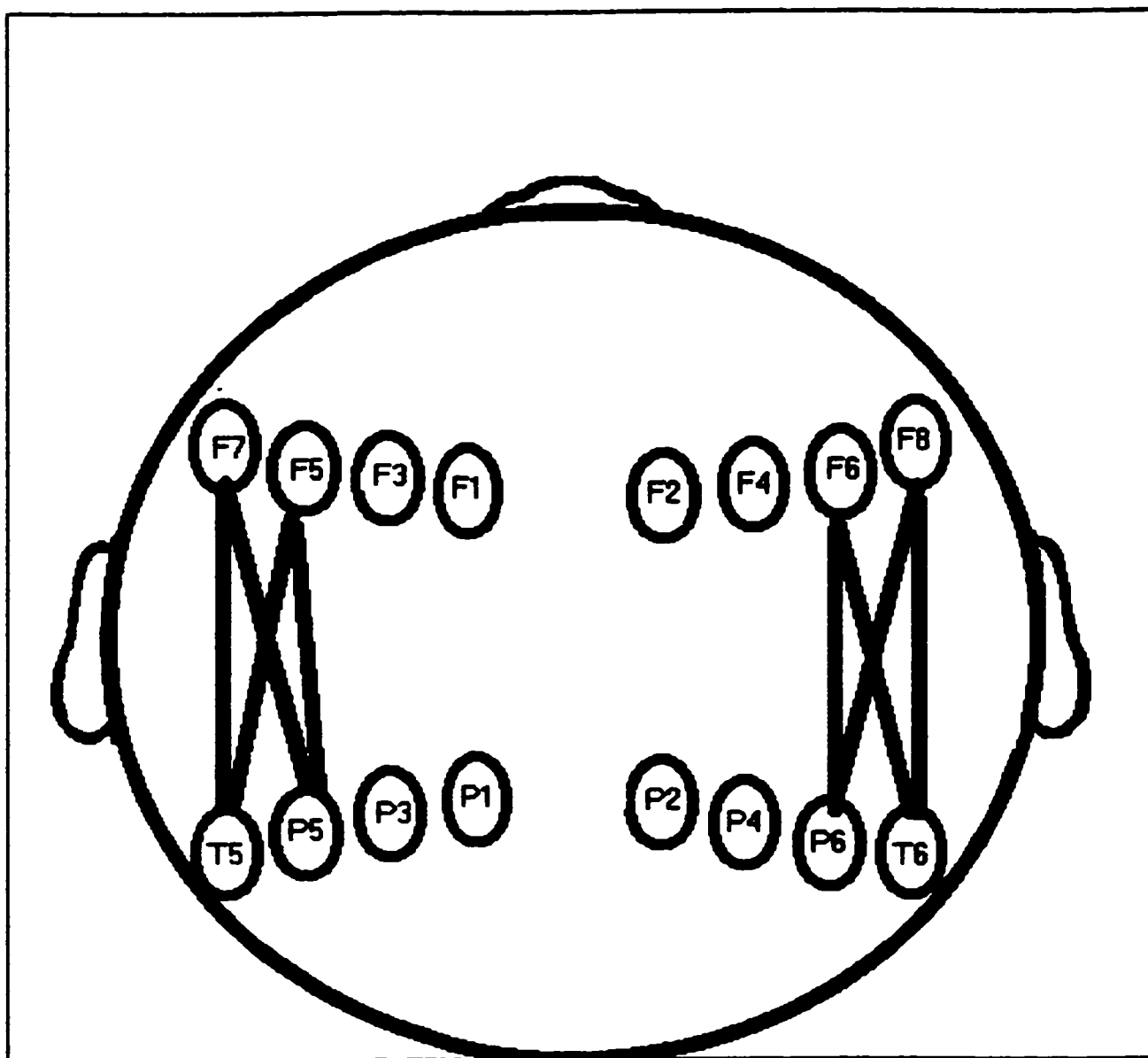
ELECTRODE DISTANCE:
F7-P5 = 13.1 cm
F7-T5 = 12.0 cm

