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PHYSIOLOGICAL MECHANISMS OF TASK-SWITCHING IN HUMAN SUBJECTS

by

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B.A. Nipissing University, 1990
M.A. Laurentian University, 1993

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for the degree of Doctor of Philosophy in Psychology

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University of Ottawa
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DEDICATION

I would like to dedicate this thesis to my parents, Olive and Ronald Moulden, whose heart-felt encouragement and support throughout my educational failures, successes, and goals, has been unwavering - from my decision to drop-out of high school after grade 10, through the night owl days of the B.A., the independence days of the M.A., the insanity days of the Ph.D., and now, the financially beleaguered days of the M.D. Your unconditional love, friendship, timely reassurances, and faith in me as your son, has enabled me to surpass the educational and vocational dreams I shared with you back in January 1987 when I was abruptly faced with the question of "What am I going to do with my life?" I thank-you for the life that has emerged, and yes, I do promise that I will not be returning to University in the pursuit of another degree after the M.D.

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2. Moulden, D.J.A., Picton, T.W., Meiran, N., Stuss, D.T., Riera, J.J., & Valdes-Sosa, P. (1998). Event-related potentials when switching attention between task-sets. *Brain and cognition*, **37**, 186-190.

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ABSTRACT

The nature, and timing, of the cerebral processes that are active when attention is switched between different tasks are not understood. The purpose of this research was to establish electrophysiological evidence for a two-stage, posterior-anterior cerebral processing model for the control of attention switching.

Reaction Times (RTs) and Event-Related Potentials (ERPs) were recorded from 22 healthy young adults as attention was cued to switch between two visuomotor tasks. One task ("horizontal") involved determining whether a circle in one of the four boxes of a 2 x 2 grid was in the left or right half of the grid whereas the other task ("vertical") involved determining whether it was in the upper or lower half. Cues designating the appropriate task occurred 200, 1200 or 1500 ms before a target. Cues were either letters (H & V) at the center of ocular fixation, or arrows (⇕ & ⇔) at the periphery. The identity of the letters, and spatial location of the arrows, informed subjects what task to perform, what hand to respond with, and whether the task was the same (repeat) or different (switch) from the previous trial.

The RT was longer for switch than repeat trials but only during short (200 ms) cue-target intervals. This demonstrates that subjects are able to completely switch attention prior to target stimuli when the cue-target interval was 1200 or 1500 ms.

The cues evoked a sequence of potentials that were larger in the switch trials than in the repeat trials: an occipital N200, a parietal P390, and a mid-frontal negative wave with a latency between 400 and 800 ms. The N200 probably represents processing of the stimulus in the extrastriate cortex. The P390 peak was larger for arrow than letter cues at centroparietal electrodes (CP1, CP2), and the inverse was true at temporal-parietal sites (P7, P8). The P390 was also 55 to 59 ms earlier for the dorsal than ventral waveform. This demonstrates that at least two separate neurophysiological events contribute to the amplitude and latency characteristics of the

scalp recorded P390. These processes are specific for the physical features of the cues and may correspond to the dorsal "where" and ventral "what" visual streams. Only the mid-frontal negative wave was found to be specifically with the switch in task. This wave may represent activity in the supplementary motor area or anterior cingulate as response rules are changed for the new task.

The readiness potential (RP) showed complex relations to switching or repeating the task. In general, this potential was larger over the hemisphere contralateral to the hand that was being prepared for response. When there was some urgency in the task, the readiness potential was bilateral on switch trials, perhaps because the previous hand was automatically activated in case it might be needed.

Left and right lateral pre-frontal slow waves occurred throughout each trial. These may represent task monitoring and/or working memory processes.

These results suggest that both posterior and anterior brain regions participate in attention switching. Posterior ERPs seem to be associated with identifying the physical features of stimuli that signal the need to switch attention between tasks, whereas the mid-frontal negativity appears to be related to carrying out the switch once the need to switch has been identified. The RP indicates the preparation of a hand for response. The strategy of this preparation varies with the urgency of the switch. Other anterior processes may monitor task performance.

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GENERAL INTRODUCTION

The ability to switch attention rapidly and appropriately between different tasks according to the demands of the situation is essential for human cognition (Allport, Styles, & Hsieh, 1994). Switching attention is necessary for goal-directed behavior which involves: 1) choosing among alternative strategies for processing exogenous or endogenous information, 2) activating the chosen strategy to perform the task, 3) monitoring the execution of planned behavior during task performance, and 4) disabling a strategy if it becomes inappropriate (Logan, 1985).

Deficits in attention-switching, frequently observed following damage to the frontal regions of the brain (Stuss & Benson, 1986), can cause two main errors. First, subjects are often unable to switch, and therefore perseverate with responses no longer appropriate to the task. Perseverative errors have been interpreted as an inability to overcome an established response (response inflexibility) or as an inability to switch attention from one criterion to another (conceptual inflexibility) (Luria, 1965; Milner, 1963). Second, subjects may fail to maintain set and through distractibility or impulsivity may switch inappropriately (Heaton et al., 1993; Sullivan et al., 1993). Caring for patients with attention-switching deficits is difficult since we do not know how the attention-switching system is organized in the brain.

Our understanding of attention-switching disorders would be improved if we could identify the processing steps that the brain works through when an individual switches attention between different tasks. My research is designed to determine the sequence of neurophysiological events that occur in the brain when behavior is switched to new goals. The experiments involve recording both behavioral data and event-related potentials (ERPs) when a subject switches attention between different conceptual and response sets. The goal is to identify specific ERP components that occur when subjects succeed in switching attention between tasks. These electrophysiological data should allow us to delineate both when and where in the brain attention-switching occurs.

PSYCHOLOGICAL AND NEUROLOGICAL THEORIES OF ATTENTIONAL CONTROL

Historically, cognitive theorists have attempted to describe attention in terms of a central processing system. Attention has also been characterized as an aggregate of processes that require controlled processing (Shiffrin & Schneider, 1977), as a unitary central executive or Supervisory Attentional System (Norman & Shallice, 1986), as a prefrontal mediator of cross-temporal contingencies of behavior (Fuster, 1985), and as a dichotomous anterior/posterior system of voluntary control over automatic brain processes (Posner & Peterson, 1990; Posner & Raichle, 1994, pp. 168-174).

There can be no single theory of attention since the computational aspects of attention are functionally diverse (Allport, 1993). Selective deficits of either divided or focused attention in patients with frontal lobe injury (Godefroy, Lhullier, & Rousseaux, 1996) indicate that a unitary concept of attention is inappropriate. Any advance in our understanding of differential control will need a framework that fractionates the attentional system into testable component processes. Optimally, the identified sub-processes should be described psychologically in terms of their function in cognition, and physiologically in terms of discrete cerebral processes.

The hypothesized central executive, or Supervisory Attentional System, has come to be identified with the functioning of the frontal lobes (Shallice, 1988). More recently, Stuss, Shallice, Alexander, & Picton (1995) have postulated that this frontal control of attention occurs on tasks that elicit non-routine shifts of attention between different tasks. Although the neuroanatomical correlates of the cognitive processes evoked during attention switching tasks remain poorly understood, several theories have localized important sub-components of attention (Colby, 1991; Fuster, 1985; Posner & Raichle, 1994). In general, these theories have focused on anterior and posterior attentional processes. This dichotomy derives from studies of delayed performance, selective attention, and hemispatial neglect.

The prefrontal cortex is especially important during the performance of delay tasks, wherein subjects must retain information over a short delay period and subsequently switch or maintain a previous task-set (Fuster, 1985; 1989). Deficient performance on delayed alternation depends on the complexity of the task with deficiencies becoming more pronounced as the similarity between competing stimuli or responses increases (Fuster, 1980, 1985). Several explanations can account for impaired performance on delayed alternation tasks, but none has proven entirely satisfactory. These explanations have included abnormalities in functions such as perseverative tendencies, short term (working) memory, anticipatory and preparatory set, response inhibition, temporal chunking, and control or suppression of interference (for reviews see, Fuster, 1985, 1989; Goldman-Rakic, 1987; Oscar-Berman, McNamara, & Freedman, 1991). Despite the lack of agreement concerning the precise function(s) tapped by delay tasks, these tasks are sensitive measures of frontal (Stuss & Benson, 1986), possibly orbitofrontal (Freedman, Black, Ebert & Binns, 1998) functions, and successful performance on these tasks depends on the organism's ability to adjust actions to temporally distant events and objectives (e.g. between a warning cue and a subsequent target) through working memory (Fuster, 1985).