FIGURE 6. DORSAL FRONTAL - DORSAL CENTRAL COHERENCE PAIRINGS.
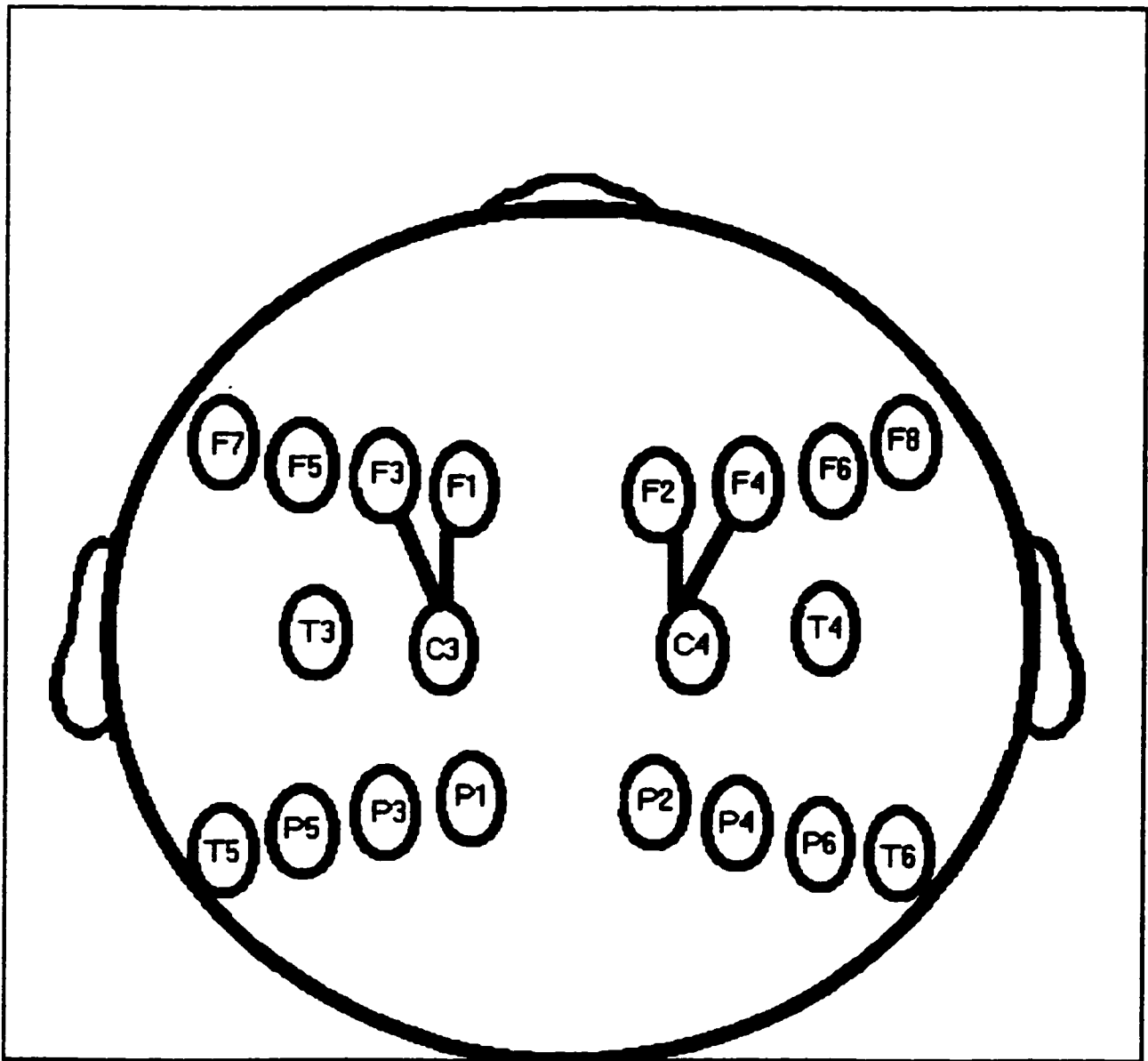
FIGURE 7. DORSAL FRONTAL - VENTRAL CENTRAL COHERENCE PAIRINGS.
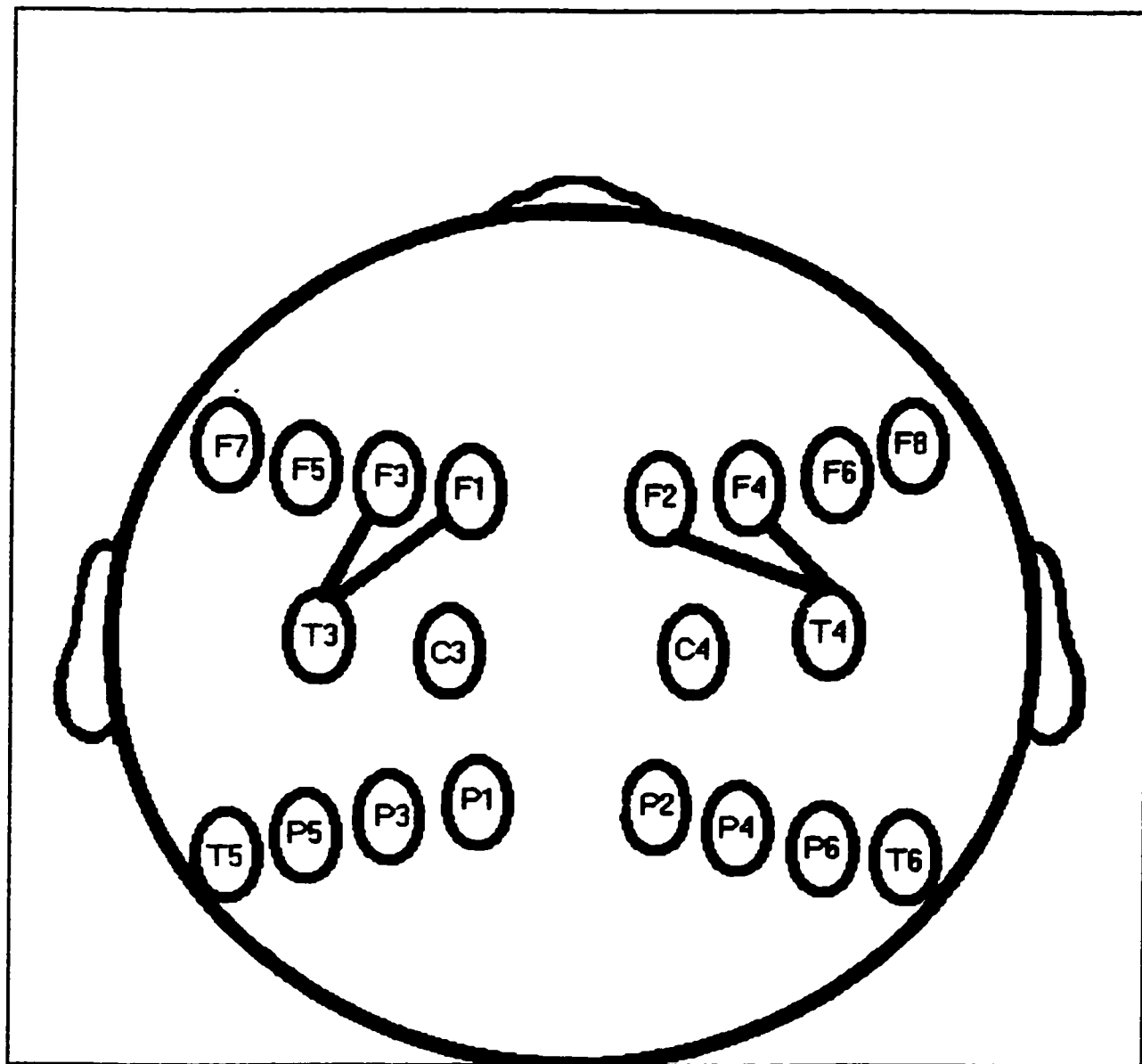
FIGURE 8. VENTRAL FRONTAL - DORSAL CENTRAL COHERENCE PAIRINGS.
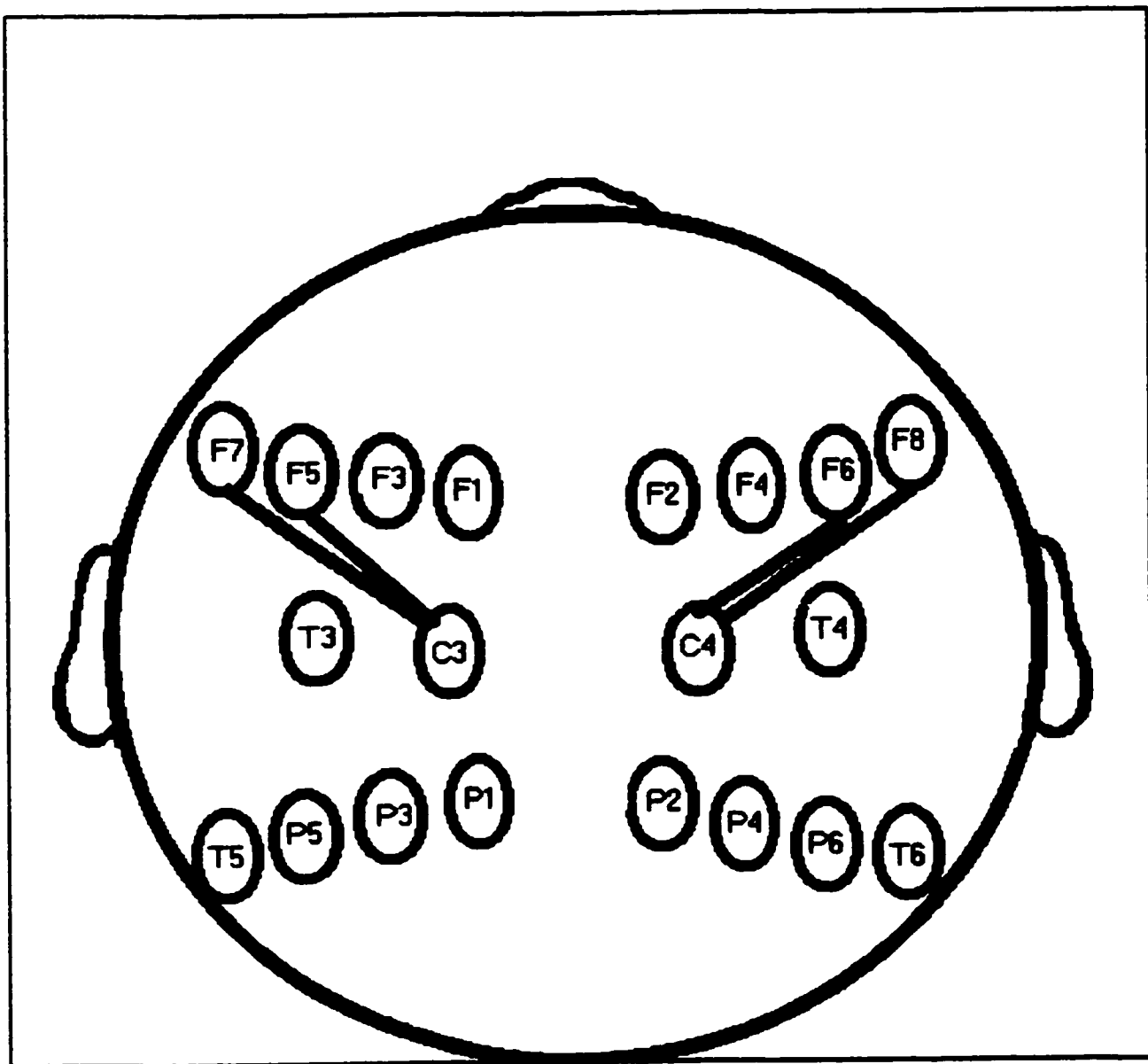
FIGURE 9. VENTRAL FRONTAL - VENTRAL CENTRAL COHERENCE PAIRINGS.
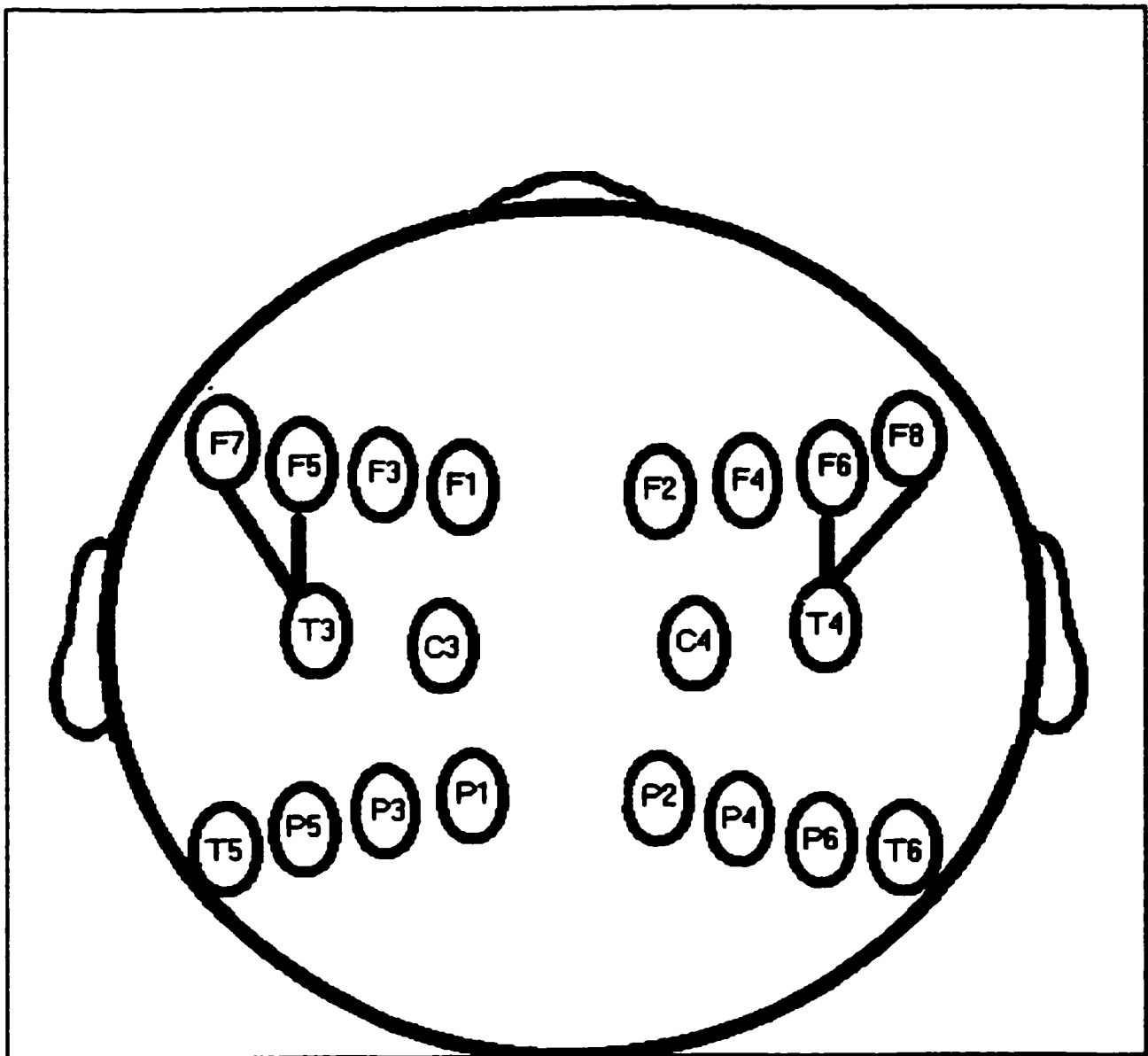
FIGURE 10. DORSAL CENTRAL - DORSAL POSTERIOR COHERENCE PAIRINGS.
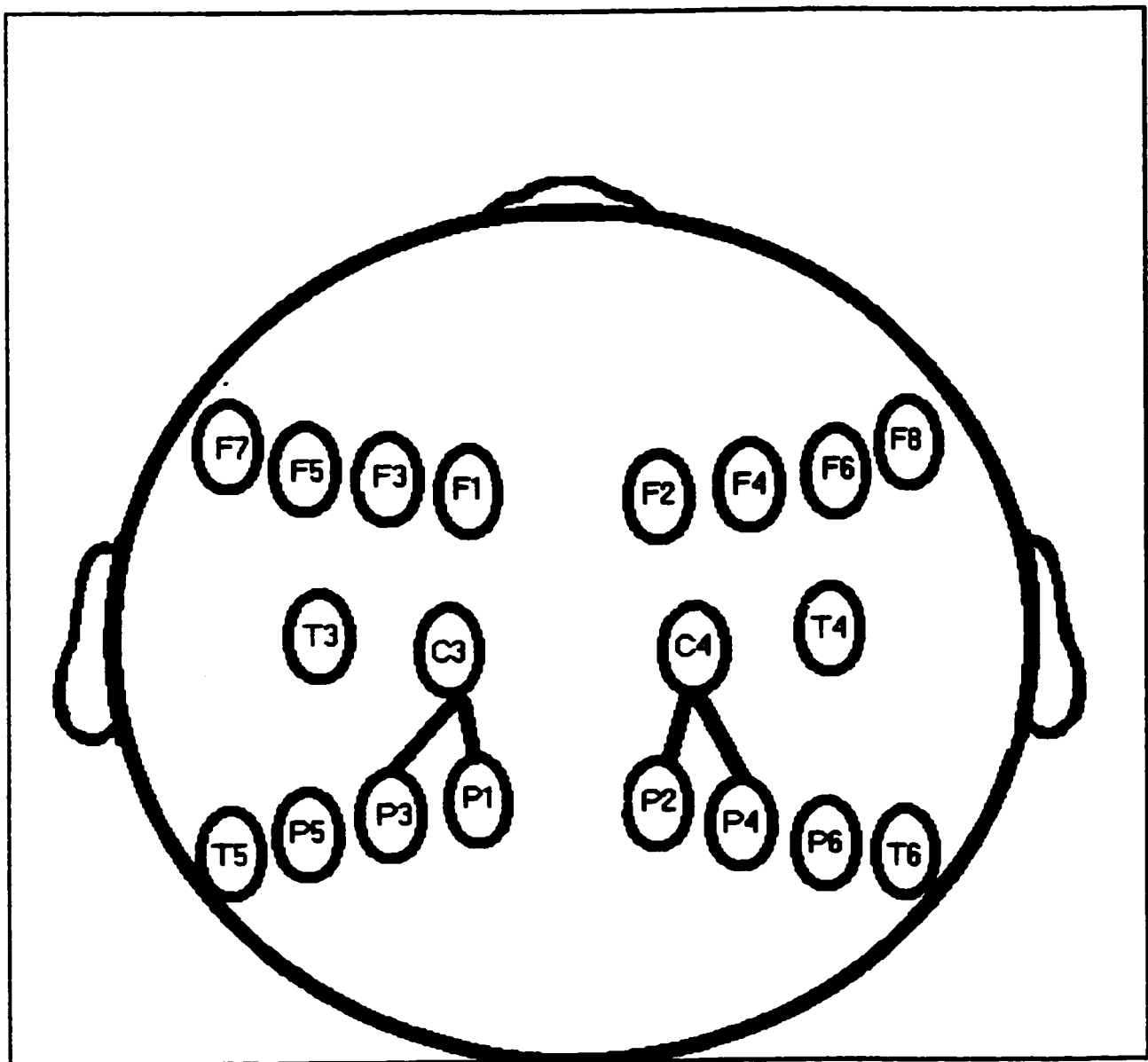
FIGURE 11. DORSAL CENTRAL - VENTRAL POSTERIOR COHERENCE PAIRINGS.
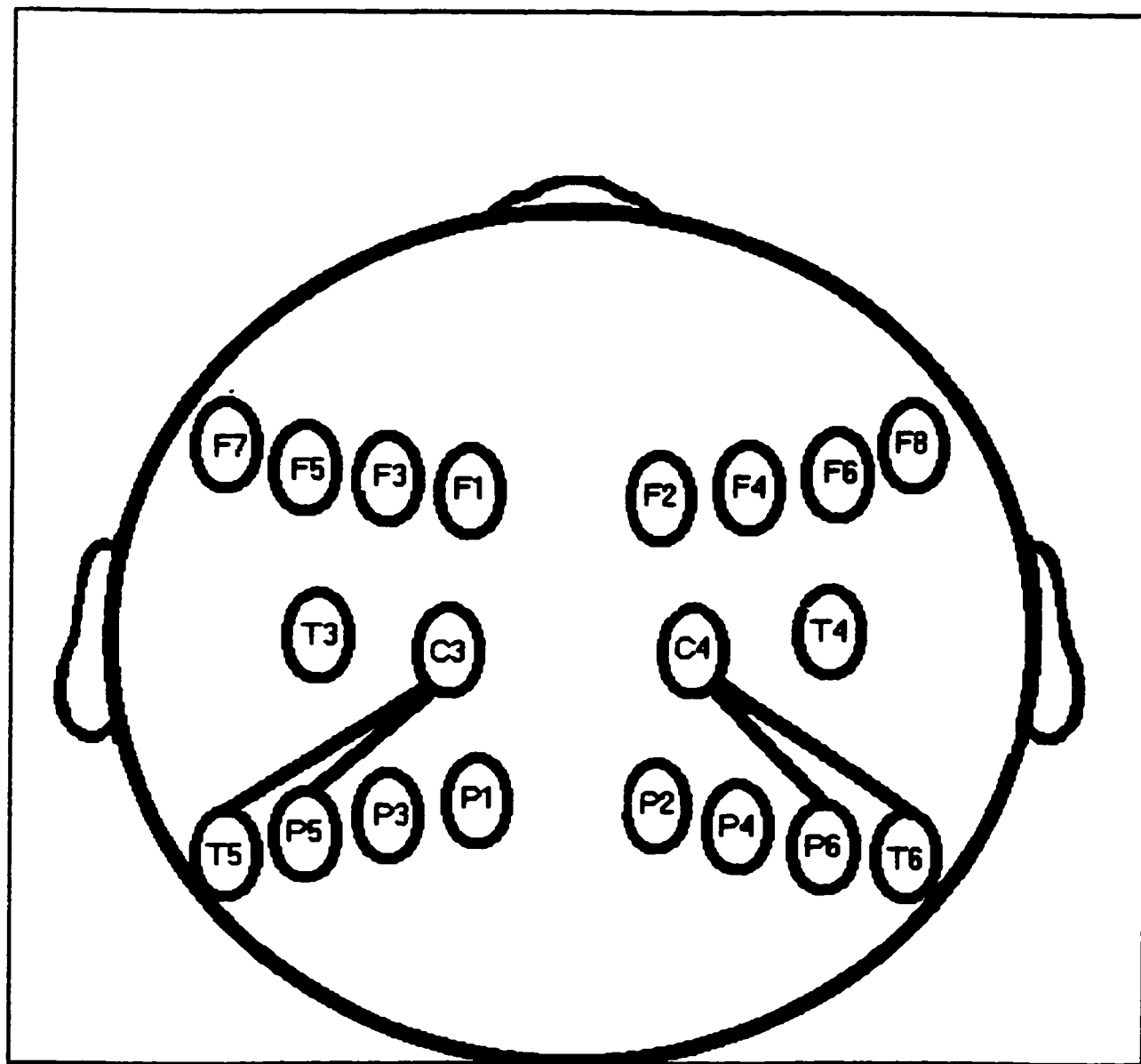
FIGURE 12. VENTRAL CENTRAL - DORSAL POSTERIOR COHERENCE PAIRINGS.
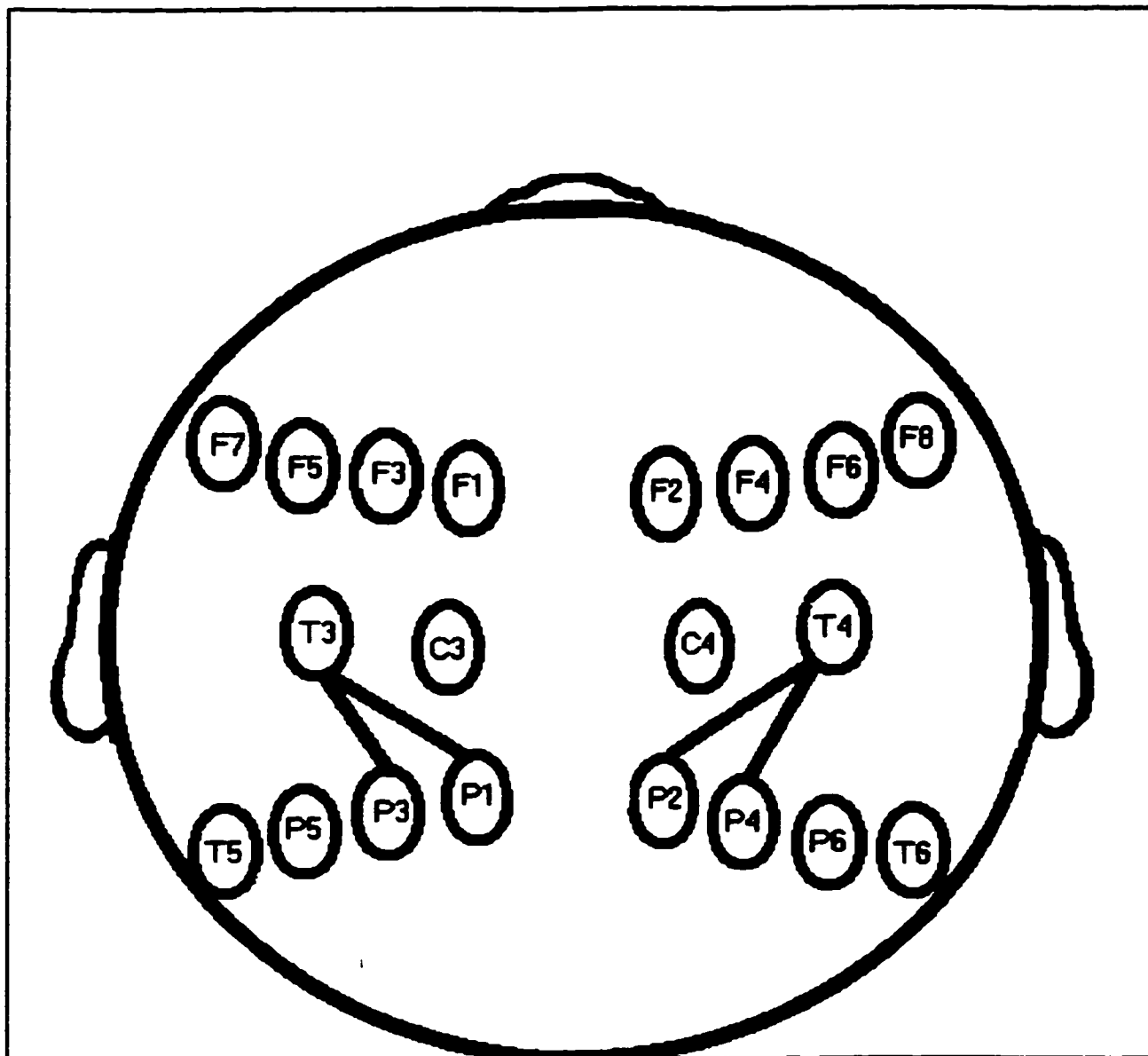
FIGURE 13. VENTRAL CENTRAL - VENTRAL POSTERIOR COHERENCE PAIRINGS.
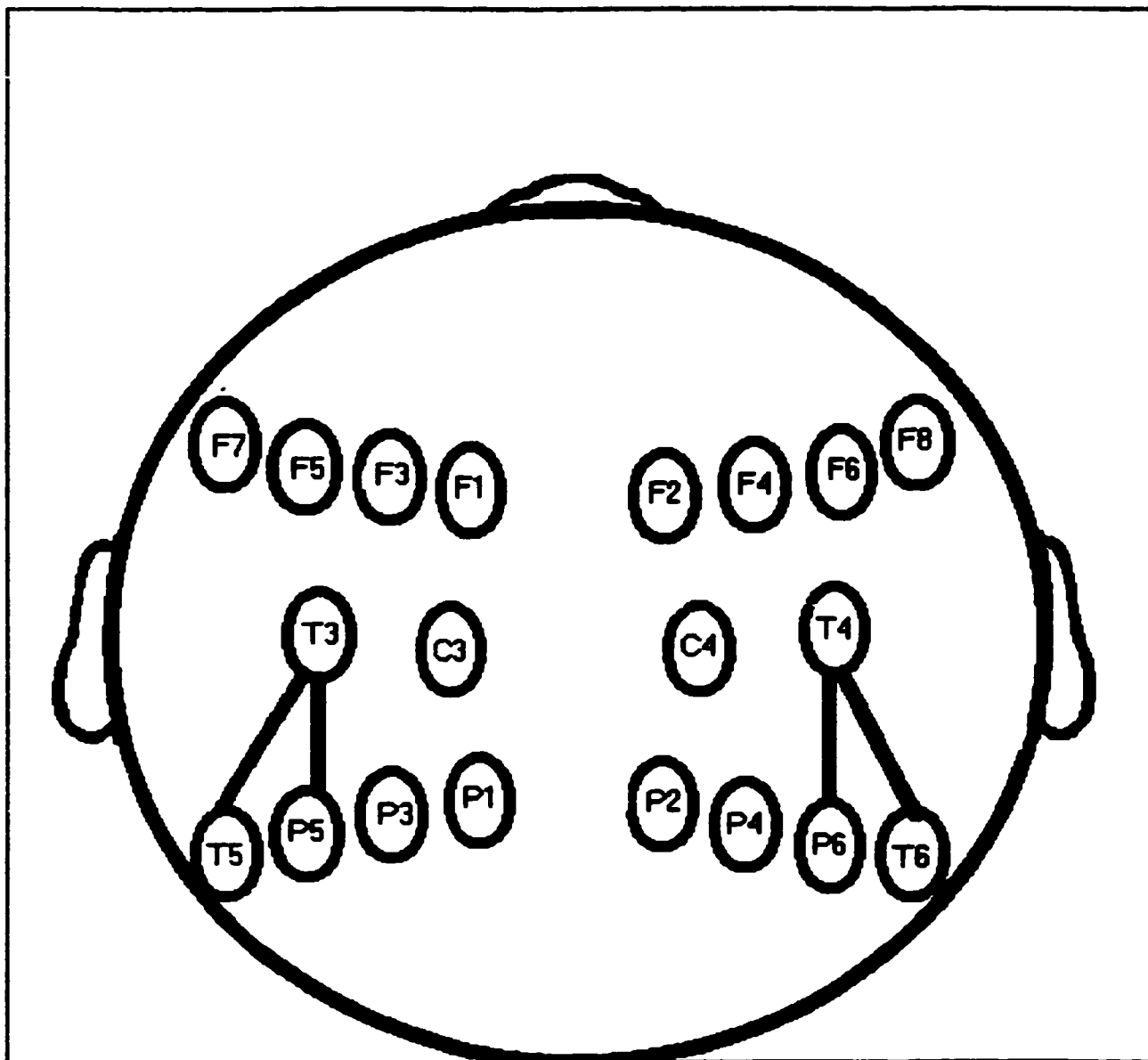
APPENDIX C

TASK INSTRUCTIONS

0-Spatial Back

In this task, you are to press the space bar every time you see a letter appear in the top, center space on the screen. It does not matter what letter it is that you see, as long as it is in the top center space, you press the space bar. Do you understand? The letters are going to appear in many different places on the screen and quite quickly, so pay careful attention.

1-Spatial Back

In this task, you are matching the spaces that appear 1-back in the series. You are to press the space bar every time you see a letter appear in a space that matches the space the letter just before was presented in. In other words, when a letter appears in a space two times in a row, you are to press the space bar. Again, it does not matter what the letters are, just pay attention to the spaces the letters are appearing in. So if you see the letter 'B' in the center space, and then the letter 'D' in the center space, you are to press the space bar. Do you understand?

2-Spatial Back

This time you are matching the spaces that appear 2-back in the series. You are to press the space bar every time you see a letter appear in a space that matches the space the letter was in two letters before. In other words, when a letter appears in a space, and then in a different space, and then in that first space again, you are to press the space bar. Again, it does not matter what the letters are, just pay attention to the spaces the letters are appearing in. So if you see the letter 'B' in the center space, and then the letter 'C' in the top right space, and then the letter 'D' in the center space, this is matching two spaces back and you are to press the space bar. Do you understand?

3-Spatial Back

This time you are matching the spaces that appear 3-back in the series. You are to press the space bar every time you see a letter appear in a space that matches the space the letter was in three letters before. In other words, when a letter appears in a space, then in a different space, and then another different space, and then in that first space again, you are to press the space bar. Again, it does not matter what the letters are, just pay attention to the spaces the letters are appearing in. So if you see the letter 'B' in the center space, then the letter 'C' in the top right space, then the letter 'P' in the bottom center space, and then the letter 'D' in the center space, this is matching three spaces back and you are to press the space bar. Do you understand?

0-Verbal Back

In this task, you are to press the space bar every time you see the letter 'B' appear. It does not matter what space the 'B' appears in, just whenever you see that letter you press the space bar. Do you understand? The letters are going to appear in many different places on the screen and quite quickly, so pay careful attention.

1-Verbal Back

In this task, you are matching the letters that appear 1-back in the series. You are to press the space bar every time you see a letter appear that matches the letter seen just before. In other words, when a letter appears two times in a row, you are to press the space bar. Again, it does not matter what spaces the letters are seen in, just pay attention to the letters that are appearing. So if you see the letter 'B' in the center space, and then the letter 'B' again but in the top left space, you are to press the space bar. Do you understand?
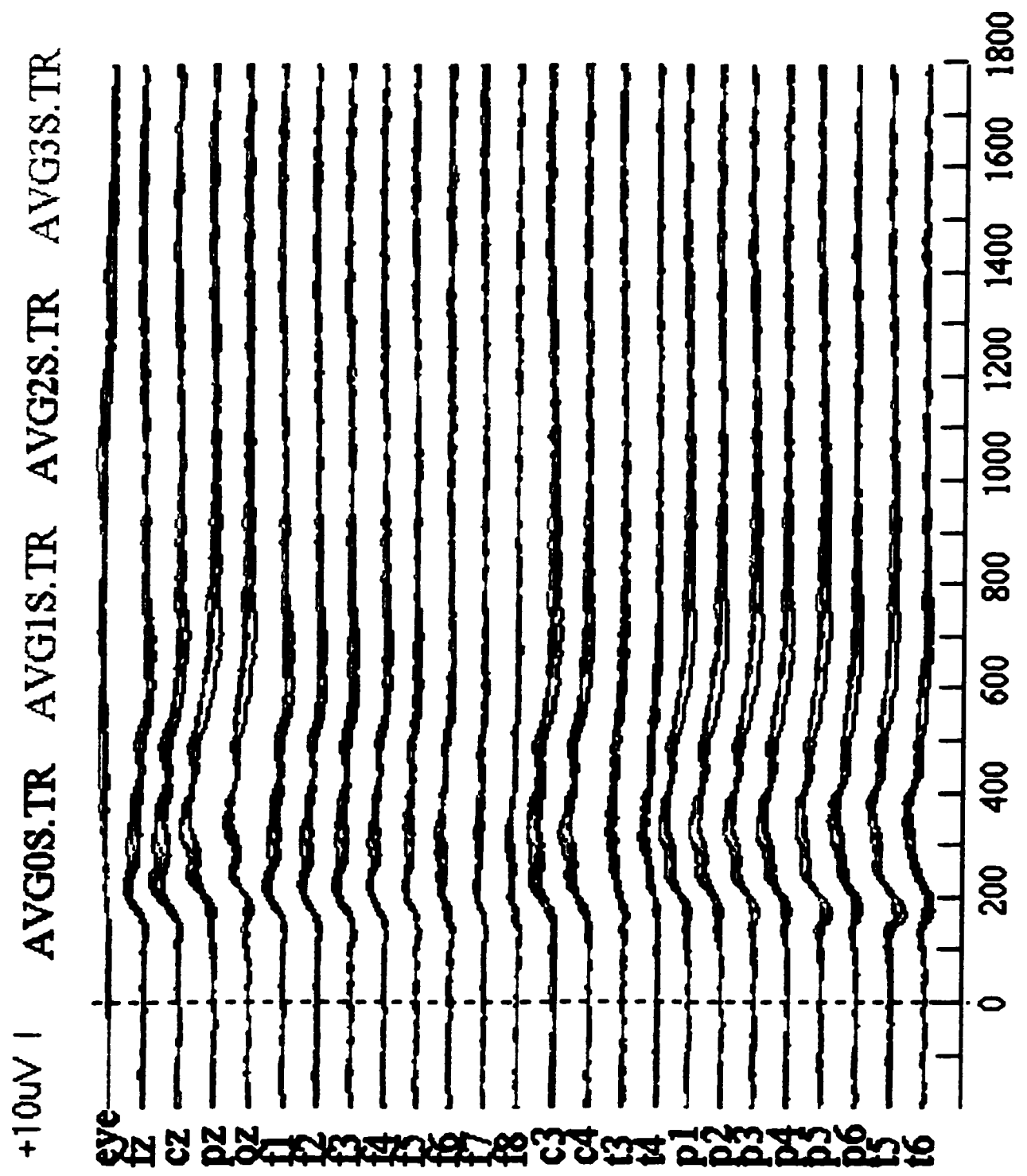
2-Verbal Back

This time you are matching the letter that appear 2-back in the series. You are to press the space bar every time you see a letter appear that matches the letter that was seen two letters before. In other words, when a letter appears, then a different letter appears, and then the first letter is seen again, you are to press the space bar. Again, it does not matter what spaces the letters are in, just pay attention to the letters that are appearing. So if you see the letter 'C' in the center space, and then the letter 'B' in the top right space, and then the letter 'C' in the bottom left space, this is matching two letters back and you are to press the space bar. Do you understand?

3-Verbal Back

This time you are matching the letter that appear 3-back in the series. You are to press the space bar every time you see a letter appear that matches the letter seen three letters before. In other words, when a letter appears, then a different letters appears, and then another different letter appears, and then that first letter is seen again, you are to press the space bar. Again, it does not matter what spaces the letters are seen in, just pay attention to the letters that are appearing. So if you see the letter 'C' in the center space, then the letter 'B' in the top right space, then the letter 'P' in the center space, and then the letter 'C' in the bottom left space, this is matching three letters back and you are to press the space bar. Do you understand?

APPENDIX D

ERP WAVEFORMS

Group Averaged ERPs to Verbal 0,1,2, and 3 back task

+10uV | AVG0V.TR   AVG1V.TR   AVG2V.TR   AVG3V.TR
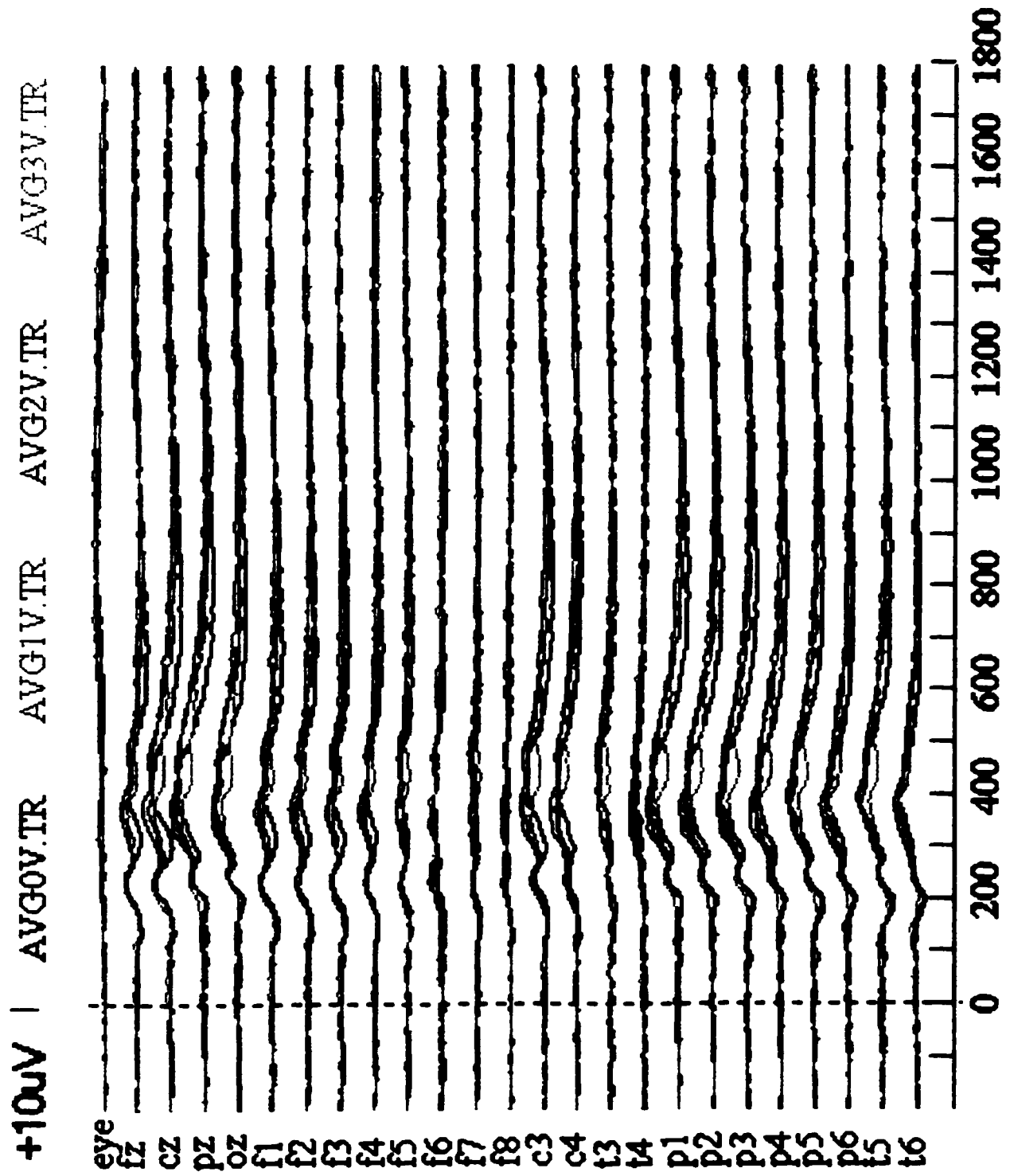
Group Averaged ERPs to Spatial 0,1,2, and 3 back task

+10uV | AVG0S.TR   AVG1S.TR   AVG2S.TR   AVG3S.TR

APPENDIX E

TABLES

Table 1. Behavioural Data for the n-Back Tasks Across Levels of Difficulty: Mean (Standard Deviation) of Total Trials Correct, Total Commission Errors, Total Omission Errors and Reaction Time.

LEVEL OF DIFFICULTY	TOTAL CORRECT	COMMISSION ERRORS	OMISSION ERRORS	REACTION TIME
0-Back	53.88 (.16)	.41 (.09)	.27 (.09)	469.85 (24.44)
1-Back	28.65 (.22)	.41 (.12)	25.35 (.22)	548.18 (29.83)
2-Back	24.68 (.63)	2.35 (.24)	29.27 (.65)	560.97 (28.61)
3-Back	15.50 (.80)	2.88 (.40)	38.50 (.80)	679.25 (37.46)

Table 2. Mean (Standard Deviation) P300 Latencies Across Posterior Sites at 4 Levels of WM load.

ELECTRODE SITE	0-BACK	1-BACK	2-BACK	3-BACK
P1/P2	344.02 (11.75)	341.97 (10.73)	336.81 (8.66)	342.32 (9.09)
P3/P4	343.82 (11.34)	341.85 (11.47)	337.19 (8.75)	346.13 (9.34)
P5/P6	344.04 (10.77)	349.22 (11.66)	341.13 (8.65)	351.91 (9.87)
T5/T6	346.46 (11.16)	357.02 (12.43)	351.66 (8.97)	351.74 (8.35)

Table 3. Mean (Standard Deviation) of Area Under the Curve at Frontal Sites at Each Level of WM Load - 600-900 ms (Time 2)

LEVEL OF WM LOAD	AREA UNDER THE CURVE
0-BACK	-.24 (.34)
1-BACK	.54 (.46)
2-BACK	-.71 (.47)
3-BACK	.58 (.37)

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Table 4. Mean (Standard Deviation) of Area Under the Curve of Ventral and Dorsal Frontal Sites.

ELECTRODE	TIME 1 (300-600 ms)	TIME 2 (600-900 ms)	TIME 4 (1200-1500 ms)
F1/F2	2.13 (.54)	-.45 (.44)	1.43 (.32)
F3/F4	2.31 (.48)	-.01 (.39)	1.42 (.34)
F5/F6	2.1 (.44)	.24 (.30)	.98 (.29)
F7/F8	1.4 (.30)	.44 (.21)	.72 (.22)

Table 5. Mean (Standard Deviation) of Area Under the Curve At Posterior Sites Across Levels of Wm Load.

LEVEL OF WM LOAD	AREA AT TIME 2 (600 to 900 ms)	AREA AT TIME 3 (900 to 1200 ms)
0-BACK	.035 (.45)	-.026 (.36)
1-BACK	1.82 (.45)	1.06 (.44)
2-BACK	-.53 (.55)	-.46 (.43)
3-BACK	1.27 (.51)	.21 (.54)

Table 6. Mean (Standard Deviation) of Area Under the Curve At Posterior Sites Across Levels of Wm Load for the Verbal and Spatial Back Tasks.

LEVEL OF WM LOAD	TIME 1 (300-600 ms)		TIME 2 (600-900 ms)	
	VERBAL BACK	SPATIAL BACK	VERBAL BACK	SPATIAL BACK
0-BACK	5.79 (.82)	4.49 (.84)	1.05 (.53)	-.98 (.48)
1-BACK	6.86 (.94)	6.92 (.87)	2.23 (.48)	1.51 (.63)
2-BACK	6.85 (.81)	5.23 (.87)	.55 (.70)	-1.61 (.51)
3-BACK	4.40 (.109)	7.21 (.76)	1.09 (.76)	1.45 (.48)

Table 7. Mean (Standard Deviation) of Area Under the Curve At Posterior Ventral-Dorsal Sites.

ELECTRODE SITE	TIME 1 (300-600 ms)	TIME 2 (600-900 ms)	TIME 4 (1200-1500 ms)
P1/P2	7.19 (.75)	.92 (.44)	1.22 (.35)
P3/P4	6.76 (.74)	.92 (.43)	1.25 (.35)
P5/P6	5.59 (.65)	.63 (.39)	1.00 (.31)
T5/T6	4.33 (.54)	.12 (.33)	.71 (.26)

Table 8. Mean (Standard Deviation) of Reaction Times for the Spatial and Verbal n-Back Tasks Across Levels of Difficulty

LEVEL OF DIFFICULTY	SPATIAL-BACK TASKS	VERBAL-BACK TASKS
0-Back	449.51 (26.11)	490.19 (24.25)
1-Back	548.28 (34.61)	548.08 (28.75)
2-Back	528.48 (26.58)	593.47 (33.98)
3-Back	617.93 (41.03)	740.57 (39.64)

Table 9. Percentage of Total Correct and Omission Errors for the Spatial and Non-Spatial n-Back Tasks Across Levels of Difficulty

LEVEL OF DIFFICULTY	TOTAL # CORRECT		OMISSION ERRORS	
	SPATIAL	NON-SPATIAL	SPATIAL	NON- SPATIAL
0-Back	99.46 %	100 %	.32 %	.25 %
1-Back	54.15 %	51.96 %	26.71 %	27.58 %
2-Back	46.19 %	45.20 %	31.21 %	31.46 %
3-Back	28.31 %	29.09 %	41.75 %	40.71 %

Table 10. Mean (Standard Deviation) Posterior Alpha and Beta FFT Values for Verbal and Spatial n-Back Tasks

ELECTRODE SITE	SPATIAL TASKS		VERBAL TASKS	
	MEAN ALPHA	MEAN BETA	MEAN ALPHA	MEAN BETA
P1/P2	7.76 (.72)	13.86 (.75)	7.27 (.61)	14.11 (.77)
P3/P4	7.65 (.70)	13.92 (.76)	7.19 (60)	14.18 (.79)
P5/P6	7.41 (.65)	13.95 (.73)	6.99 (.57)	14.27 (.81)
T5/T6	6.99 (.62)	13.75 (.77)	6.69 (.54)	14.52 (.89)

Table 11. Alpha and Beta Mean (Standard Deviation) Coherence Values of Dorsal Frontal Paired with Dorsal Posterior versus Dorsal Frontal Paired with Ventral Posterior Electrode Sites for Verbal and Spatial n-Back Tasks Combined

LOCATION	ELECTRODE PAIR	MEAN COHERENCE VALUE	
		ALPHA	BETA
Dorsal Frontal with Dorsal Posterior	F1-P1	.542 (.022)	.536 (.026)
	F1-P3	.533 (.021)	.520 (.025)
	F3-P1	.535 (.021)	.471 (.028)
	F3-P3	.539 (.021)	.468 (.027)
	F2-P2	.527 (.022)	.503 (.028)
	F2-P4	.511 (.023)	.485 (.029)
	F4-P2	.517 (.022)	.457 (.029)
	F4-P4	.508 (.023)	.446 (.030)
Dorsal Frontal with Ventral Posterior	F1-P5	.469 (.023)	.451 (.028)
	F1-T5	.421 (.021)	.396 (.026)
	F3-P5	.481 (.023)	.409 (.028)
	F3-T5	.440 (.022)	.365 (.026)
	F2-P6	.448 (.025)	.418 (.029)
	F2-T6	.380 (.028)	.340 (.033)
	F4-P6	.448 (.025)	.386 (.030)
	F4-T6	.384 (.029)	.320 (.033)

Table 12. Alpha and Beta Mean (Standard Deviation) Coherence Values of Ventral Frontal Paired with Dorsal Posterior versus Ventral Frontal Paired with Ventral Posterior Electrode Sites for Verbal and Spatial n-Back Tasks Combined

LOCATION	ELECTRODE PAIR	MEAN COHERENCE VALUE	
		ALPHA	BETA
Ventral Frontal with Dorsal Posterior	F5-P1	.492 (.019)	.394 (.024)
	F5-P3	.517 (.018)	.404 (.024)
	F7-P1	.431 (.020)	.411 (.024)
	F7-P3	.466 (.020)	.431 (.027)
	F6-P2	.369 (.023)	.277 (.019)
	F6-P4	.373 (.022)	.279 (.020)
	F8-P2	.415 (.019)	.361 (.021)
	F8-P4	.431 (.020)	.369 (.023)
Ventral Frontal with Ventral Posterior	F5-P5	.488 (.019)	.369 (.024)
	F5-T5	.468 (.019)	.341 (.023)
	F7-P5	.461 (.019)	.408 (.026)
	F7-T5	.469 (.020)	.395 (.026)
	F6-P6	.347 (.023)	.253 (.020)
	F6-T6	.312 (.026)	.216 (.021)
	F8-P6	.420 (.021)	.350 (.024)
	F8-T6	.400 (.026)	.317 (.027)

Table 13. Mean (Standard Deviation) FFT Values for Alpha and Beta Bandwidths for Ventral and Dorsal Posterior Sites in Both Hemispheres.