In terms of selective attention, Colby (1991) has characterized the contribution of the frontal cortex as response selection and that of the parietal cortex as target selection. This distinction is supported by Positron Emission Tomography (PET). Both superior parietal and superior frontal cortex are active when attention switches from central to peripheral locations (Corbetta, Miezin, Shulman. & Petersen, 1993). However, the parietal region is active when the direction of attention is determined by sensory cues independently of any motor response, whereas the frontal region is only active when responses are made (Corbetta, Miezin, Shulman. & Petersen, 1993).

Posner and colleagues (Posner, 1980; Posner, Petersen, Fox, & Raichle, 1988; Posner & Petersen, 1990; Posner & Raichle, 1994) have emphasized the role of posterior brain regions in visuospatial selective attention to location, and the role of an anterior mid-line attentional system (cingulate) in high-level selection of information, targets, and cognitive procedures for output. For example, PET studies have demonstrated no change in the blood flow in the anterior cingulate during the simple reading of visually presented words, but robust activation of the anterior cingulate occurs when the words are more complexly processed during semantic monitoring and verb generation tasks, or under conditions of Stroop interference (Pardo, Pardo, Janer, & Raichle, 1990; Petersen et al., 1988b, 1989; Posner et al., 1988b; see also Janer & Pardo, 1991). Moreover, the degree of blood flow in the anterior cingulate increases as the number of targets in a detection task increases (Posner et al., 1988b).

One of the more widely accepted theories for the allocation of attentional resources within the brain concerns the special role of the right parietal lobe (Corbetta, Miezin, Shulman & Petersen, 1993) in directing spatial attention (Mesulam 1981, 1990). Mesulam's theory attempts to account for the high frequency of left-sided neglect after right hemisphere damage (McFie & Zangwill, 1960) by proposing that the left and right hemispheres are both capable of directing visuospatial attention contralaterally, but that the right hemisphere is also specialized to direct spatial attention ipsilaterally. Attention to right-sided extrapersonal space is supported by both the left and right parietal lobes, whereas attention to the left is only mediated by the right parietal lobule. Thus, neglect of right-sided extrapersonal space after a left parietal lesion is uncommon since the intact right parietal lobule can compensate. Neglect of the left after a right parietal lesion is common since the intact left parietal lobule cannot compensate.

Right-hemisphere dominance for the distribution of spatial attention within both ipsilateral and contralateral extrapersonal space has been verified in clinical populations with visuomotor scanning and tactile exploration (Weintraub & Mesulam, 1987) and in normal subjects with tasks requiring covert shifts of visuospatial attention to location (Corbetta, Miezin, Shulman. & Petersen, 1993). Moreover, cognitive analyses have indicated that the focus of spatial attention processing is shifted from one to another location (or target) through a series of simpler operations that are localized to discrete posterior and sub-cortical brain regions (Posner, Cohen, & Rafal, 1982; Posner, Walker, Friedrich, & Rafal, 1984).

The frontal lobes are also involved in attentional control (Stuss et al., 1995). The perseverative errors observed on alternation tasks after prefrontal injury are consistent with this view (Luria, 1973 p. 207-211; Stuss & Benson, 1986). However, it is also clear that the ability to switch attention, at least in the visuospatial modality, depends upon posterior brain regions. Thus, in describing the neurocognitive basis of attention switching, it will be important to distinguish between paradigms that emphasize spatial (stimulus location) and non-spatial (response set) switches of attention.

SPATIAL AND NON-SPATIAL ATTENTION-SWITCHING

Switching Location

Most paradigms for studying spatial attention switching have used variations of the spatial cueing paradigm of Posner (1980). This paradigm manipulates the locus of directed attention while the eyes remain fixed on a central fixation point (i.e. a covert switch of attention). Subjects are required to press a button as soon as a target stimulus appears. At the beginning of each trial, subjects are given a cue that indicates the probable location of the target and is intended to draw attention to one side of the visual field prior to the target onset. On most trials the target is presented in the location indicated by the cue (valid trial), but occasionally it is in a different location (invalid trial). Performance is analyzed in terms of the benefits from knowing where in space the target will occur, and the cost when the target occurs at a position other than the expected position.

Compared to a neutral condition without a cue, reaction times (RT) are faster and more accurate for targets occurring at validly cued locations and slower and less accurate for targets at invalidly cued locations (Posner, 1980; Posner & Cohen, 1984). The RT benefits are seen with cues providing spatial location, but not with other cues that focus on the identity or shape of the cue stimulus (Posner, Snyder, & Davidson, 1980). This finding suggests that the behavioral facilitation effects of warning cues are specific to the shifting of the focus of attention to the cued location.

Studies using the spatial cueing paradigm in focal brain-injured patients have revealed systematic deficits in shifting of covert visual attention as a function of three brain areas - damage to any of these areas results in a reduced ability to covertly shift visual attention to location (Posner, 1988), and each area appears to produce a unique type of deficit. First, the RT of patients with parietal lesions is equivalent to that of normal subjects on valid trials but impaired on invalid trials that require the patient to respond to a stimulus presented to the contralesional visual field (Posner, Walker, Friedrich, & Rafal, 1984). Thus, posterior parietal lesions disrupt the disengaging of attention from an ipsilesional focus (Posner & Cohen, 1984; Posner & Petersen, 1990). Second, patients with progressive deterioration in the superior colliculus (i.e. supranuclear palsy) show an overall slowing in RT to both cued and uncued targets whether or not attention is first engaged elsewhere (Posner, 1988; Posner & Cohen, 1984). This finding is consistent with the idea that the lesion interferes with the movement of attention. Third, patients with posterior pulvinar lesions have difficulties engaging (orienting) attention to a spatial location opposite to the side of the lesion (Rafal & Posner, 1987) irrespective of the time allowed to do so. This pattern suggests a deficit in the ability to engage attention at a new spatial focus.

In summary, spatial cueing paradigms indicate that shifting attention to different locations depends on distinct computations that are carried out at specific neuroanatomical sites within posterior and sub-cortical brain regions. Attention must disengage (parietal) from its present focus, move to the new location (superior colliculus), and engage (posterolateral pulvinar) at the new location (Posner & Petersen, 1990). This model is supported by lesion studies in human patients and neurophysiological studies in humans and monkeys (Posner & Petersen, 1990). The specific role of the parietal cortex in shifting the spatial focus of attention is clearly demonstrated with PET studies. Repetitive shifting of attention between spatial locations causes significant parietal activity (Corbetta, Miezin, Shulman. & Petersen, 1993), whereas sustained focal attention to one location only activates stimulus selection processes in ventral extrastriate cortex with minimal blood flow changes in the parietal lobes (Heinze et al., 1994).

Switching Tasks

Switching attention between tasks differs from switching attention in space by being based on stimulus-response contingencies rather than just on stimuli. Many studies in cognitive psychology have looked at the switching of attention between different tasks both within and across blocks of trials (Allport et al., 1994; Allport & Styles, 1990; Gopher, 1996; Meiran, 1996; Shaffer, 1965; Sudevan & Taylor, 1987; Rogers & Monsell, 1995; Rubenstein, Meyer, & Evans, 1994).

Task switching paradigms present stimuli that can be processed in different ways. For example, if the stimuli contain both a number and a letter, the subject can decide if the letter is a vowel or consonant, or whether the number is odd or even in order to make a discriminative button press response (Rogers & Monsell, 1995). The tasks change over a sequence of trials. On one type of trial (switch) the subject has to switch from performing the task of the previous trial to a different task; on the other type of trial (repeat) the subject performs the same task as on the previous trial. A switch cost is calculated by subtracting the mean RT when the subject repeats a task from the mean RT when the subject switches to a different task. This switch cost reflects the extra time taken to switch attention between tasks.

Switch cost studies of attention switching have proceeded along two fronts. First, the time available for switching attention between tasks has been evaluated by decreasing the time available for switching. This can be accomplished by decreasing the inter-trial interval (from 1200 to 150 ms) when the task switch is predictably based on the ordering of the trials (Rogers & Monsell, 1995). Alternatively, if a warning cue is provided that identifies the upcoming task as a switch trial, the duration of the cue to target interval can either be long (1200 ms) or short (200 ms) (Meiran, 1996). Secondly, studies have manipulated the difficulty of the attention-switching paradigm by increasing or decreasing the complexity of the rules of the task (Allport & Styles, 1990; Rubenstein, Meyer, & Evans, 1994).