ELECTRODE PAIRS	ALPHA BAND		BETA BAND	
	LEFT HEMISPHERE	RIGHT HEMISPHERE	LEFT HEMISPHERE	RIGHT HEMISPHERE
P1/P2	7.71 (.65)	7.51 (.68)	14.08 (.79)	13.89 (.73)
P3/P4	7.56 (.63)	7.28 (.67)	14.45 (.81)	13.66 (.73)
P5/P6	7.53 (.60)	6.87 (.62)	14.84 (.82)	13.76 (.74)
T5/T6	7.26 (.57)	6.42 (.60)	15.05 (.89)	13.23 (.76)

Table 14. Mean (Standard Deviation) Frontal-Posterior Coherence Vaules of Frontal Sites in the Left and Right Hemisphere.

ELECTRODE PAIRS	ALPHA BAND		BETA BAND	
	LEFT HEMISPHERE	RIGHT HEMISPHERE	LEFT HEMISPHERE	RIGHT HEMISPHERE
F1/F2	.50 (.02)	.47 (.02)	.48 (.03)	.44 (.03)
F3/F4	.50 (.02)	.47 (.02)	.43 (.03)	.40 (.03)
F5/F6	.50 (.02)	.35 (.02)	.38 (.02)	.26 (.02)
F7/F8	.46 (.02)	.42 (.02)	.41 (.03)	.35 (.02)

Table 15. Mean (Standard Deviation) Frontal-Posterior Coherence Vaules of Posterior Sites in the Left and Right Hemisphere.

ELECTRODE PAIRS	ALPHA BAND		BETA BAND	
	LEFT HEMISPHERE	RIGHT HEMISPHERE	LEFT HEMISPHERE	RIGHT HEMISPHERE
P1/P2	.50 (.02)	.46 (.02)	.45 (.02)	.40 (.02)
P3/P4	.51 (.02)	.46 (.02)	.46 (.02)	.40 (.02)
P5/P6	.48 (.02)	.42 (.02)	.41 (.02)	.35 (.02)
T5/T6	.45 (.02)	.37 (.03)	.37 (.02)	.30 (.03)

Table 16. Mean (Standard Deviation) Local Coherence Values for Alpha and Beta Bandwidths for Both Hemispheres.

ELECTRODE PAIRS	ALPHA BAND		BETA BAND	
	LEFT HEMISPHERE	RIGHT HEMISPHERE	LEFT HEMISPHERE	RIGHT HEMISPHERE
F1/F3 - F2/F4	.956 (.01)	.963 (.01)	.864 (.03)	.913 (.03)
F3/F5 - F4/F6	.883 (.02)	.677 (.04)	.691 (.05)	.506 (.04)
F5/F7 - F6/F8	.868 (.02)	.685 (.04)	.661 (.04)	.503 (.03)

APPENDIX F

GRAPHS

FIGURE 1. FRONTAL SPECTRAL ANALYSIS
OF TASK DIFFICULTY - BETA BANDWIDTH.

150
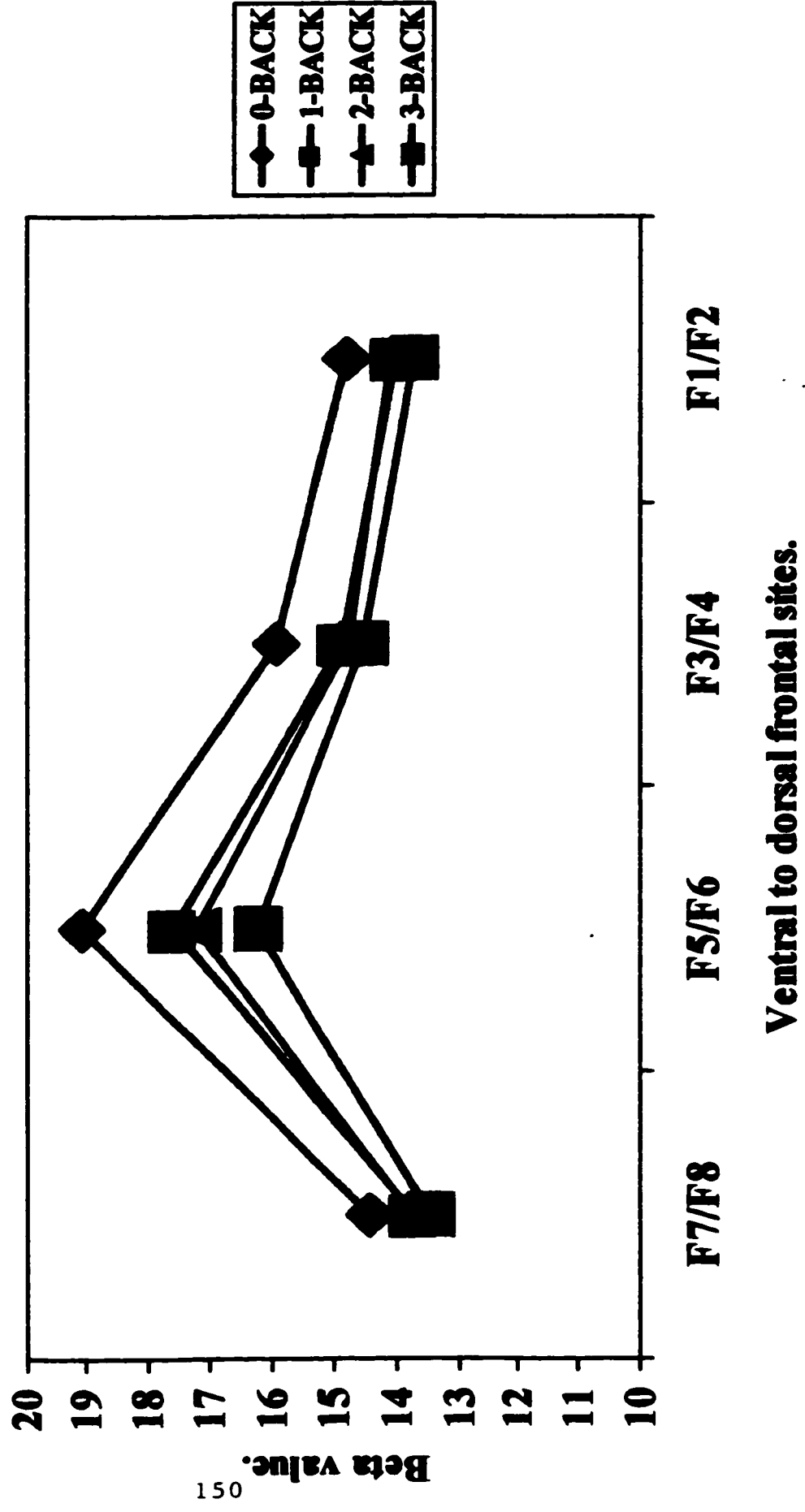
FIGURE 2. COHERENCE VALUES OF FRONTAL ELECTRODES ACROSS LEVELS OF WM LOAD - LEFT HEMISPHERE