There are four main findings concerning the timing of task switching. First, it takes longer to perform a task when the subject switches rather than repeats the same task within (Meiran, 1996; Rogers & Monsell, 1995) or across blocks of trials (Allport, Styles, & Hsieh, 1994; Rubenstein, Meyer, & Evans, 1994). Switching between tasks is associated with a switch cost of about 15-30% in RT (Biederman, 1972; Meiran, 1996; Rogers & Monsell, 1995). This indicates that switching takes time. Second, as the time available for switching between tasks increases, there is a significant, although incomplete (Meiran, 1996; Rogers & Monsell, 1995), decline in the RT switch cost. This indicates an early stage in the switching process that can occur in anticipation of the switch if the identity of the new task is known in advance (i.e. an early goal-identity stage). Third, the time required to complete this early goal-switching stage is between 150 and 450 ms (Rogers & Monsell, 1995). Fourth, even when a subject knows the identity of an upcoming task ahead of time, by means of a w9arning cue (Meiran 1996) or by the ordering of the stimuli (Rogers & Monsell, 1995), and is provided with adequate time to prepare, a residual switch cost remains - as large as 120 ms if the S-R mapping is difficult (i.e. competing tasks share overlapping response sets) (Rogers & Monsell, 1995). The residual switch cost indicates that a late step in the switching process does not occur until the stimulus arrives and the response rules associated with the new task are correctly acted upon - the "stimulus-cued completion hypothesis" (Rogers & Monsell, 1995)

Three findings derive from manipulations of task complexity. First, the size of the residual switch cost increases with the complexity of the stimulus-response mapping rules (i.e. when both tasks produce overlapping responses) (Meiran 1996; Rogers & Monsell, 1995). Second, RT increases as the difficulty of discriminating between stimuli increases - although the switch cost remains constant (Allport & Styles, 1990; Allport, Styles, & Hsieh,1994; Rubenstein, Meyer, & Evans, 1994). This indicates that the executive control of switching is central to the process of stimulus evaluation.

Importantly, the increases in switch cost due to complexity and timing are additive (Rubenstein, Meyer, & Evans, 1994). Performance is worse when task-cues are absent (poor goal identity) and response rules are complex (difficult response activation).

CLINICAL TESTS OF ATTENTIONAL CONTROL

In humans, perseveration and failure to maintain set can be evaluated using standard neuropsychological tests such as the copying of alternating graphic sequences (e.g.□◇□◇□◇...) (Luria, 1973) or the Wisconsin Card Sorting Test - WCST (Heaton, 1981, 1993). With graphic alternation tasks patients with prefrontal lesions (most frequently bilateral) are often unable to switch between copying the two designs, perseverate on the first drawing (e.g. □□□) and may fail to notice their mistakes. They have lost the ability not only to switch their actions, but also to check their results (Luria, 1973, p. 206-210). On the WCST, Milner's (1963) classic paper indicates that the area of the frontal lobe most likely to lead to perseveration is the dorsolateral prefrontal region of either hemisphere.

However, the WCST has been nonspecific in indicating the physio-anatomical basis of attention switching. The WCST requires many processing sub-components. Impaired performance may be attributed to concentration, vigilance, working memory, behavioral monitoring, conceptual problems, and motor inefficiencies (Bornstein, 1986; Dehaene &

Changeux, 1991; Drewe, 1974; Milner, 1963, 1964; Sullivan et al., 1993; Robinson, Heaton, Lehman, & Stilson, 1980; Stuss & Benson, 1984; Taylor, 1979). Patients with diffuse cerebral lesions can perform as poorly on the WCST as patients with focal frontal lesions (Robinson, Heaton, Lehman, & Stilson, 1980), near perfect scores can be achieved despite bilateral orbital and dorsolateral damage (Heck & Bryer, 1986), and posterior lesions can disrupt card sorting performance (Anderson et al., 1991; Drewe, 1974; Teuber, 1964). In particular, Drewe (1974) observed that patients with either a left frontal or right parietal lesion required many indications of a correct response in order to achieve only partial success on the WCST. Nevertheless, it has been suggested that good performance by frontally damaged patients may occur because the examiner provides the structure and direction normally given by the patients' own frontal lobes (Stuss & Benson, 1986).

Neuropsychological studies that have used more controlled paradigms than the WCST have identified at least two processes involved in attention-switching (Owen et al., 1991) - the ability to engage attention or switch attention to particular perceptual dimensions. Owen et al. (1993) have since demonstrated that these processes are differentially affected by frontal lobe damage (disengage deficit) and Parkinson's disease (engage deficit) (Owen et al., 1993).

Since abnormalities on neuropsychological tests such as the WCST are not specific as to the underlying pathology, the cerebral basis of switching attention between tasks remains the least understood of the hypothesized anterior executive functions. Perhaps a more realistic approach to understanding deficits in switching attention after frontal lobe damage is to determine the cerebral basis of the different processes that underlie task-switching.

PHYSIOLOGY OF HUMAN ATTENTION-SWITCHING

PET & fMRI

In a PET study of visual attention switching to locations across the visual hemi-fields, Corbetta et al. (1993) observed that areas within the superior frontal and parietal lobes were involved in programming the switch of attention to the contralateral hemi-field. The authors further noted that the switching mechanisms of the parietal lobes are not symmetric. The right parietal lobe was involved in attention shifts in both visual fields, whereas the left parietal lobe appeared to be restricted to rightward shifts of attention. Similarly, utilizing a spatial switching paradigm, Shedden (1995) recorded fMRI and ERPs as subjects covertly switched visual attention between numeric stimuli that were either to the left or right of a central fixation point. Attention could switch within or across the left and right visual fields. A region lateralized to the right superior parietal cortex was active when attention was switched between locations, independent of the location within or across the visual hemi-fields. Regions in the right inferior parietal and left superior parietal cortices were also active during the shift conditions.

ERPs as a Means to Study Cognition

ERPs are voltage changes generated in the brain, following a transient visual, auditory, or somatosensory stimulus, or preceding a motor response. Sensitive amplifying equipment, and use of an averaging technique (Dawson, 1954) is required to record these "stimulus-locked" voltage changes from electrodes placed on the scalp, since the potentials are small (0.5 to 100 μV) in comparison to the background electroencephalographic "EEG" potentials with which they are intermixed. By averaging together epochs of the EEG that are time-locked to the onset of a stimulus (e.g. 200 ms before to 2800 ms later), the randomly varying background potentials decrease in size, and we are left with voltage changes specifically related to the brain's response to the stimulus - the Event Related Potential.

The ERP averaged from the human scalp is an indirect measure of the electrical changes that occur in neurons within the brain as they process the stimuli and cognitive demands relevant to a particular task. In many cases, depending on the size, orientation, and depth of the generator, and relative location of the recording electrodes, potentials of opposite polarity can be picked up from the scalp at opposite ends of this dipolar field. The standard nomenclature for labeling the ERPs in these dipolar fields includes an identification of the polarity (P = positive; N = negative) as well as the latency (ms) of the potential relative to the evoking stimulus. For example, a "P300" is a positive potential that is maximally recorded 300 msecs after an evoking stimulus. This same potential might also be called an "N300" if it is measured at the opposite end of its dipolar field.

There are both early and late ERPs. The early potentials, usually recorded within 200 ms of stimulus delivery, principally reflect activity generated in an afferent pathway and its primary cortical receiving area in the brain. The later potentials are more clearly influenced by mental processes such as attention to the stimulus or the expectation that a particular stimulus will, or will not, occur. Other ERPs may be recorded in association with awaiting a stimulus ("expectancy wave" or "contingent negative variation" - CNV) or when preparing to make a motor response ("readiness potential"). These latter ERPs are recorded as gradually rising negativities over the fronto-central cortex lasting for one or more secs before the relevant event. For the purposes of this manuscript, the terms "exogenous" ERPs will be used to distinguish responses evoked by direct stimulation of the sensory system, whereas "endogenous" ERPs will refer to those in which an additional, cognitive activity is presumed to be required by the subject.

Since the major goal of cognitive psychology is to; "identify the cognitive processes that mediate between the environment and overt behavior, the representations on which these processes operate, the ways in which they interact, and their temporal properties " (Rugg & Coles, 1995, p. 26), then the ERP appears to be a good candidate of study since it can be recorded at the time these processes are occurring. This is advantageous for directly studying fast-acting cognitive processes that control the rapid identification, classification, and response to stimuli - processes that can only be inferred in retrospect from behavioral experiments that rely solely on reaction-time (RT) techniques.