FIGURE 3. P300 AMPLITUDE ANALYSIS OF FRONTAL AND POSTERIOR SITES.
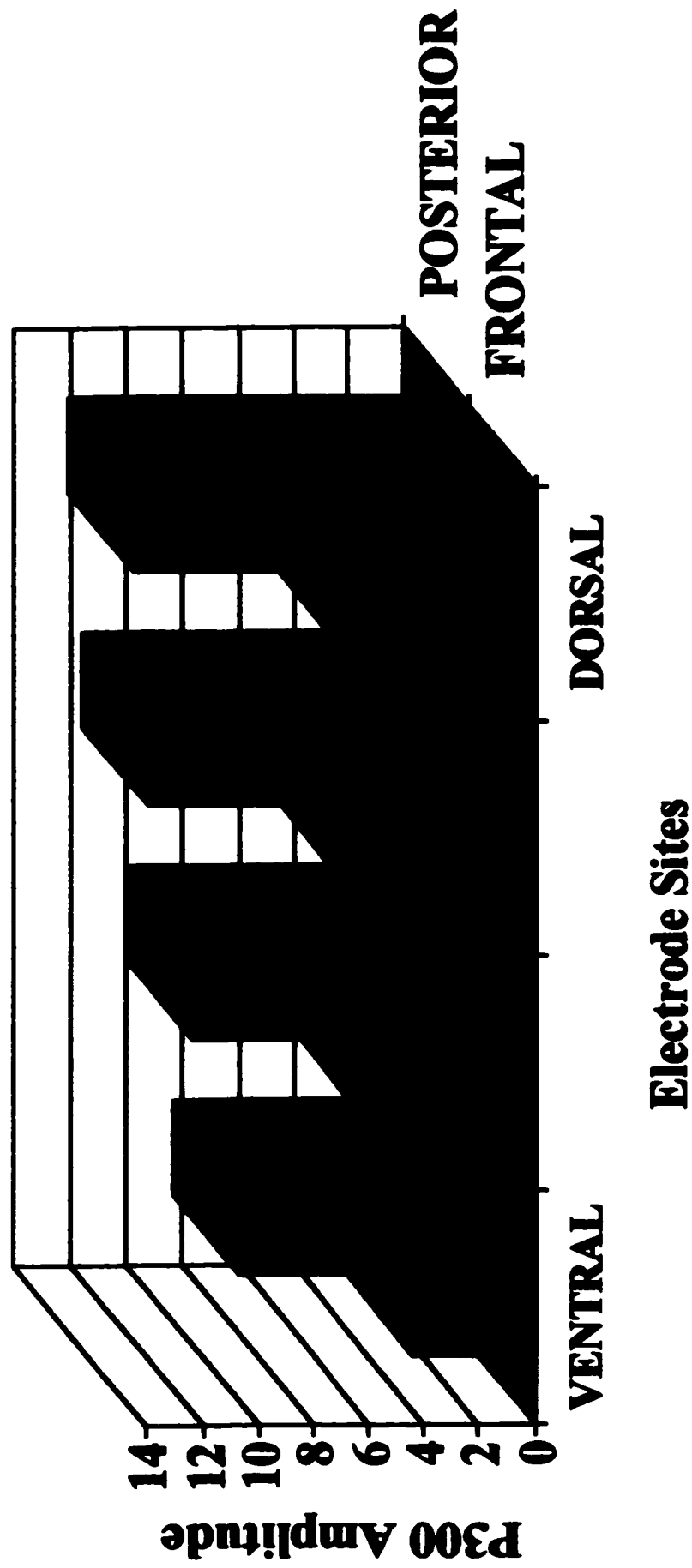
FIGURE 4. P300 LATENCY ANALYSIS OF POSTERIOR SITES.
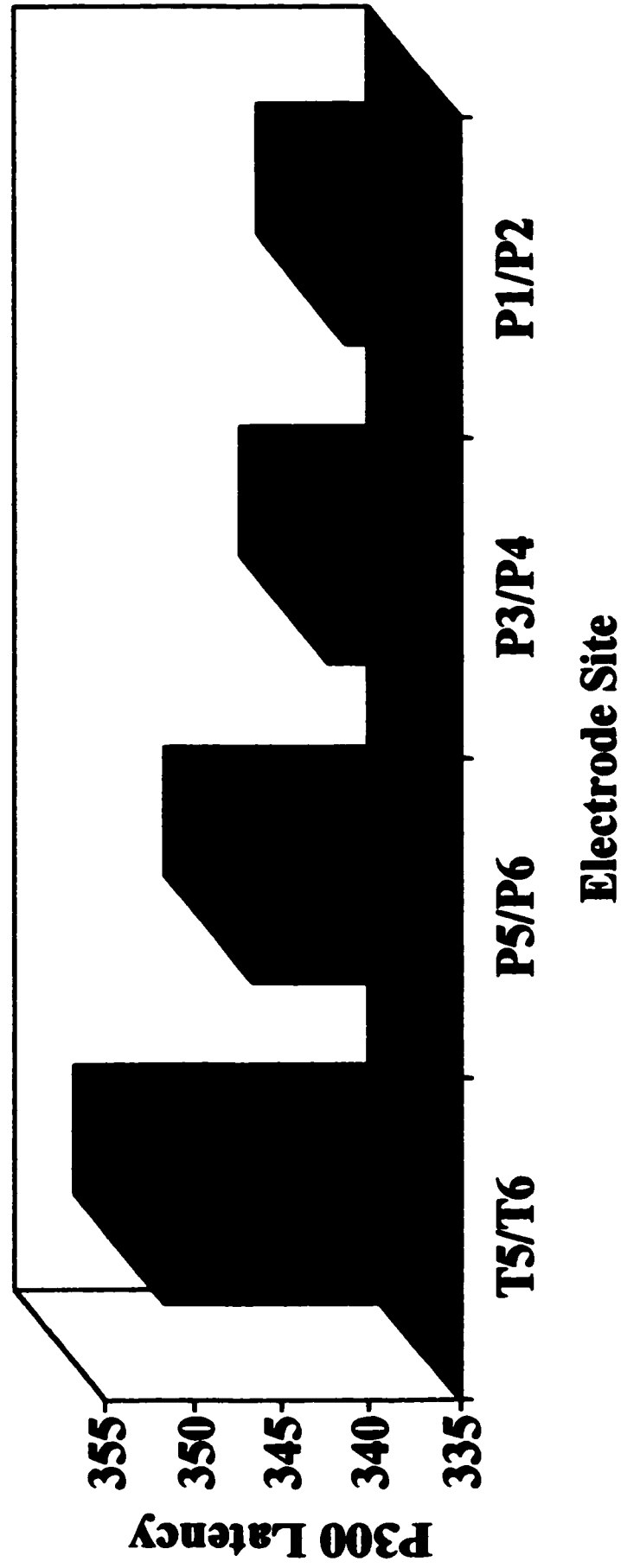
FIGURE 5. P300 AMPLITUDE ANALYSIS OF FRONTAL SITES BY LEVEL OF WM LOAD
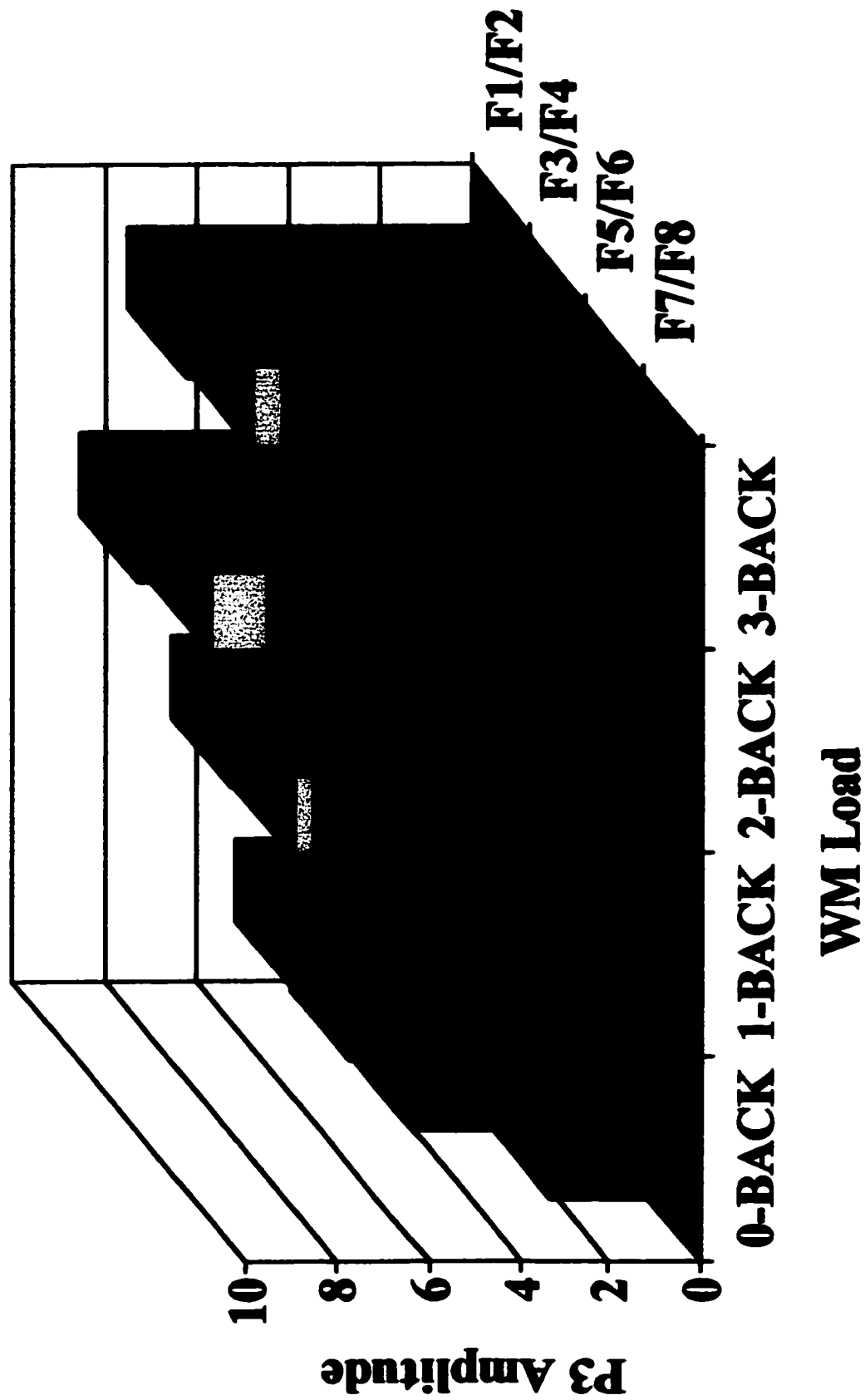
FIGURE 6. POSTERIOR P300 LATENCIES ACROSS TASKS AND WM LOAD
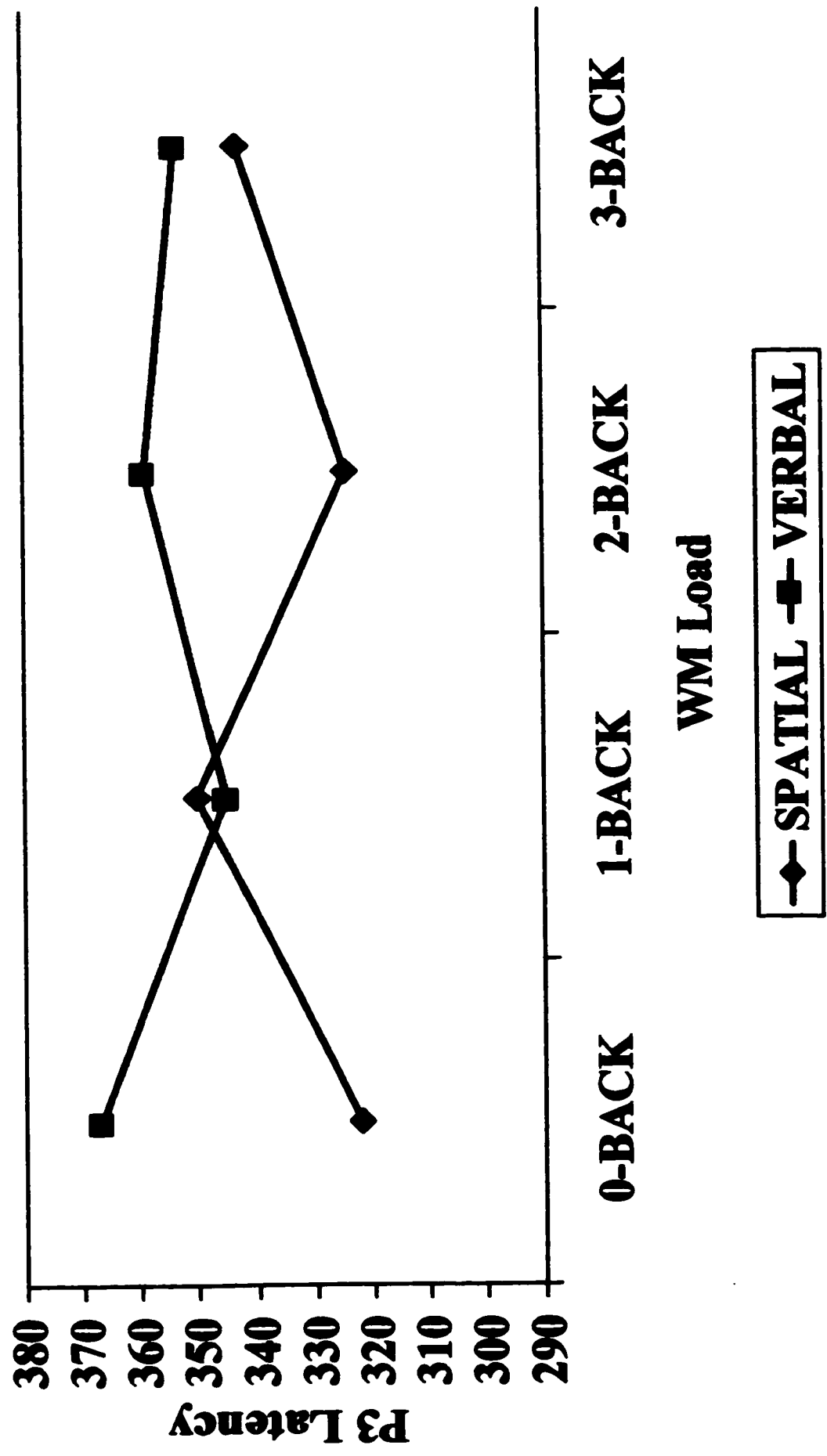
FIGURE 7. AREA UNDER THE CURVE ACROSS TASK AND WM LOAD (300-600 ms)
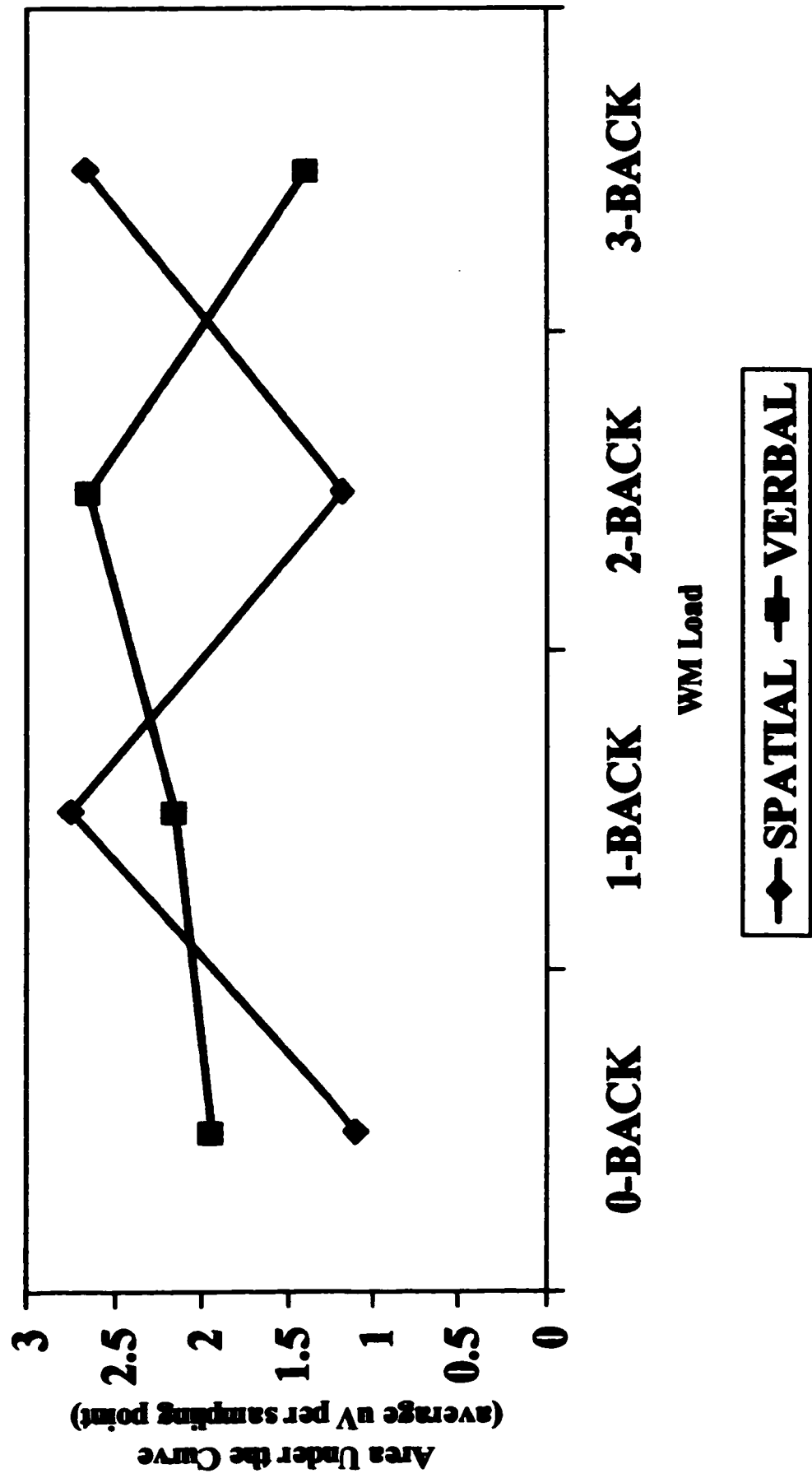
FIGURE 8. AREA UNDER THE CURVE AT FRONTAL SITES ACROSS LEVEL OF WM LOAD AND TASK (300-600 ms)
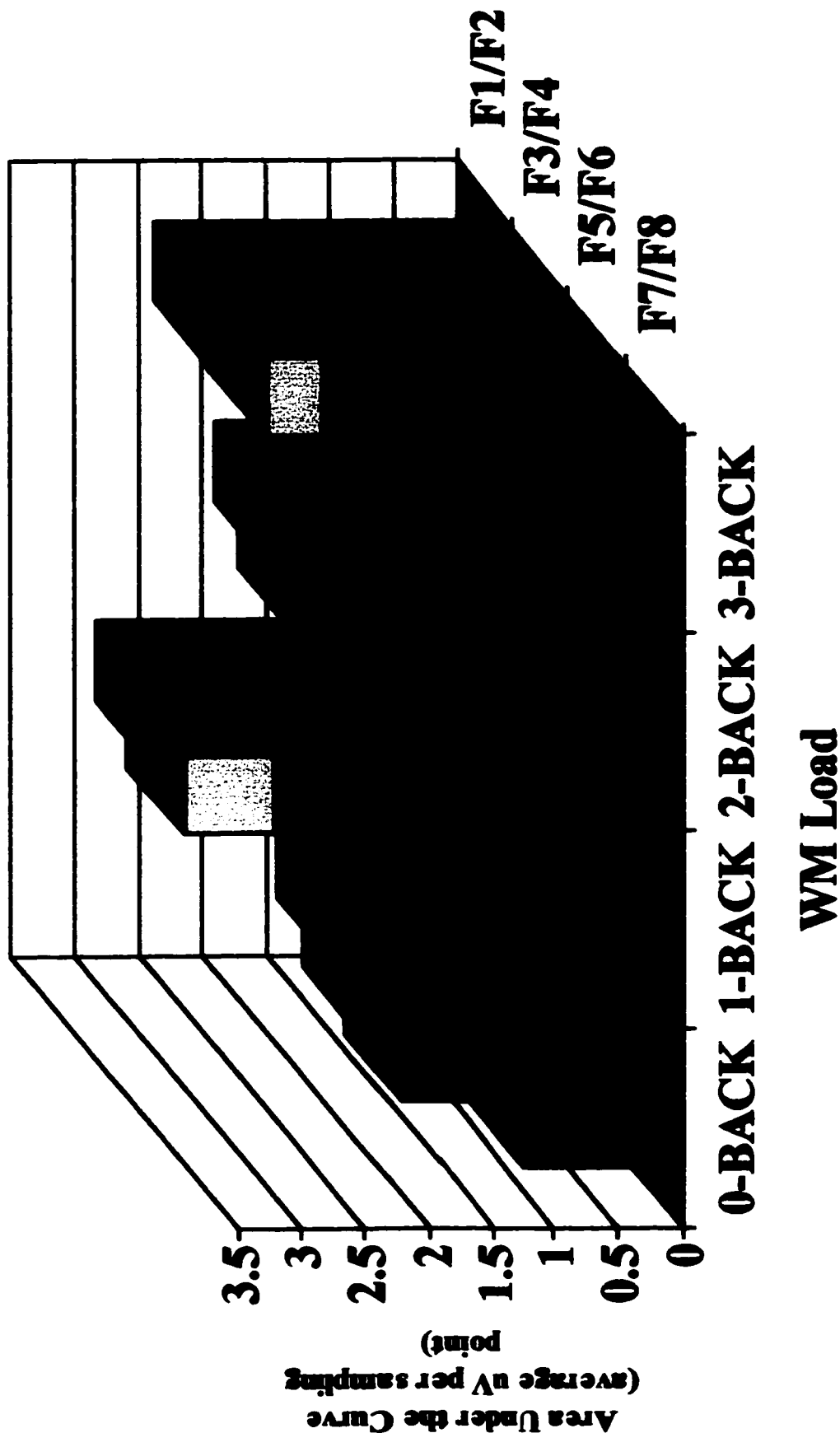
FIGURE 9. AREA UNDER THE CURVE AT FRONTAL SITES ACROSS LEVEL OF WM LOAD - SPATIAL TASK (300-600 ms)
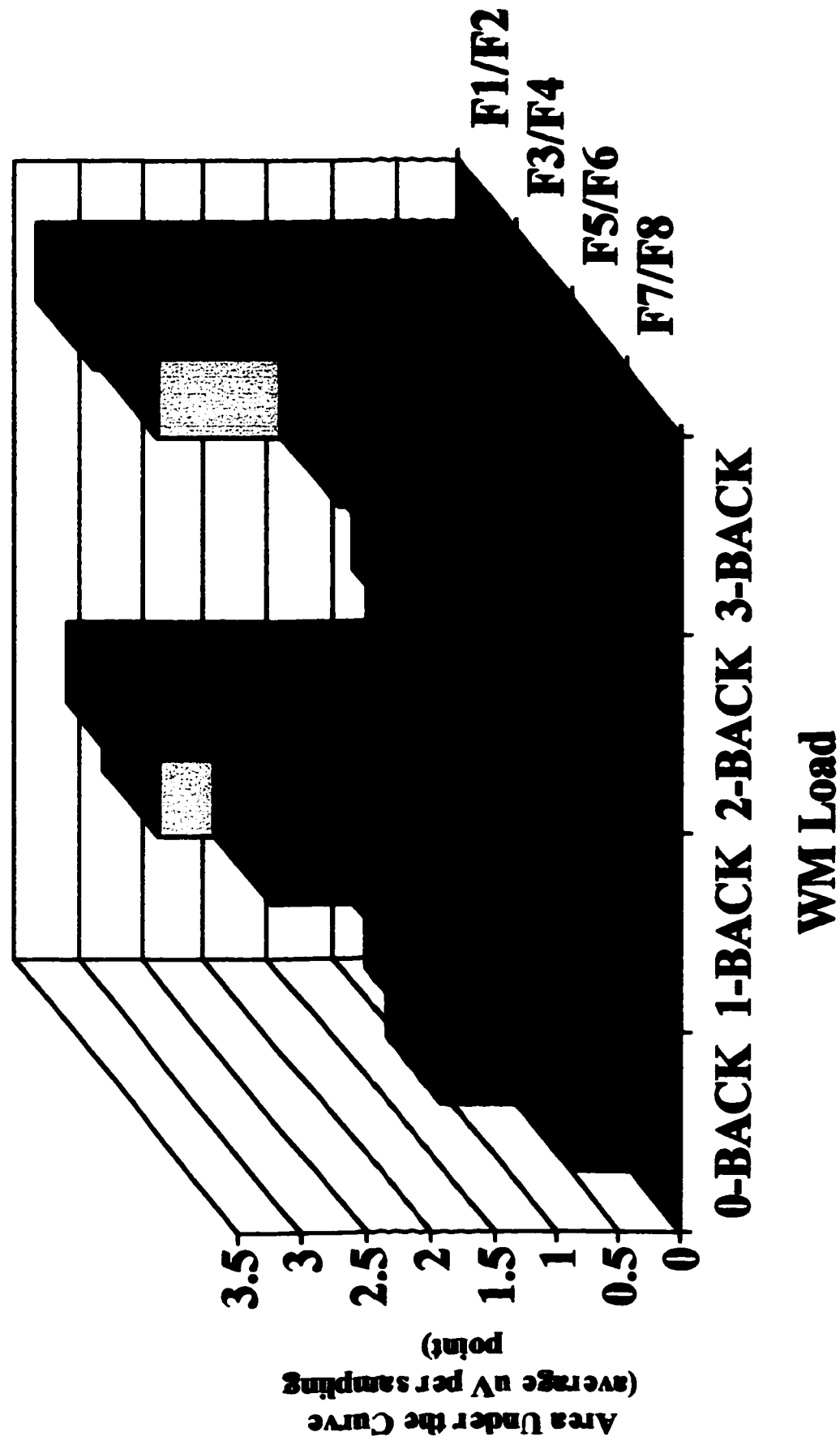
FIGURE 10. AREA UNDER THE CURVE AT FRONTAL SITES ACROSS LEVEL OF WM LOAD - VERBAL TASK (300-600 ms)
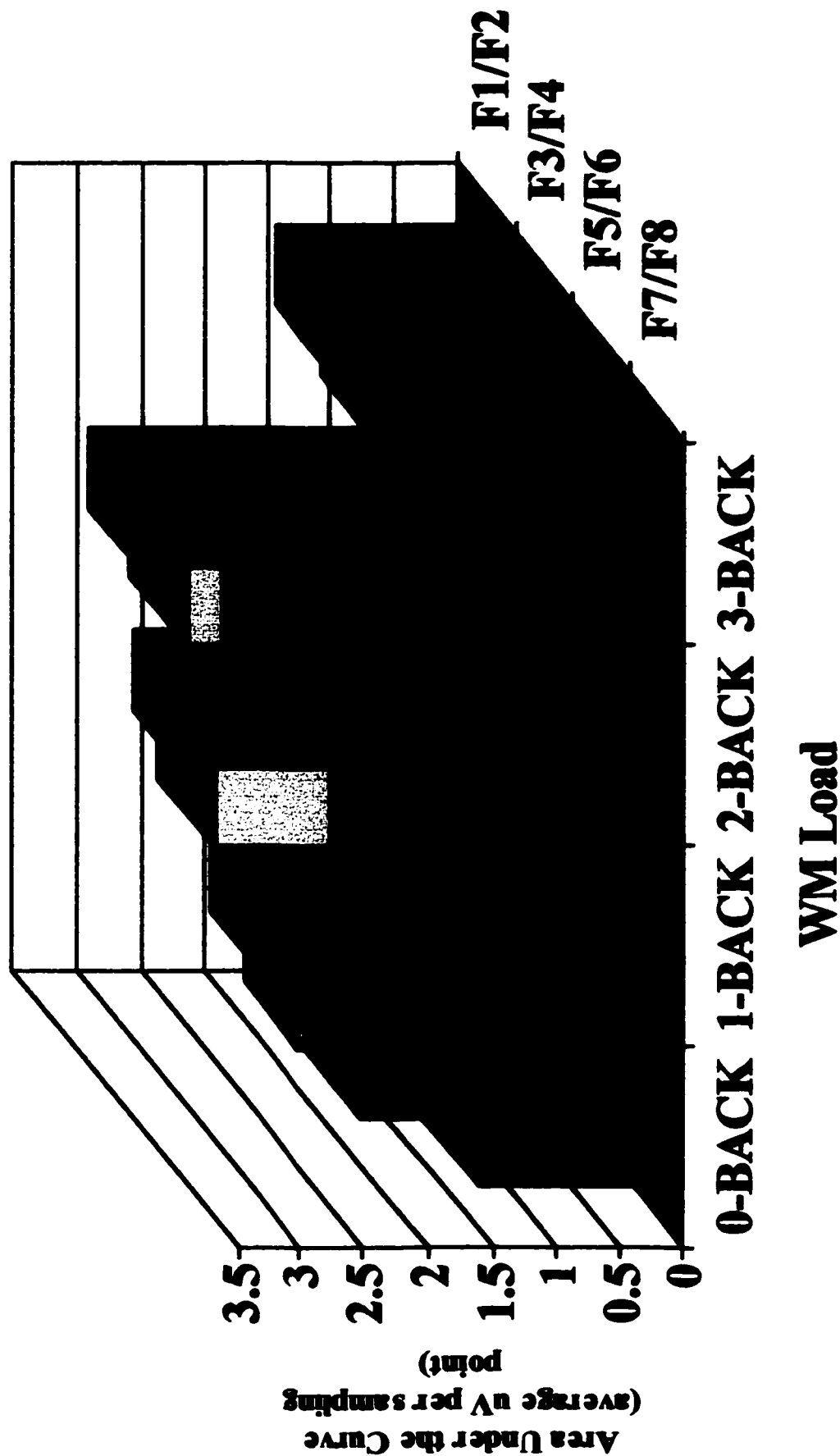
FIGURE 11. AREA UNDER THE CURVE ANALYSIS OF POSTERIOR SITES ACROSS TASKS (600-900 ms)
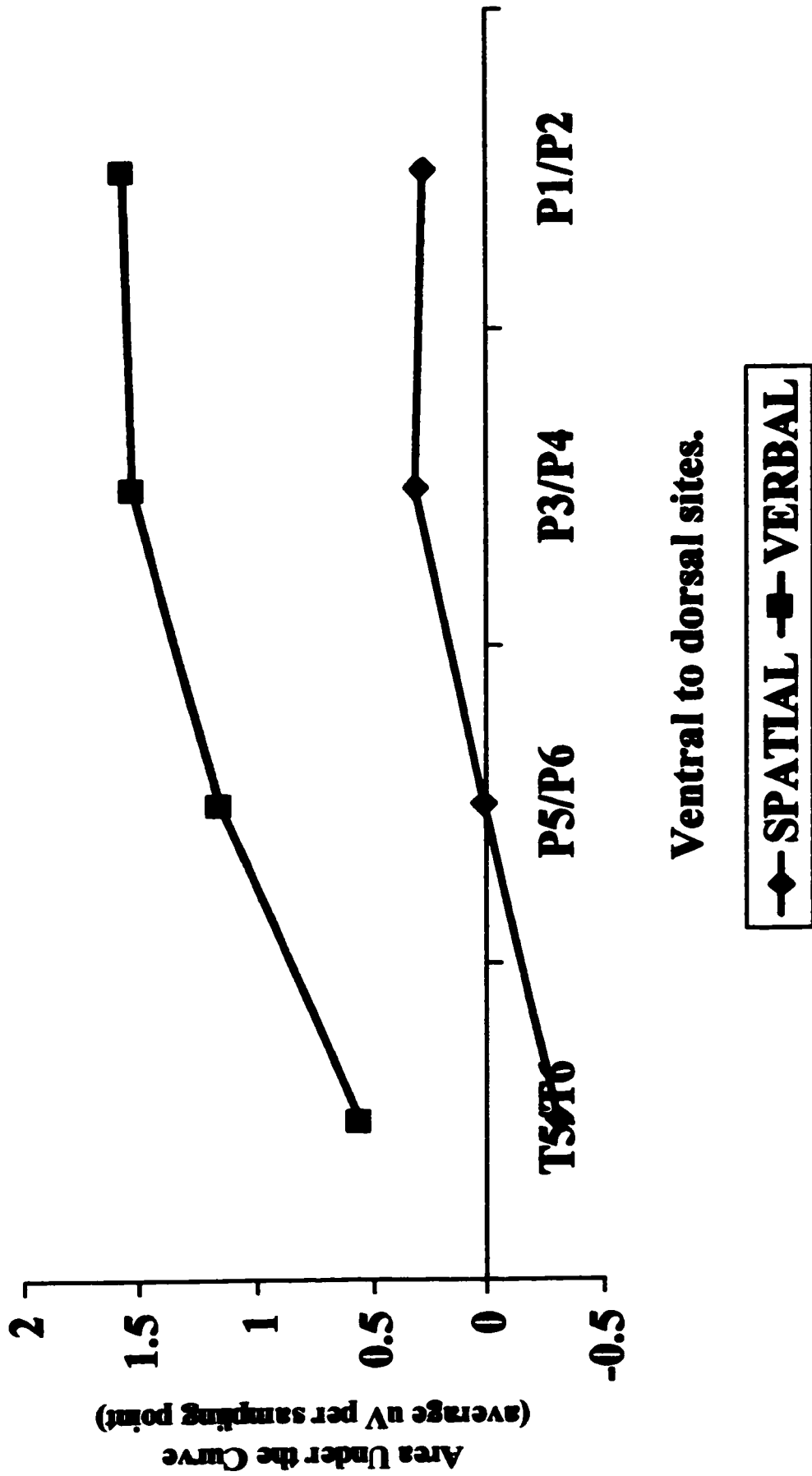
FIGURE 12. AREA UNDER THE CURVE AT POSTERIOR SITES ACROSS LEVEL OF WM LOAD - VERBAL TASK (300-600 ms)
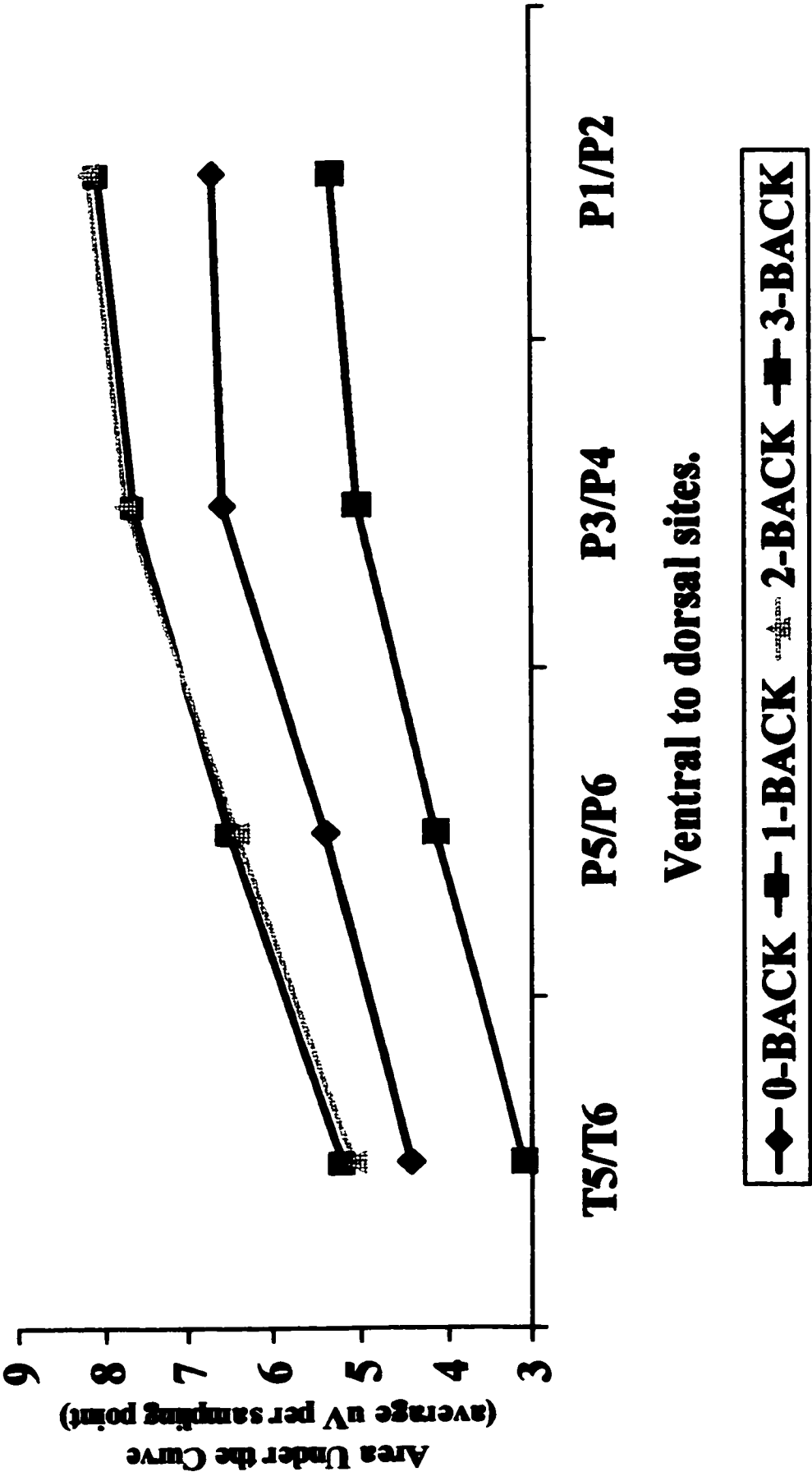
FIGURE 13. AREA UNDER THE CURVE AT POSTERIOR SITES ACROSS LEVEL OF WM LOAD - SPATIAL TASK (300-600 ms)

Ventral to dorsal sites.

0-BACK 1-BACK 2-BACK 3-BACK

Area Under the Curve (average uV per sampling point)

T5/T6   P5/P6   P3/P4   P1/P2
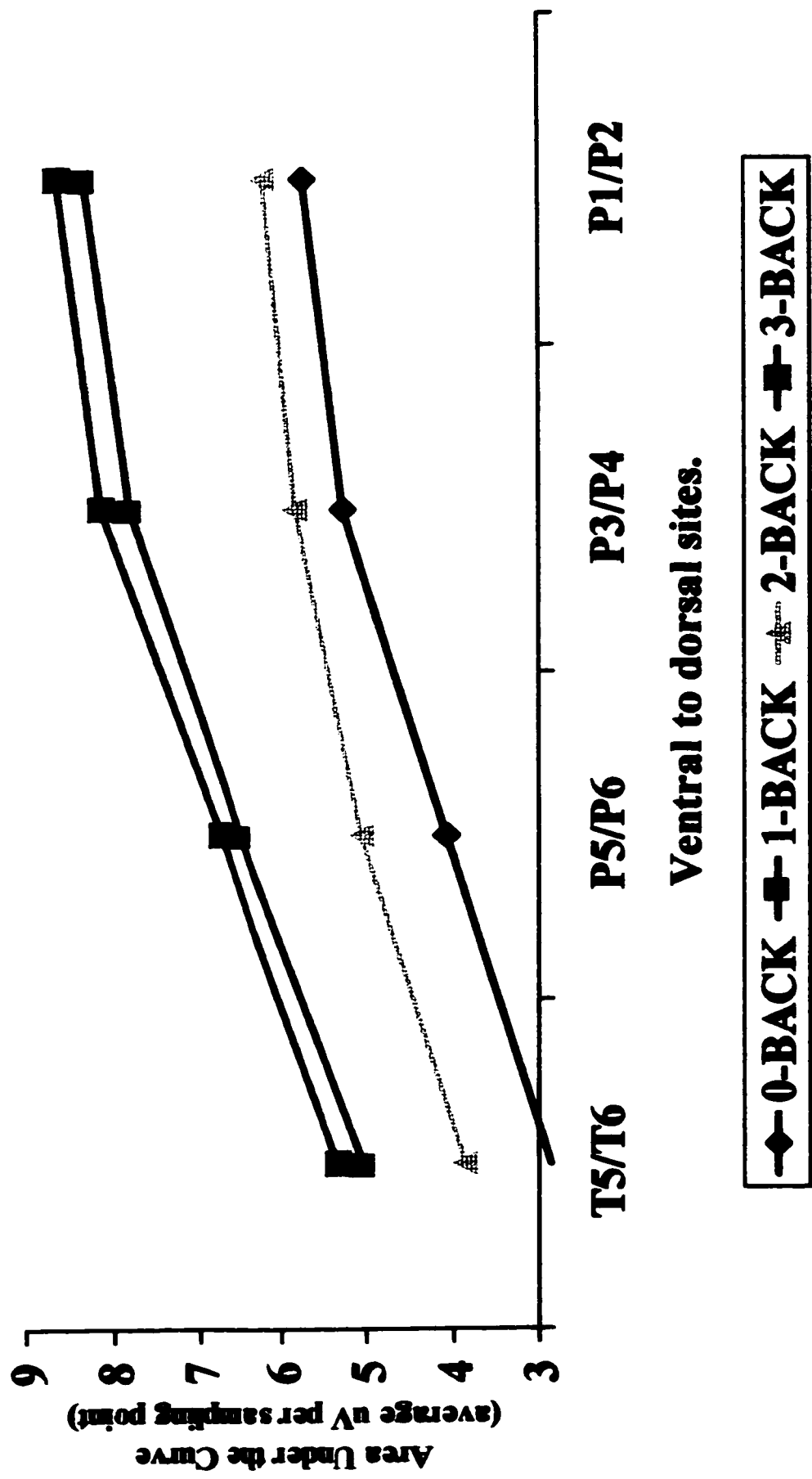
FIGURE 14. AREA UNDER THE CURVE AT POSTERIOR SITES ACROSS LEVELS OF WM LOAD - VERBAL TASK (600-900 ms)

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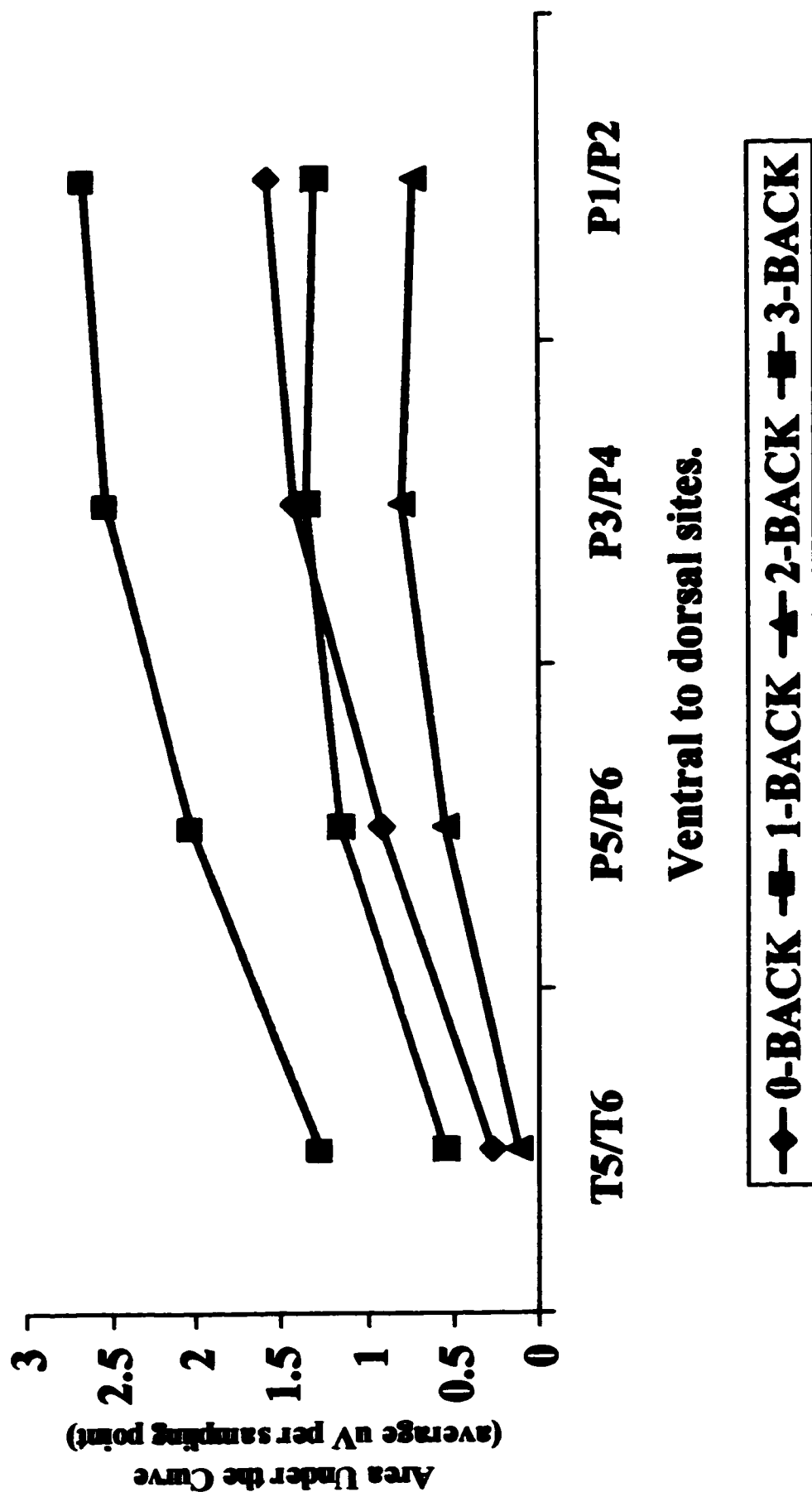
FIGURE 15. AREA UNDER THE CURVE AT POSTERIOR SITES ACROSS LEVELS OF WM LOAD - SPATIALTASK (600-900 ms)

Ventral to dorsal sites.