Although ERPs are well suited for telling us when particular neurophysiological events occur during the processing of a specific cognitive task, they are less efficient in conveying the location within the brain that the events originated. These locations must be estimated based on the scalp topography, and/or hypotheses derived from related neuroimaging and clinical data. Another problem arises when the investigator attempts to determine the causal role, in information processing terms, of brain activity reflected by the ERP - what is the functional significance of a physiological correlate of a hypothesized cognitive process? The answer, although less than perfect, derives from a comparison of the defining characteristics of an ERP between different experimental conditions. If an ERP varies significantly between two experimental conditions, and if we assume that underlying cognitive events contribute to this variance, then we can also infer that the cognitive processing associated with the two conditions differs in a meaningful way. This meaning, however, will depend upon the nature of the cognitive tasks that are being compared.

ERPs

Five ERP studies have specifically looked at the physiological basis of attention-switching. Two focused on switching in visual space (Harter & Anllo-Vento, 1991; Shedden, 1995), one was concerned with switching between and within task modalities (Courchesne &

Askhoomoff, 1993), the other two focused on concept formation during tasks that were similar in design to the WCST (Delisle, Stuss, & Picton, 1986; Stuss & Picton, 1978).

Harter and Anllo-Vento's (1991) study looks specifically at the preparatory processes occurring prior to an attentional switch. The ERP was averaged relative to a warning cue. The cue was an arrow at fixation that directed attention to the left or right visual field, or to the middle as a control in which attention need not switch. Subjects only responded to targets that appeared in the cued location. Two slow potentials were detected following the cue and preceding the target for both switching to the left and right hemi-space as compared to the middle control - an early anterior negativity (200 - 500 ms) and a late posterior positivity (500 - 700 ms). The anterior component was interpreted as the selective recruitment of cognitive processes involved with directing attention in space, whereas the posterior wave was interpreted as the switching of spatial attention because of its latency, and because it was greater in amplitude over posterior areas contralateral to the direction of attention as indicated by the cue.

Shedden (1995) recorded ERPs during switch versus fixed attention in visual space. Spatial attention switching was cued by the offset of a visual stimulus. Four ERP components were amplitude modulated following the offset of the cue stimulus on switch compared to fixed attention conditions. These components included a larger anterior (128 ms, frontocentral) and posterior (156 ms, occipital) negative peak (N1), a larger (maximal contralateral to the direction of attention) posterior parietal peak (P2, 200 ms), and a negative slow difference (switch - fixed) wave (N2, 250 - 450 ms) that was maximally recorded over central anterior electrode sites. Shedden interpreted the N1-P2-N2 switching complex as indicating orienting, preparing to switch, and disengaging attention to location, respectively.

In contrast to the visuospatial switching paradigms, Courchesne and colleagues (Akshoomoff & Courchesne, 1994; Courchesne & Askhoomoff, 1993; Courchesne et al., 1993) recorded ERPs from subjects while attention switched between ongoing sequences of auditory and visual stimuli. Similar to the switching in space paradigms, an enhanced positive parietal ERP wave was associated with the attention switching trials. Stuss and Picton (1978) also recorded amplitude enhancements at parietal (P_3 - 355 ms) and parieto-occipital (P_4 - 647 ms) regions during trials that preceded the subjects successful adoption of a new response strategy (i.e. switch in strategy) during the trial-and-error learning of a sorting criterion during the presentation of complex visual stimuli. A general negative baseline shift, recorded after a successful switch in criterion, was tentatively related to the formulation of new hypotheses. In a similar concept-formation task with simpler visual stimuli, Delisle, Stuss and Picton (1986) compared ERPs between trials wherein auditory tones prompted subjects to either maintain (positive feedback), or switch (negative feedback) conceptual hypotheses based on the color (black, white) or form (square, triangle) of stimuli. The negative feedback conditions were associated with a frontally (F3, F4) enhanced negative wave at about 400 msec after onset of the visual stimuli. Delisle et al. (1986) cautiously speculated that this "N400" may represent the supervisory attentional function of a frontal lobe executive system (Shallice, 1982).

The Posner paradigm has also been studied with electrophysiological techniques (Eason et al., 1969; Mangun & Hillyard, 1990a; Mangun & Hillyard, 1990b; Mangun & Hillyard, 1991; Mangun, Hansen, & Hillyard, 1987; Mangun, Hillyard, & Luck, 1993). The general finding has been that stimuli falling in the "spotlight" of spatial attention during valid trials elicit enhanced early P1 (80 to 120 ms) and N1 (160 to 200 ms) ERP components over posterior scalp regions as compared to invalid trials. Although these papers show the preparation following valid (and invalid) cues, data were not analyzed according to whether the task switched (from one hemisphere to another).

General Rationale for Experiments

The rationale for conducting the experiments in this thesis was three-fold. First, we were interested in determining if the ERPs can provide evidence for the hypothesized posterior (goal identity) and anterior (response rule selection) attention switching dichotomy. Second, we evaluated the stimulus-cued completion hypothesis that the mental set cannot be completely reconfigured until an imperative (target) stimulus is presented that completes the switch. This was investigated electrophysiologically by an analysis of the readiness potential, and behaviorally through the RTs. We hoped to replicate the RT reports of previous task-set switching studies that have demonstrated the presence of both early and late switching stages. The existence of these stages would be supported by a decline in the RT switch cost between short and long cue-target-interval trials, and by a residual switch cost even though subjects were provided with ample time to complete the switch in mental set. The ERPs would support the stimulus-cued completion hypothesis if the readiness potential demonstrated less than optimal response preparation prior to the imperative target stimulus. Third, assuming that a residual RT switch cost would be recorded, we hoped to identify an ERP that occurred at the switch cost latency range, as this may provide a physio-anatomical correlate of one of the key steps in the executive control of attention.

EXPERIMENT #1

INTRODUCTION

The brain lesion literature suggests that two distinct cerebral processes occur during task switching. Posterior brain regions may process stimulus information relevant to the task, and a frontal process may be involved in setting up or switching stimulus-response rules, - - the posterior-anterior attention switching dichotomy. The task-set switching literature suggests that two independent cognitive stages take part in switching - an early goal identity stage, and a late response selection stage. The early stage is supported by a decline in the RT switch cost with increasing cue to target intervals, whereas support for the late stage is based on the residual RT switch cost that remains during trials when the cue-to-target interval is long. The model that has emerged is known as the stimulus-cued-completion hypothesis (Rogers & Monsell, 1995). Because this term generates confusion in paradigms that use a "cue" to warn the subject to switch prior to the target, we shall henceforth refer to this as the stimulus or target-evoked completion hypothesis. The model asserts that attention cannot be completely switched until the stimulus requiring the switched response rules has been presented. In paradigms that use separate cue and target stimuli, switching is initiated by the cue and completed by the target.

Unfortunately, although lesion and behavioral studies provide useful insights, they cannot unequivocally inform us as to the exact number of switching stages, the time at which these stages are carried out (i.e. before or after an evoking stimulus), the precise locus of attention switching effects within the information processing system, or the nature of each process in relation to its locus. Nor can they specify the neural mechanisms that give rise to the ability to successfully switch attention between tasks. It is possible, however, to apply neurophysiological methods to address these questions and to help identify the transitional neural events that contribute to switching successfully, and ultimately, to the final behavioral output.

One of the advantages for using ERPs is that electrophysiological recordings can provide an account of what the brain is preparing to do before an overt response is made (see Brunia, 1993; Coles, 1989). For example, when the brain is preparing to make a button press response a slow negative wave develops at the central scalp location contralateral to the preparing response hand. This is the readiness potential (RP) (Coles et al., 1995), or Bereitschaftspotential (BP) (Kornhuber & Deecke, 1964). The RP clearly involves activation of the motor cortex contralateral to the responding hand. Opinions differ on whether the RP does (Ikeda, Luders, Burgess, & Shibasaki, 1992; Ikeda et al., 1996; Mackinnon et al., 1996) or does not (Bötzel, Plendl, Paulus, & Scherg, 1993) also involve the supplementary motor cortex. Nevetheless, the lateralization of the RP is accepted as a sign of specific response hand preparation (Coles, 1989). One other advantage is the high temporal resolution (i.e. milliseconds) of ERPs which provides information about the absolute and relative timing of neurocognitive events that is difficult to infer from behavior alone.

The attention-switching paradigm in our experiment #1 requires that subjects switch attention between two conceptual tasks (i.e. decide if a target is above or below or to the left or right of fixation) and two response sets (i.e. a 2 choice discriminative button press) involving either a left or right hand response. A visual cue identifies the correct task and response hand (goal-identity stage) and precedes a target stimulus whose spatial position dictates which of two possible response rules (button press response) to select and execute (response rule activation). Over a series of trials subjects may either repeat the task and response hand from the previous trial, or switch to the other task-hand.

We selected this paradigm for four reasons. First, its design follows paradigms which have been widely used in the task-set switching literature. Second, the paradigm has previously been shown to be associated with a RT switch cost (Meiran, 1996; in press). Third, in order to test the stimulus-cued completion hypothesis with ERPs, and investigate the proposal of two independent switching stages, we needed to adopt a switching paradigm that assigned the goal-identity and response rule-activation switching stages to different stimuli that were separated in time. Fourth, the cue stimuli allow the sequence of switches within a block of trials to be random and this prevents the subject from switching attention in anticipation of the upcoming trial.

In our paradigm a goal identifying cue was followed by a response rule-activating target. The cue stimulus informed subjects whether or not to switch attention to a different task, and the target served as the stimulus evoking the completion of the switch by coding for the specific button press response. Since the cue occurs before the stimulus evoking the completion of the switch (i.e. the target), it was appropriate for us to rename the stimulus-cued-completion hypothesis as the target, or simply, the stimulus-evoked completion hypothesis.

The presence of a residual RT switch cost, as well as an amplitude or latency modulated post-target ERP for switch compared to repeat trials, would support the target evoked completion hypothesis. The number of discrete switching stages would be determined by the count of ERPs varying with the stimuli to switch attention. The intra-cerebral locus of any switch-related potential would be inferred from the scalp topography of the ERPs. Finally, the role of particular ERPs in the attention-switching process would be determined by their temporal relationship to the cue and target stimuli, and preparation of the motor response (i.e. the readiness potential).

HYPOTHESES

The following hypotheses were addressed in the first experiment:

1) The RT switch cost (switch - repeat) would be largest when the time available for switching-attention prior to the target is restricted (200 ms cue-target interval). An early switching stage would be demonstrated by a decline in the RT switch cost when subjects are provided with enough time to switch attention prior to the stimulus requiring response (1200 ms cue-target interval).

2) A late switching stage would be evident by a residual RT switch cost when the cue-target interval is 1200 ms indicating that the switching process cannot be completely reconfigured in advance of the target.
3) Posterior and anterior ERP components within the critical latency of 150 to 450 ms will follow the cue to switch attention between task-hand sets.
4) An incorrectly lateralized RP prior to a forewarned switch between task and response hands will provide support for the stimulus-cued-completion hypothesis of task switching (i.e. incomplete response preparation during forewarned switches in response set).
5) The lateral frontal cortex will show increased activity during the cue-target delay interval in relation to task monitoring.

METHODS

SUBJECTS

Eight right-handed male volunteers with ages between 27 and 54 (mean 34) years participated in the experiment. All subjects were university graduates, with normal vision, and no history of neurological impairment.

PARADIGM

Task stimuli were presented on a computer monitor positioned 75 cm in front of the subject. Each subject completed 1000 task-set trials over ten separate trial blocks. Each trial consisted of a cue, target, and response and all stimuli, including the grid, were white on a black background. Cue arrows designating the task and response hand were located either to the left and right (Left Hand Task) or on the top and bottom (Right Hand Task) of a 2 x 2 grid. The grid subtended approximately 3.6° x 3.6° and was displayed continuously. The target was a circle, with a diameter of 1.5°, which was presented in one of the four grid quadrants. The position of the target in the grid determined which button to press. For example, on a Left-Right task the subject responded with the left hand by pressing one button if the target was on the **L**eft (left middle finger) and another button if the target was on the **R**ight (left index finger) half of the grid (see Figure 1, Upper panel). On a Top-Bottom task the right hand responded by pressing one button if the target was in the **T**op (right middle finger) and another button if the target was in the **B**ottom (right index finger) half of the grid.

Task-hand cues preceded the target by either 200 (20%) or 1200 (80%) ms thereby allowing subjects to use the task identifying cues to switch conceptual sets and prepare the correct response hand prior to the target (see Figure 1, Lower panel). One purpose of the short cue-target interval trials is to prevent the subjects from having enough time to complete this early attentional switch.

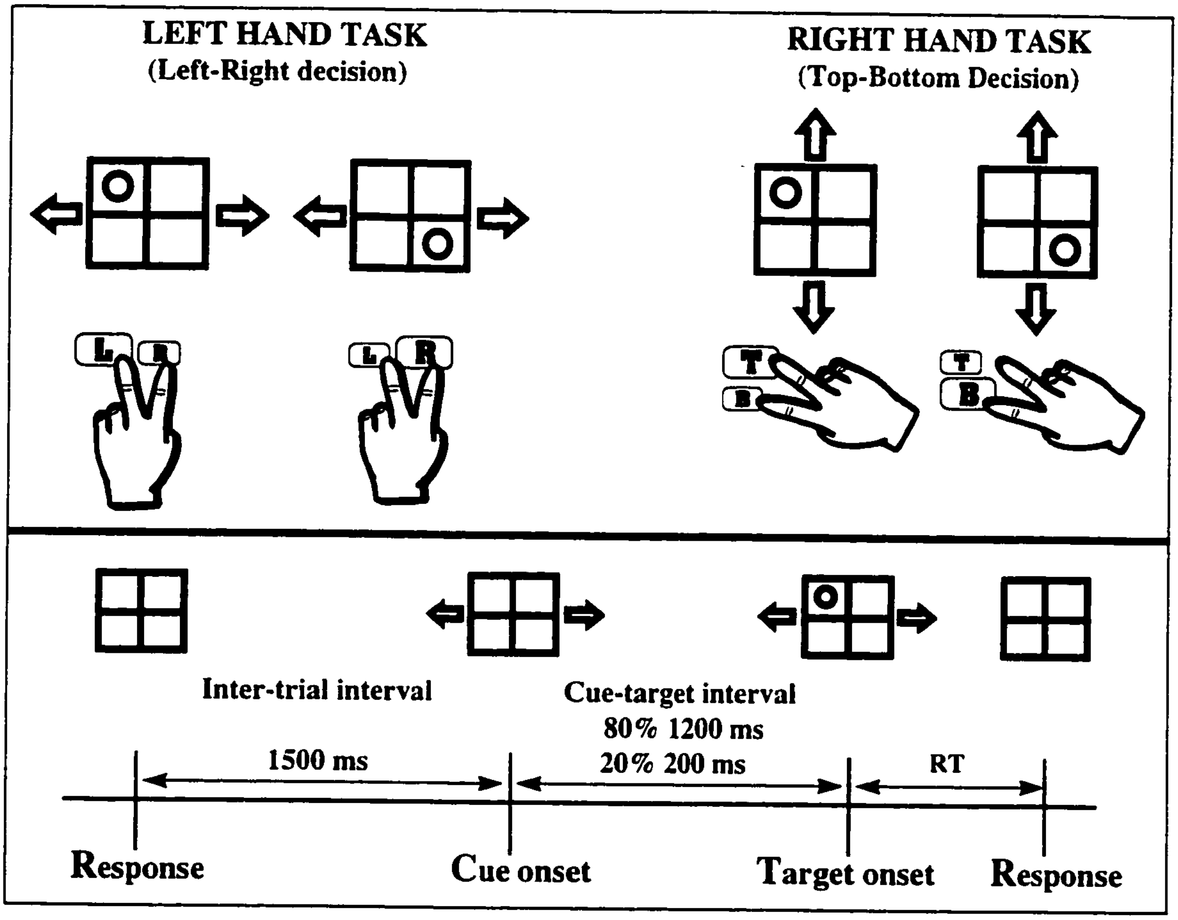

Figure 1:

Task switching paradigm. *Upper Panel*: The attention switching paradigm task decision and response-set mapping rules. During a Left Hand task the subject must decide if the target circle is on the Left or Right side of the grid and respond with one of two button presses with the left hand. During a Right Hand task the subject must decide if the target is in the Top or Bottom half of the grid and respond with the right hand. *Lower Panel*: The task-hand identifying cue arrows (task goal-identifying stage) precede the target circle (response rule activation stage) by either 200 or 1200 ms. The inter-trial interval is constant. Subjects are instructed to maintain fixation at the center of the grid during task performance. The cue and target are turned off following a response.