0-BACK 1-BACK 2-BACK 3-BACK

Area Under the Curve (average uV per sampling point)
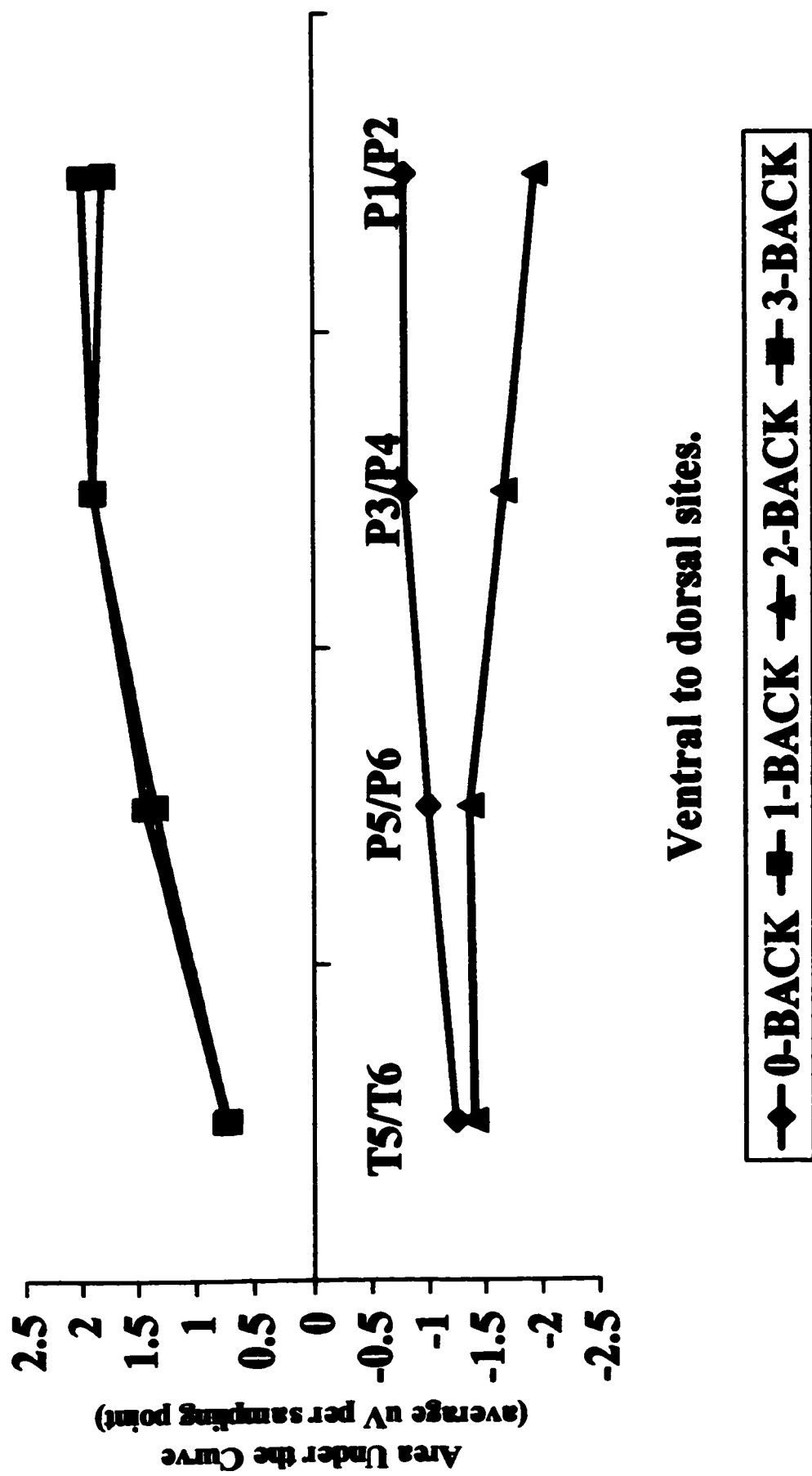
FIGURE 16. FRONTAL SPECTRAL ANALYSIS ACROSS TASKS - ALPHA BANDWIDTH.

Dorsal to ventral sites.
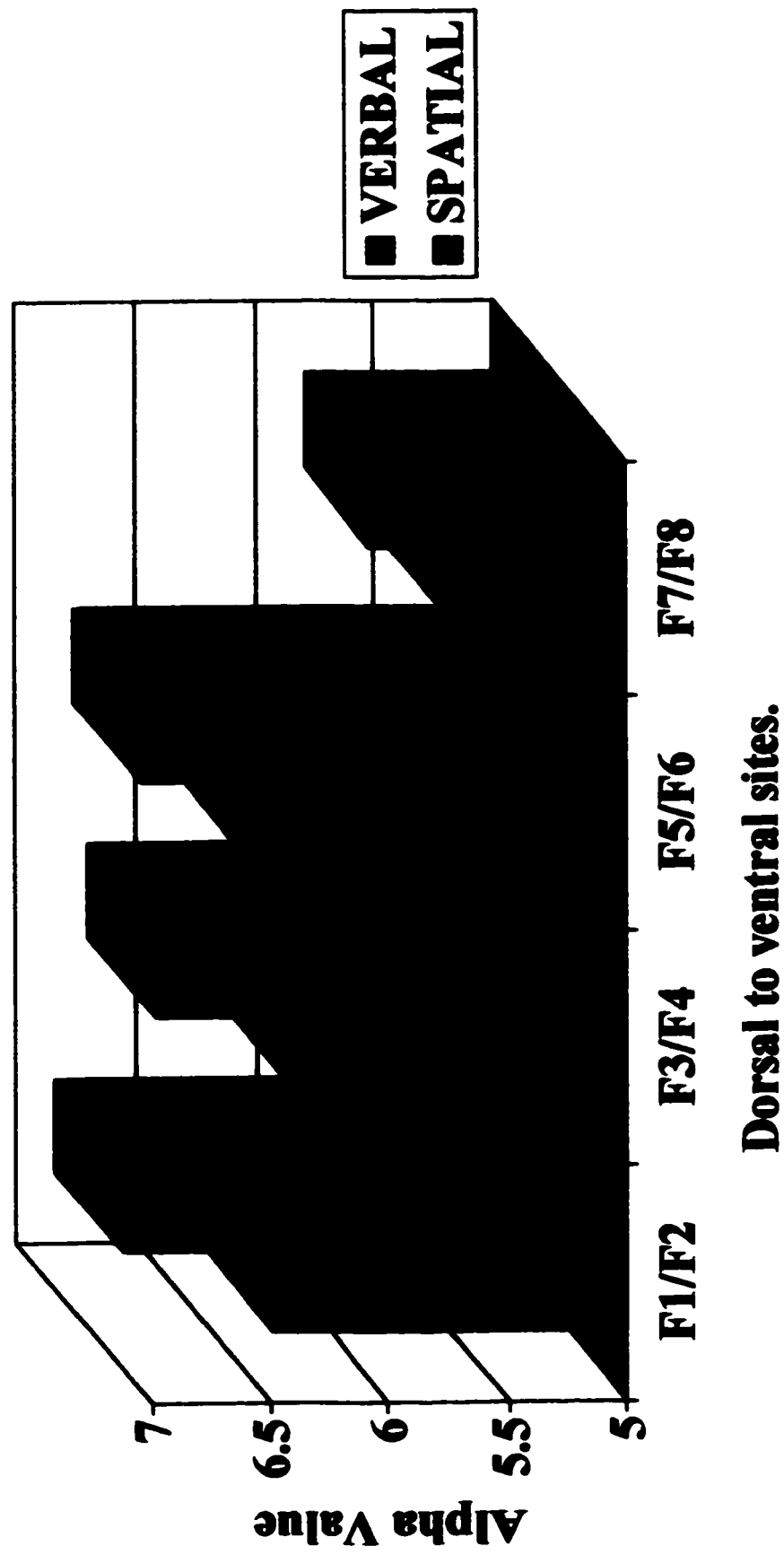
FIGURE 17. POSTERIOR SPECTRAL ANALYSIS ACROSS TASKS - BETA BANDWIDTH.
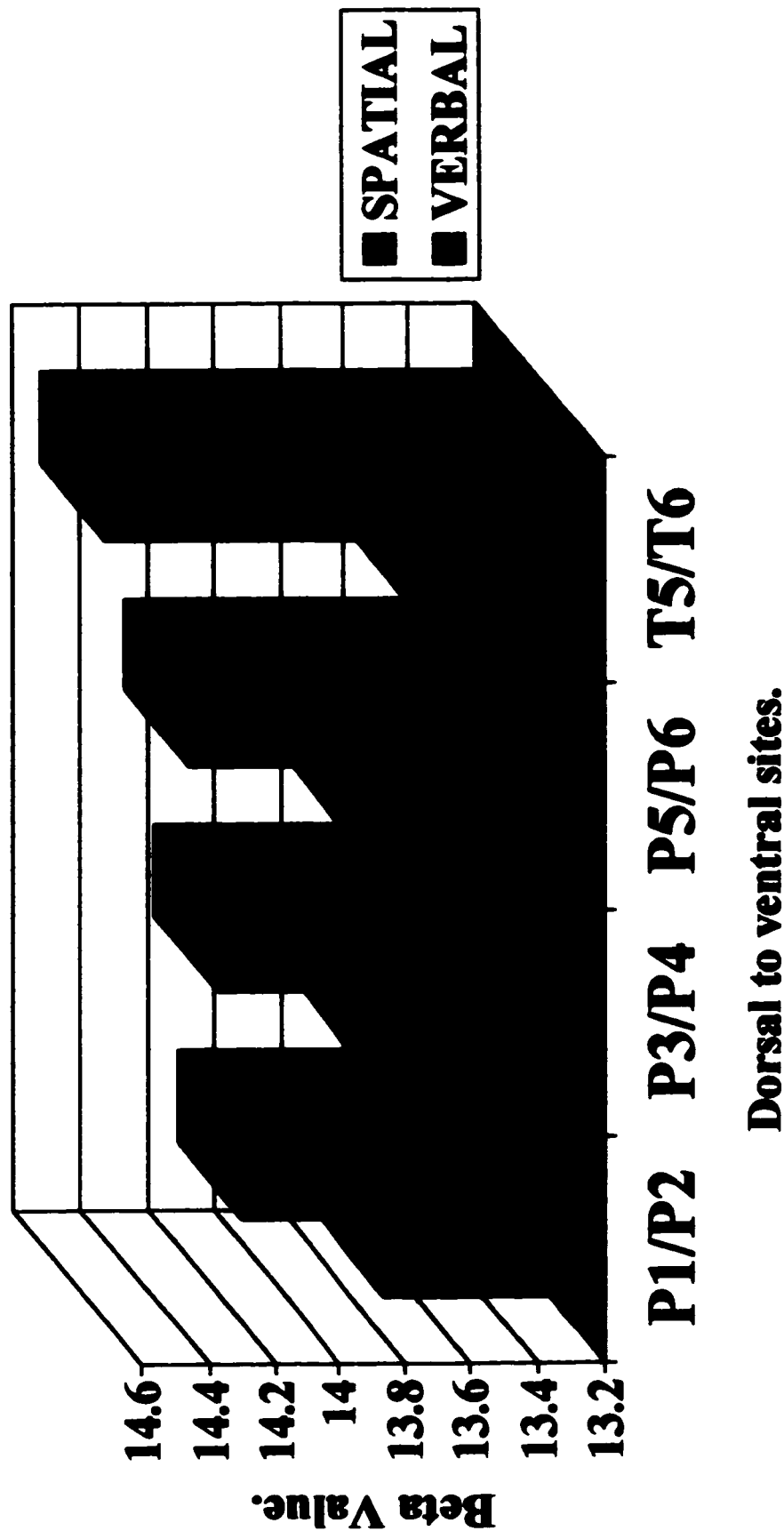
FIGURE 18. COHERENCE VALUES FOR CENTRAL-FRONTAL PAIRINGS - BETA BANDWIDTH

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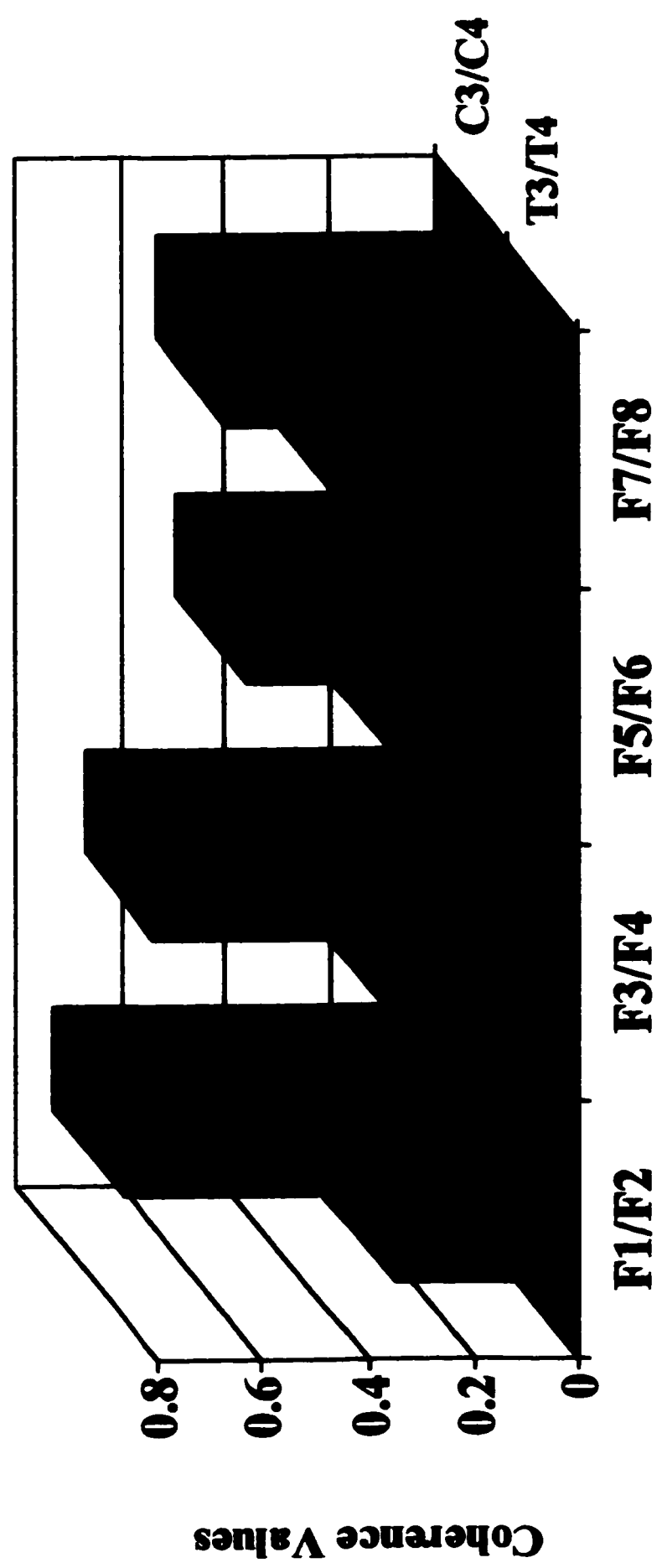
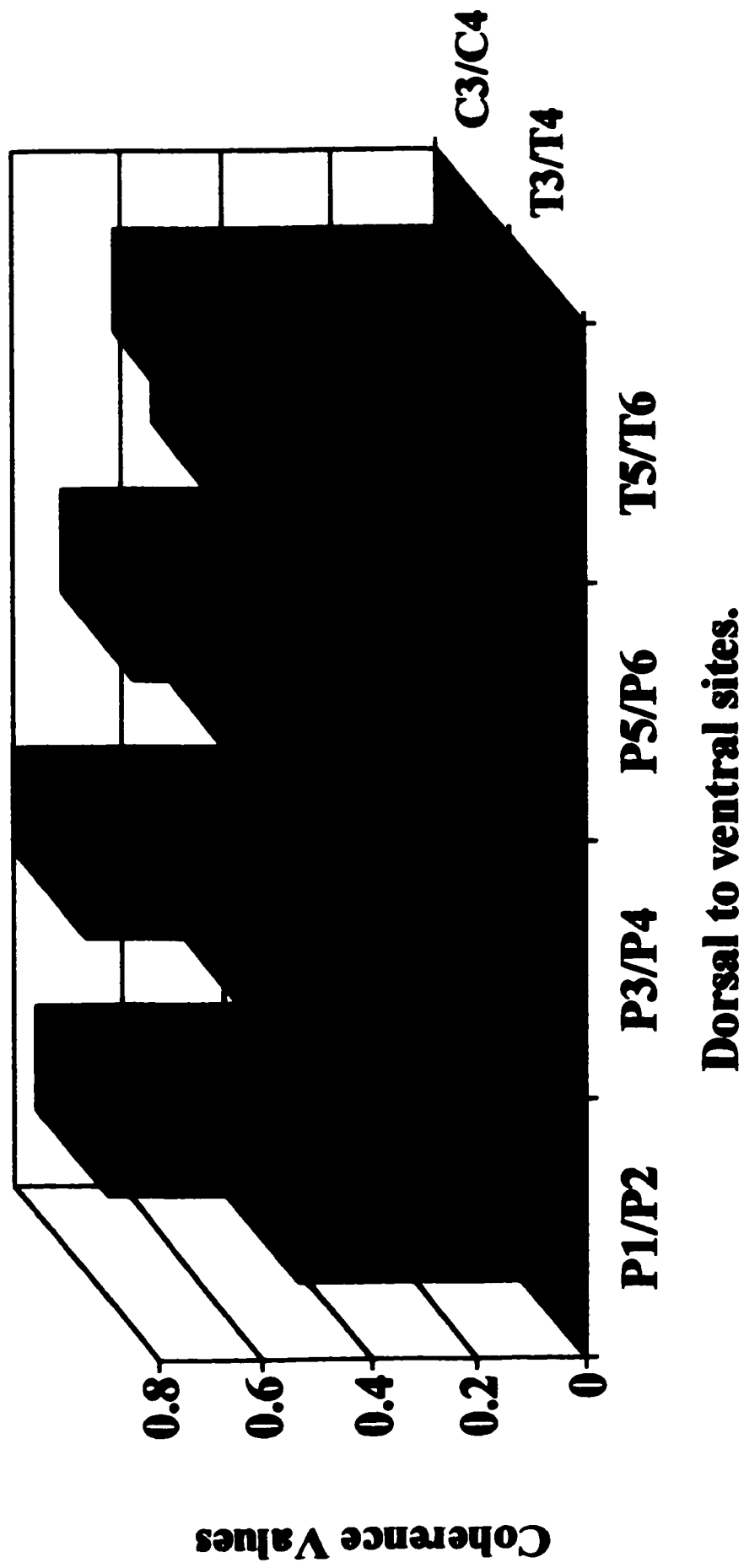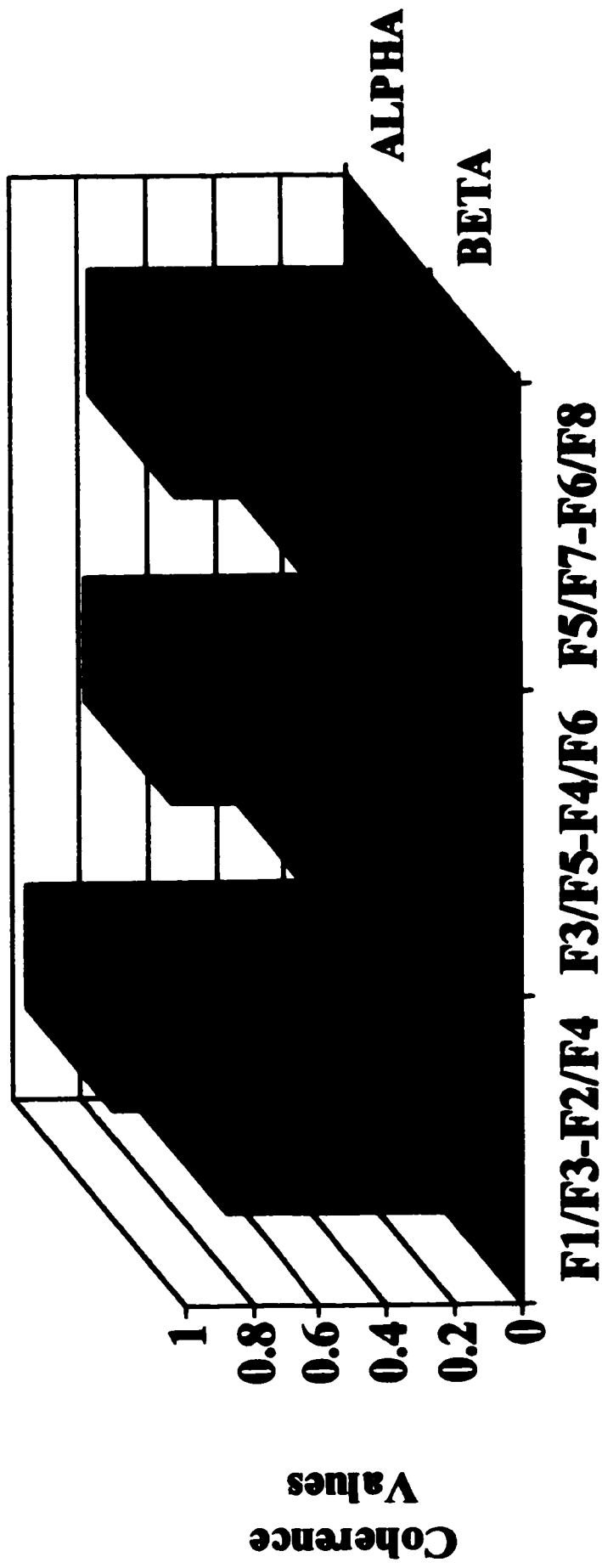FIGURE 19. COHERENCE VALUES FOR CENTRAL-POSTERIOR PAIRINGS - BETA BANDWIDTH
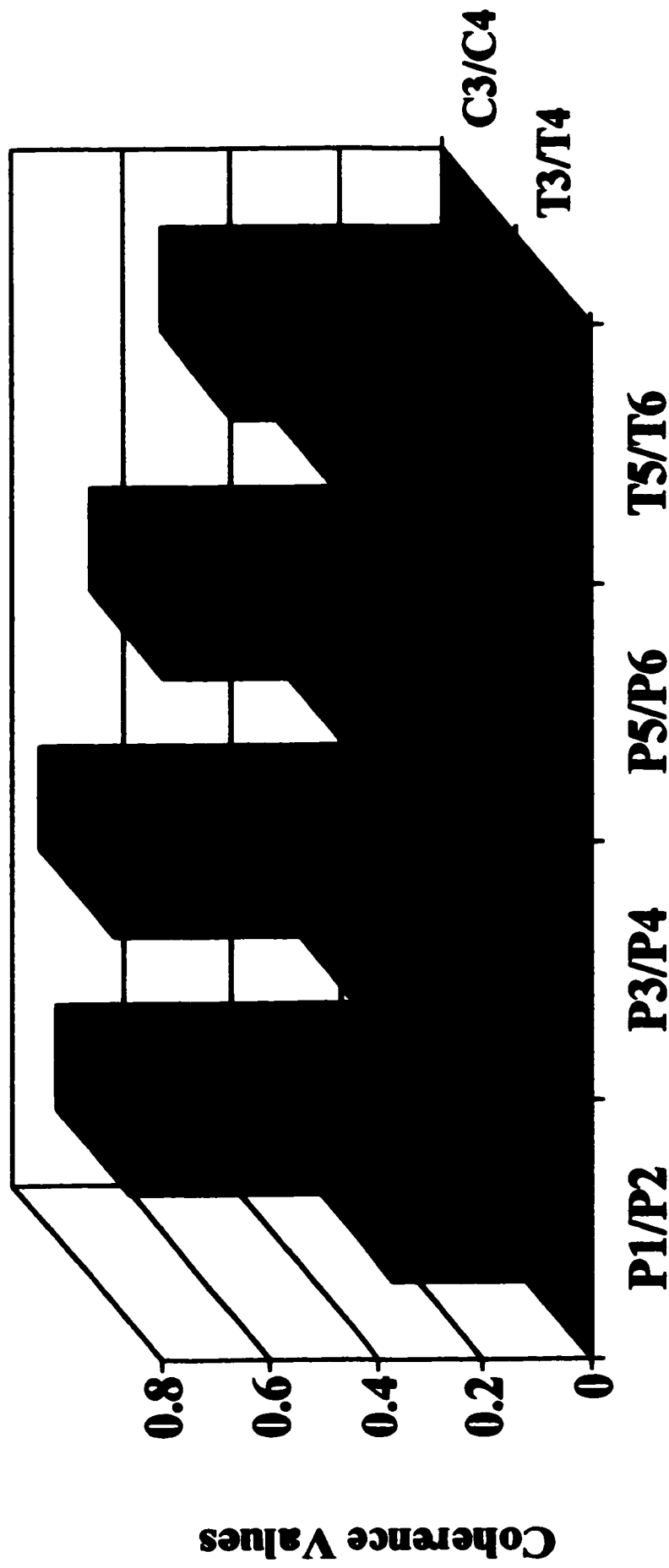
FIGURE 20. COHERENCE VALUES FOR CENTRAL-FRONTAL PAIRINGS - ALPHA BANDWIDTH