There are unfortunate confusions between the side of the stimulus, the side of the responding hand, and the side of the recording electrodes. A decision about the left or right sidedness of the stimulus requires a response with the left hand. We shall attempt to alleviate this confusion by using left and right only for the responding hand and for the recording electrode.

The sequence of tasks within a block varied randomly so that on each trial the subject either repeated the task from the previous trial (e.g. left hand task preceded by a left hand task - repeat left hand), or switched to the other task (left hand preceded by a right hand task - switch to the left hand). Subjects were instructed to respond as quickly and accurately as possible and to use the cues to prepare the correct response hand in advance of the target as this would facilitate a faster RT.

BEHAVIORAL MEASURES

The median RT was calculated for each condition for each subject. Subsequent calculations combining data across subjects used the mean of the median RTs. These RTs are presented for correct responses only. Separate averages were computed for the 200 and 1200 ms cue-target interval and for switch and repeat trials. RTs were logarithmically transformed prior to statistical analysis. Response accuracy was computed as the percentage of correct responses during the switch-repeat and short-long cue-target interval trials.

ELECTROPHYSIOLICAL MEASURES

Data Recording

The EEG was recorded with recessed tin electrodes mounted in an electrode cap with 32 standard 10-10 scalp locations (Figure 2). All electrodes were referenced to the inion (Iz) and converted to an average reference off-line prior to analyses. Inter-electrode impedance was maintained below 5 kOhms. EEG was recorded with a bandpass of DC (3 subjects) or 0.1 Hz to (5 subjects) to 50 Hz at a rate of 250 samples/sec. Epochs were collapsed off-line to 180 points representing one sample every 16.67 ms over a 3 second sweep including a 200 ms pre-cue baseline. Rejection for movement artifact was set at ± 600 μVolts on any channel.

Ocular Artifacts

Ocular source components were used to remove ocular artifacts from each subject's averaged ERP data (Berg & Scherg, 1991; Lins et al., 1993a; 1993b). Prior to the experiment the EEG was recorded for each subject as they completed a systematic series of 10 blinks, 10 vertical, and 10 horizontal eye movements. These ocular calibration trials were used as models to estimate ocular sources (Berg & Scherg, 1991; Lins et al., 1993a; 1993b). For each subject the first three ocular components were extracted that explained most of the variance in the calibration data (> 95%). These components were then used in conjunction with a four regional source (12 equivalent dipoles) surrogate EEG model in BESA (Brain Electric Source Analysis) to remove ocular artifacts from each subject's averaged ERP data.

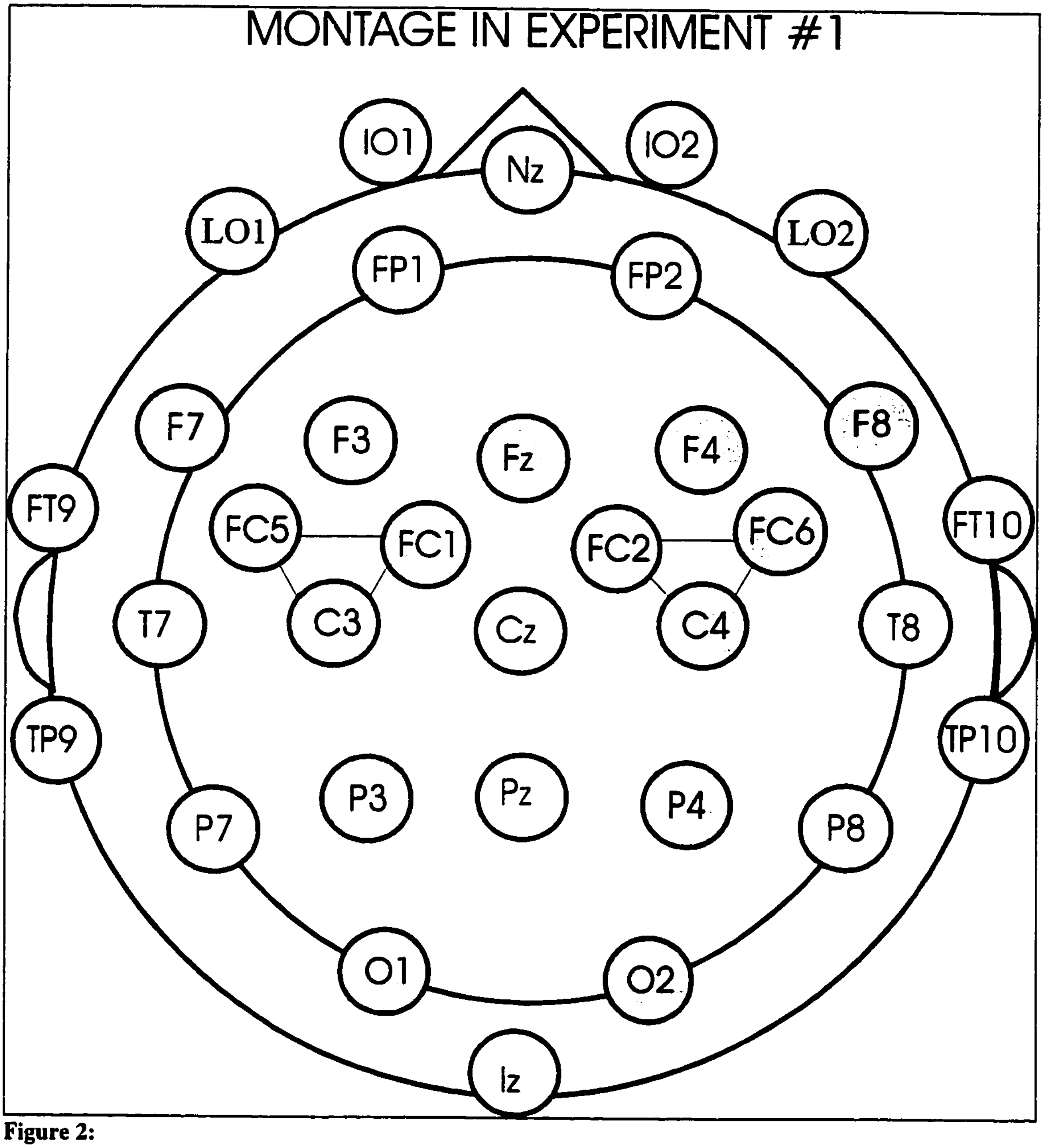

Figure 2:

Recording montage in the first experiment. Shaded circles represent electrode locations where ERPs were analyzed statistically. The ERPs were collapsed over two sets of 3 electrodes (connected by lines) for one of the readiness potential analyses (i.e. RP3).

The advantage of the ocular source component technique is that trials contaminated by eye movements are not discarded from the data analysis, and that artifact correction removes only that activity explained by the source activity of the ocular source components and not the underlying brain activity.

Analysis and Independent Variables

Behavioral data from both the 200 and 1200 ms cue-target interval trials are reported. For simplicity, ERP analyses are primarily presented for correct response 1200 ms cue-target interval trials. Correct response 200 ms cue-target interval trial ERPs are only presented for the readiness potential recordings. Independent variables are sequence (switch v. repeat), task-hand (left hand [left-right decision] v. right hand [top-bottom decision], and hemisphere (left v. right) for homologous electrode pairs. ERPs were subjected to separate repeated measures ANOVAs. Non-significant effects ($p > .05$) are only reported as they relate to the hypotheses of interest.

ERP MEASUREMENTS

Peak and latency measurements were obtained from electrode sites where the component of interest was maximally recorded. The amplitude of ERP slow waveforms was quantified as the mean voltage within a specified latency range relative to the mean voltage 200 ms prior to the cue onset. The following ERPs were identified and measured:

Cue ERPs

(i) N200, maximum negative peak at O1 and O2 within the latency range of 70 to 300 ms post-cue.

(ii) P390, maximum positive peak at P3 and P4 within the latency range of 300 to 700 ms post-cue.

(iii) Mid-Frontal Negative Wave: N430, maximum negative peak at Fz within the latency range of 300 to 700 ms post-cue.

Readiness Potentials

(iv) Readiness Potential 1: RP1, mean voltage at C3 and C4 during the latency range 600 to 900 ms post-cue (i.e. 600 to 300 ms pre-target).

(v) Readiness Potential 2: RP2, mean voltage at C3 and C4 during the latency range 900 to 1200 ms post-cue (i.e. 300 ms pre-target to target onset).

(vi) Readiness Potential 3: RP3, mean voltage collapsed over three left (C3, FC1, FC5) and right (C4, FC2, FC6) fronto-central electrodes during the latency ranges of 600 to 900 ms post-cue (i.e. 600 to 300 ms pre-target), and 900 to 1200 ms post-cue (i.e. 300 ms pre-target to target onset).

Frontal Slow Waves

(vii) Sustained Positive Wave: SPW, mean voltage at F7 and F8 during the latency range 450 to 1300 ms post-cue (i.e. 750 ms pre-target to 100 ms post-target).

(viii) Sustained Negative Wave: SNW, mean voltage at F3 and F4 during the latency range 600 to 1200 ms post-cue (i.e. 600 ms pre-target to target onset).

Target ERPs

(ix) N200T, maximum negative peak at O1 and O2 within latency range of 70 to 300 ms post-target.

(x) P390T, maximum positive peak at P3 and P4 within latency range of 300 to 700 ms post-target.

(xi) Mid-Frontal Negative Wave: N430T, maximum negative peak at Fz within latency range 300 to 700 ms post-target.

(xii) Left Lateral Frontal Negative Peak: N400T, maximum negative peak at F7 and F8 within latency range 300 to 600 ms post-target.

RESULTS

BEHAVIORAL DATA

The short cue-to-target interval switch showed a significant switch-cost and large percentage of errors (Figure 3). RT was 76 ms longer during the short cue-target interval (F (1,7) = 11.14, p < .01), and showed a significant cue-target interval x sequence interaction (F (1,7) = 7.24, p < .01). The switch RT was 40 ms longer than repeat RT on the 200 ms cue-target interval trials (482 vs. 442 ms), but not significantly different on the 1200 ms trials (383 vs. 389 ms).

The percentage of errors was significantly higher for the short cue-target intervals (F(1,7) = 16.91, p < .01), and switches (F(1,7) = 47.53, p < .001), with a significant cue-target interval by sequence interaction (F(1,7) = 34.74, p < .001) (Figure 3). Thirteen percent (98/632) of the responses to the 200 ms switch trials were incorrect, whereas the percentage error was only 3.9% (30/740), 3.7% (100/2911) and 3.2% (92/2697) for the 200 ms repeat, and 1200 ms switch and repeat trials respectively.

ERP DATA

Cue ERPs

Occipital N200, Parietal P390, Frontal negative wave N430:

Figure 4 summarizes the ERP switch effects. The occipital N200 to cue stimuli was the earliest ERP deflection to vary with the sequence manipulation. The N200 was significantly

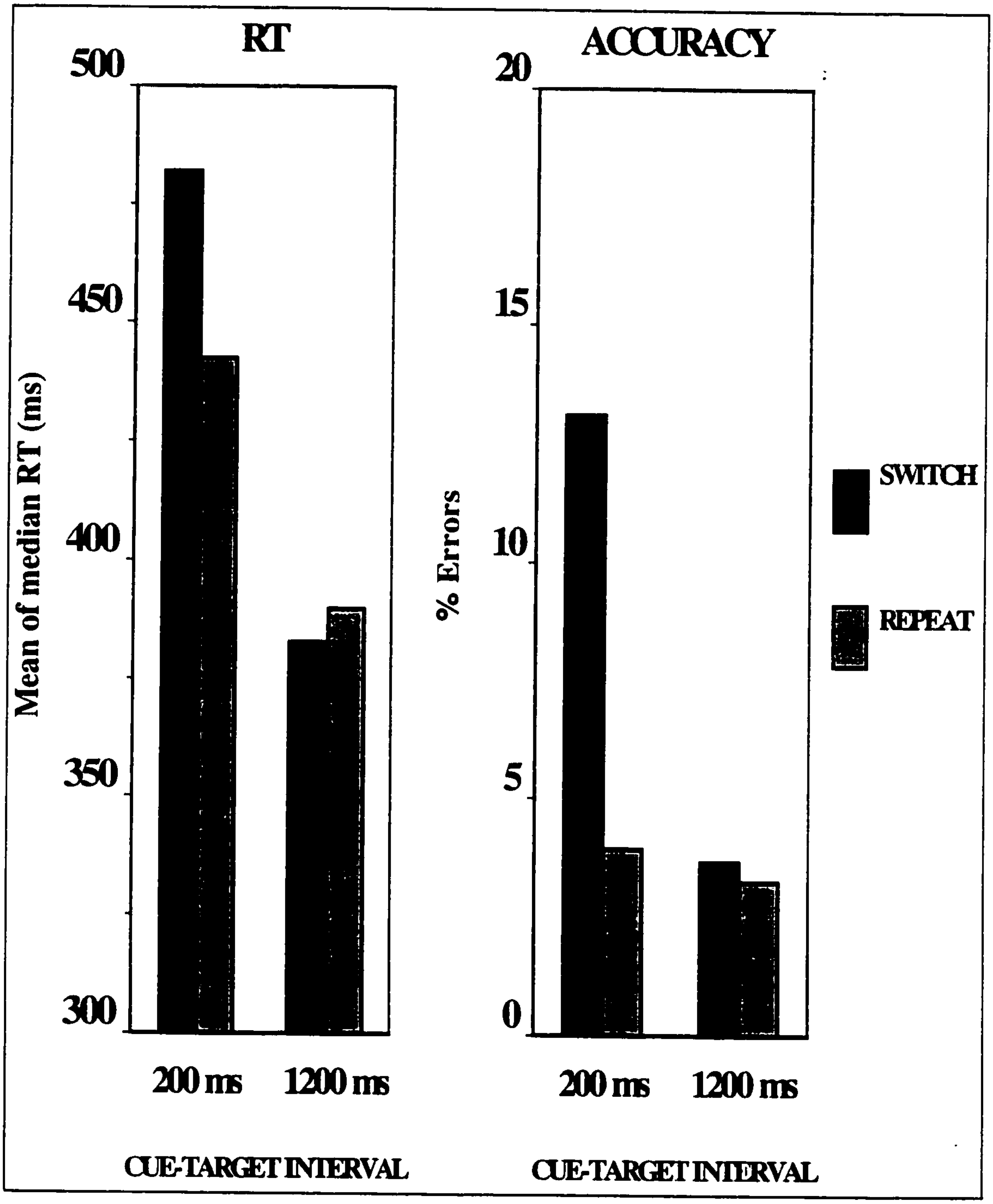

Figure 3:

Average reaction time and response accuracy for experiment #1.