Dorsal to ventral sites.
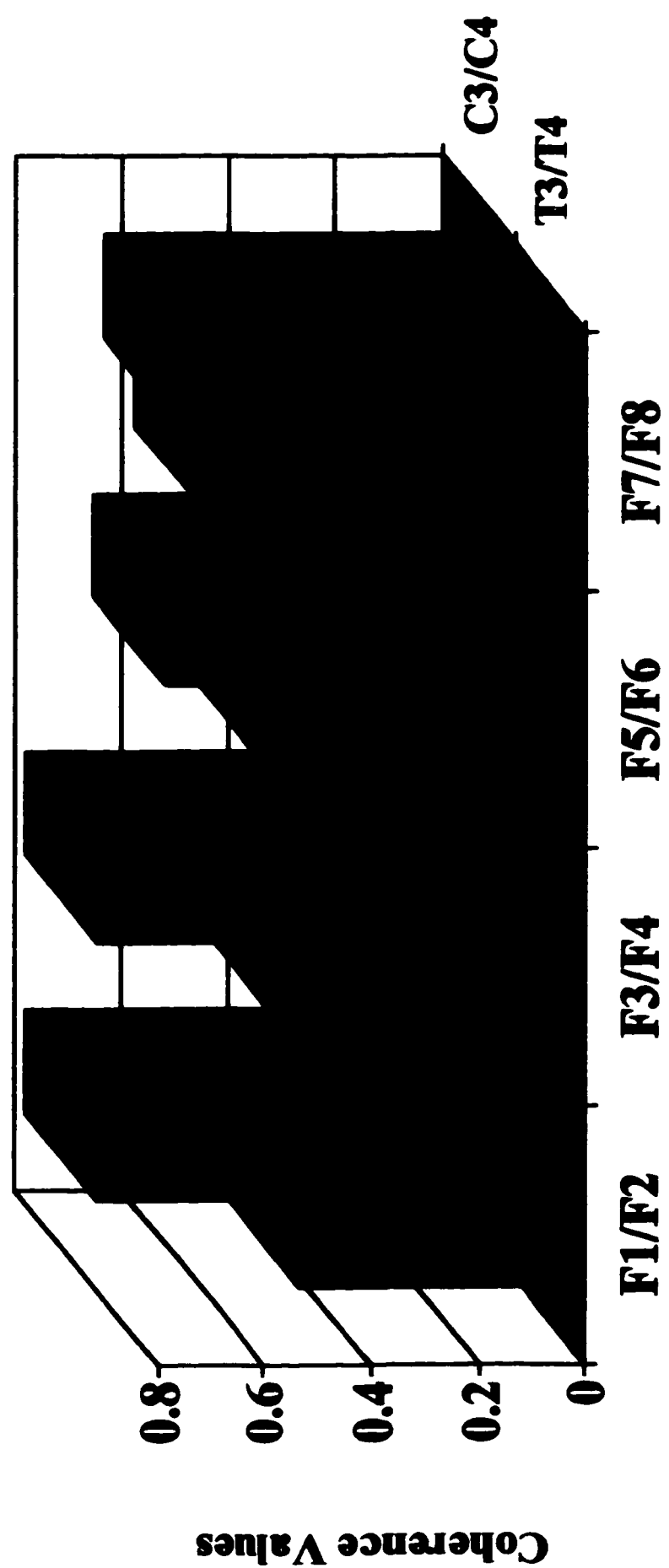
FIGURE 21. COHERENCE VALUES FOR CENTRAL-POSTERIOR PAIRINGS - ALPHA BANDWIDTH

Dorsal to ventral sites.

Coherence Values

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FIGURE 22. FRONTAL LOCAL COHERENCE VALUES OF BOTH ALPHA AND BETA BANDWIDTHS

Local Coherence Pairs.

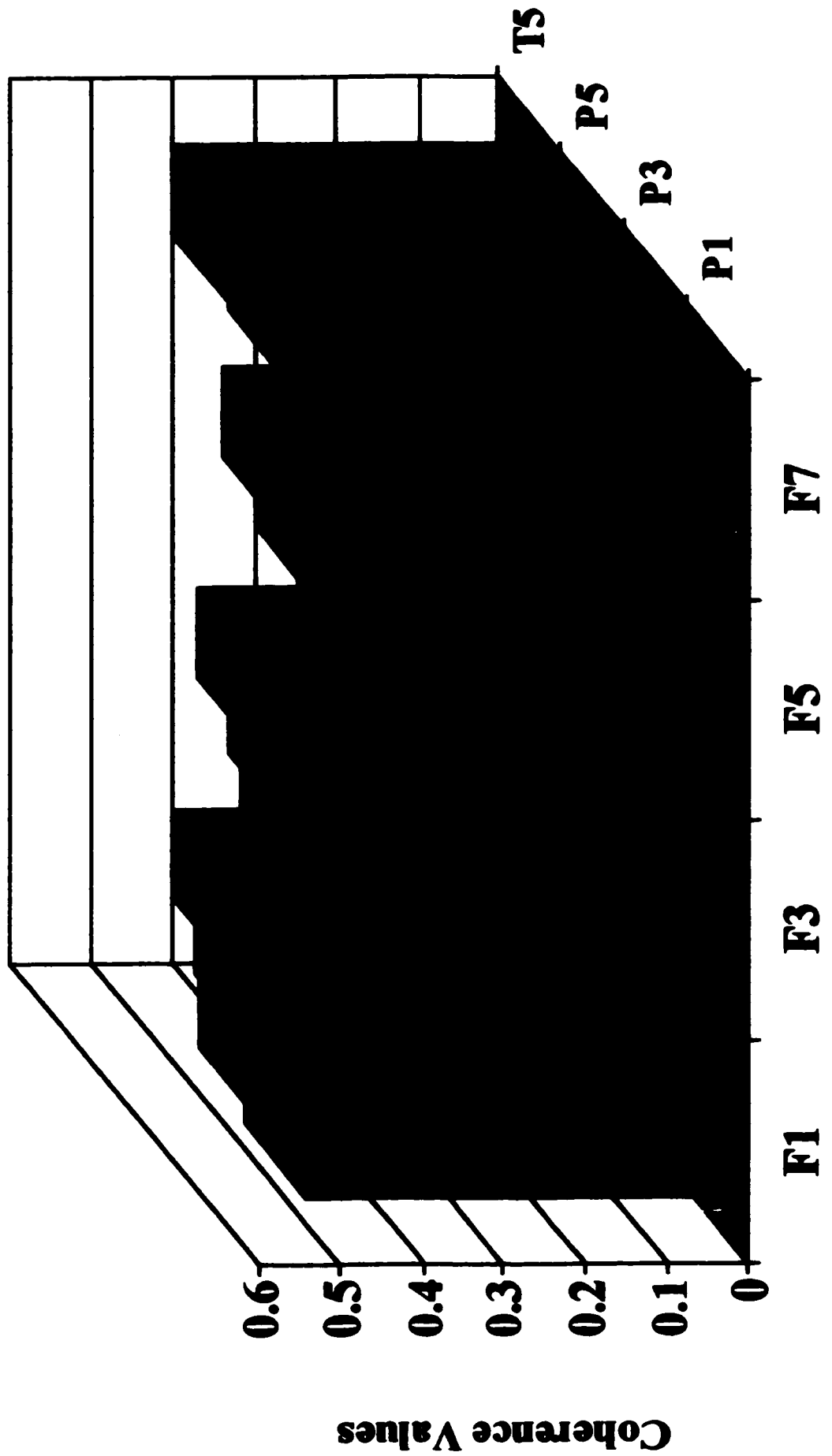FIGURE 23. BETA COHERENCE VALUES FOR FRONTAL-POSTERIOR PAIRINGS IN THE LEFT HEMISPHERE.

FIGURE 24. BETA COHERENCE VALUES FOR FRONTAL-POSTERIOR PAIRINGS IN THE RIGHT HEMISPHERE.

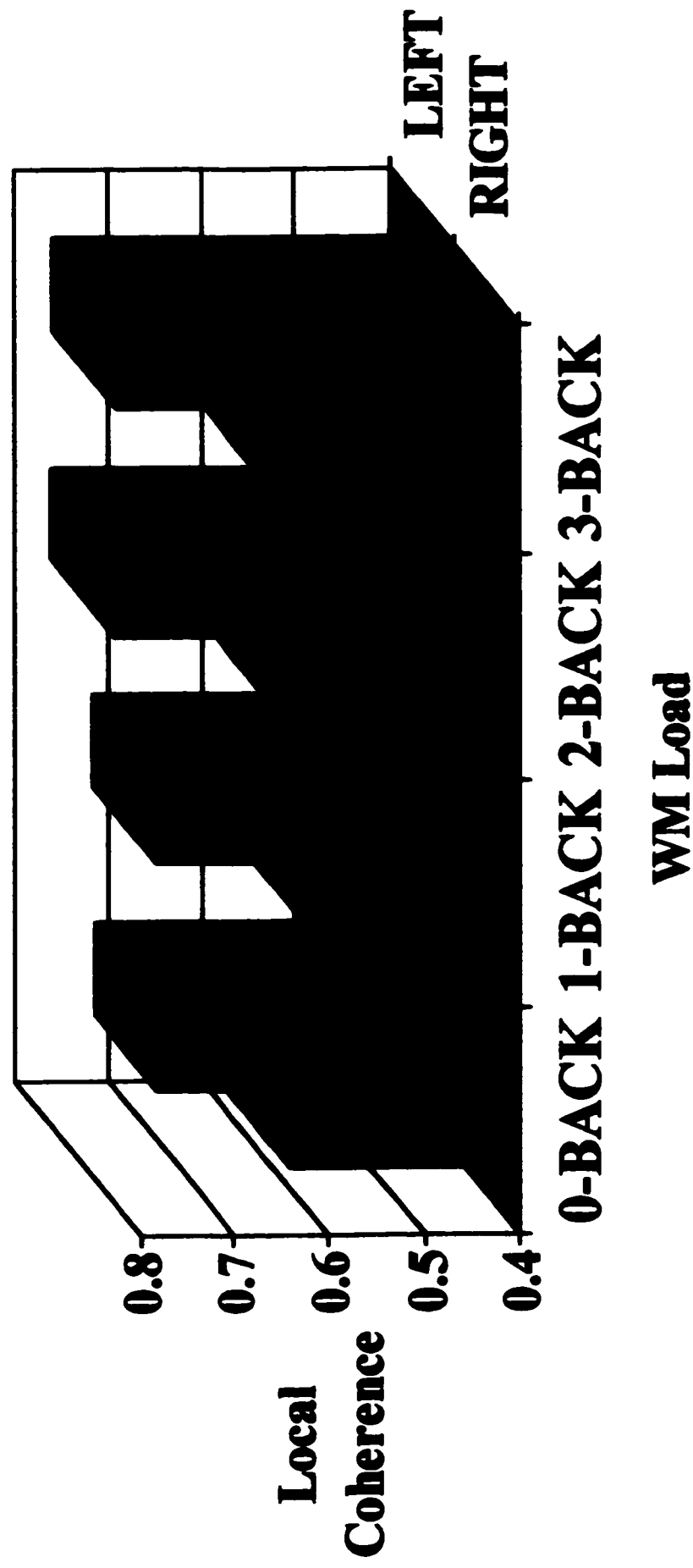FIGURE 25. LOCAL COHERENCE VALUES OF FRONTAL ELECTRODES ACROSS LEVEL OF WM LOAD

FIGURE 26. HEMISPHERIC DIFFERENCE IN P300 AMPLITUDES ACROSS LEVEL OF WM LOAD.