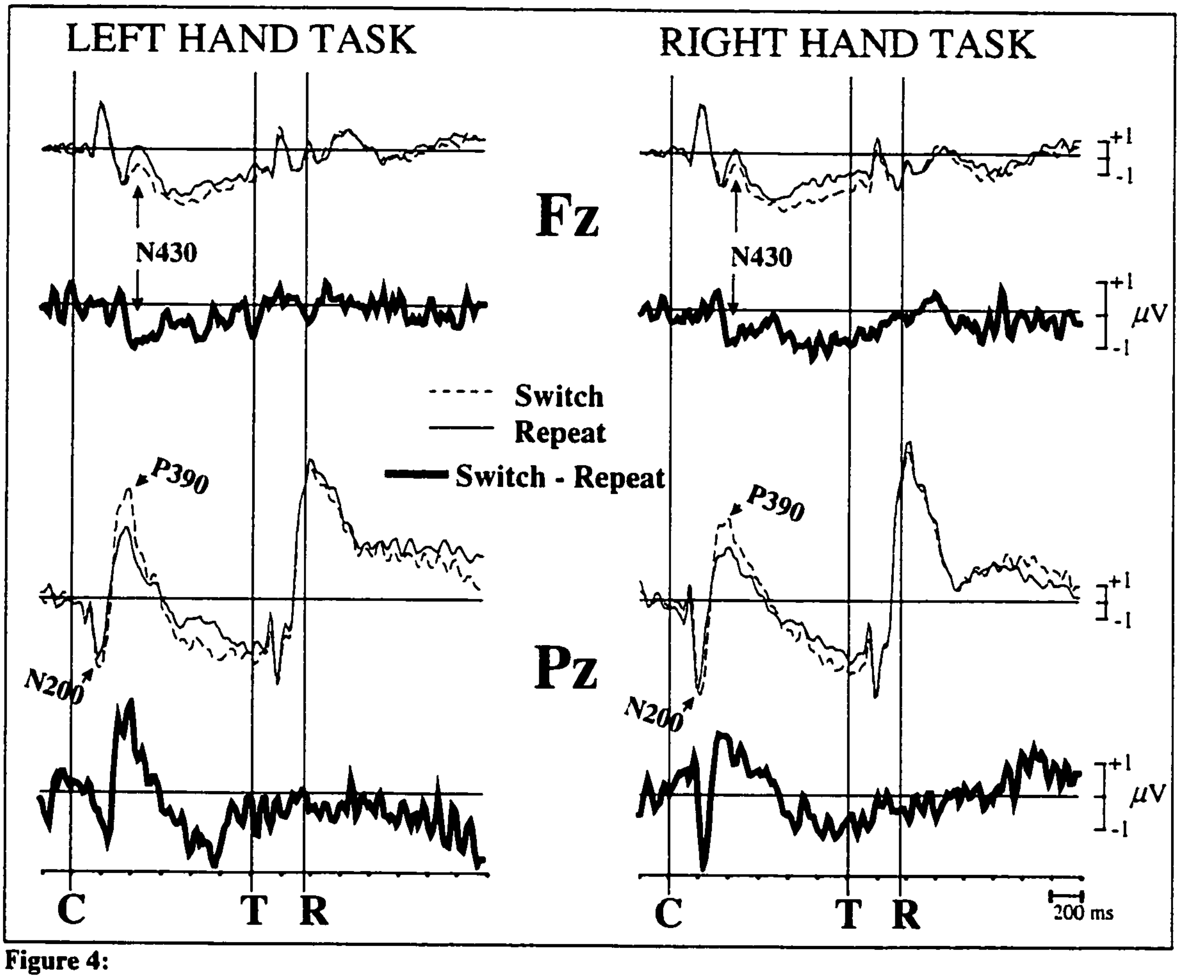

Figure 4:

Switch ERPs at mid-frontal (Fz) and mid-parietal (Pz) sites. The sweep is 3000 milliseconds long. The three vertical bars represent the Cue, Target, and Response. The cue stimulus occurs 200 ms after the onset of the sweep and the target 1200 ms after the cue. ERPs involving a left hand response are plotted at the left of the figure, and a right hand response on the right. Positivity is up. Switch trials (dotted lines) are superimposed on repeat (small smooth lines). Switch minus repeat difference waveforms are presented as thick smooth lines. The difference waveforms demonstrate that the enhanced switch ERPs are present after the cue, but not the target stimuli.

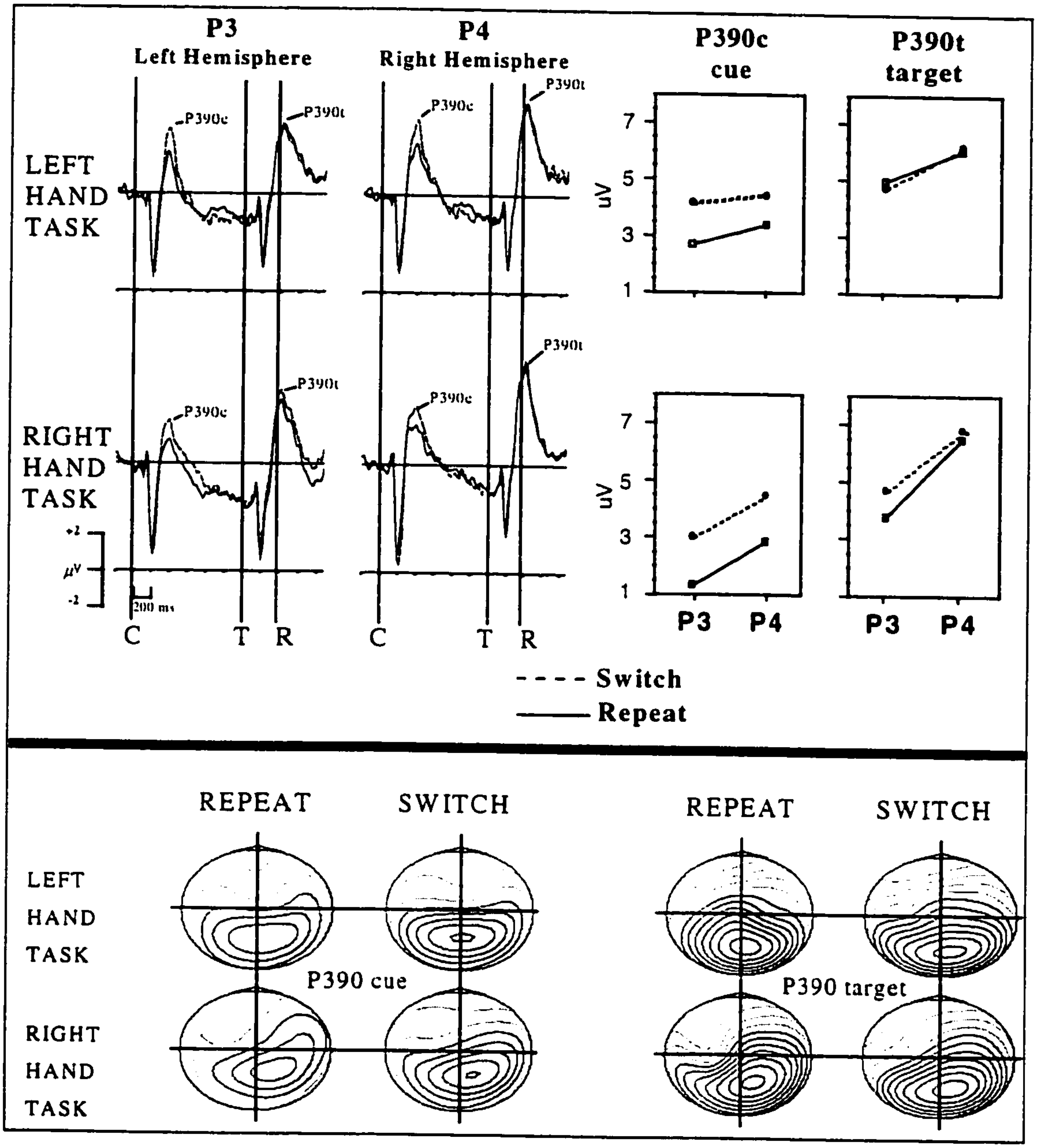

Figure 5:

Upper panel: P390 ERPs recorded from left (P3) and right (P4) superior parietal electrodes following the cue (P390) and target (P390T) stimuli. *Lower panel:* Spline maps for the P390 to cue and target stimuli. The view is looking down at the top of the head with the nose oriented towards the top of the page. Contours represent areas of equipotential voltage (surface potentials) separated from adjacent areas by differences of ± 1µV. Light areas represent negative voltage (current sinks) and dark areas correspond to positive voltage (current sources). The maps and waveforms show the right parietal focus of the P390 to the cue and target stimuli, and demonstrate that the P390 was larger for switch than repeat tasks only in response to the cue stimuli, and that the target P390 was larger than the cue P390.

larger than repeat trials (F (1,7) = 44.2, p < .001) and exhibited a bi-occipital (O1, O2) scalp distribution. The next ERP to vary with switching was the parietal P390 which was largest for switch than repeat trials (F (1,7) = 16.49, p < .01) as well as being larger over the right (P4) than left (P3) hemisphere (F (1,7) = 17.52, p < .01) (see Figure 5). Interestingly, the task-hand x hemisphere interaction was also significant (F (1,7) = 7.78, p < .05) indicating that the average amplitude of the P390 measured over the left parietal scalp was attenuated (> 1 μV) when the cue stimuli were oriented within the vertical meridian (Top-Bottom cue- Right Hand task) of the visual fields. The N200 and P390 peak latencies were both significantly earlier when the cue arrows were in the horizontal meridian of the visual fields during a Left-Hand Task (F (1,7) = 7.7 , 9.83, p < .05).

As shown in Figure 4, the larger P390 (Pz) during switch trials was followed by an enhanced negativity (N430) at the mid-frontal (Fz) site. The mid-frontal N430 peak exhibited greater negativity on switch than repeat trials (F (1,7) = 9.82, p = .01) with a peak latency that was significantly later (40 ms) than that of the P390 (F (1,7) = 5.77, p <

.05). That the N430 and P390 represent distinct ERP components is further demonstrated by the P390 being recorded in response to both the cue and target stimuli, whereas the N430 was primarily recorded following the cue (Figure 4).

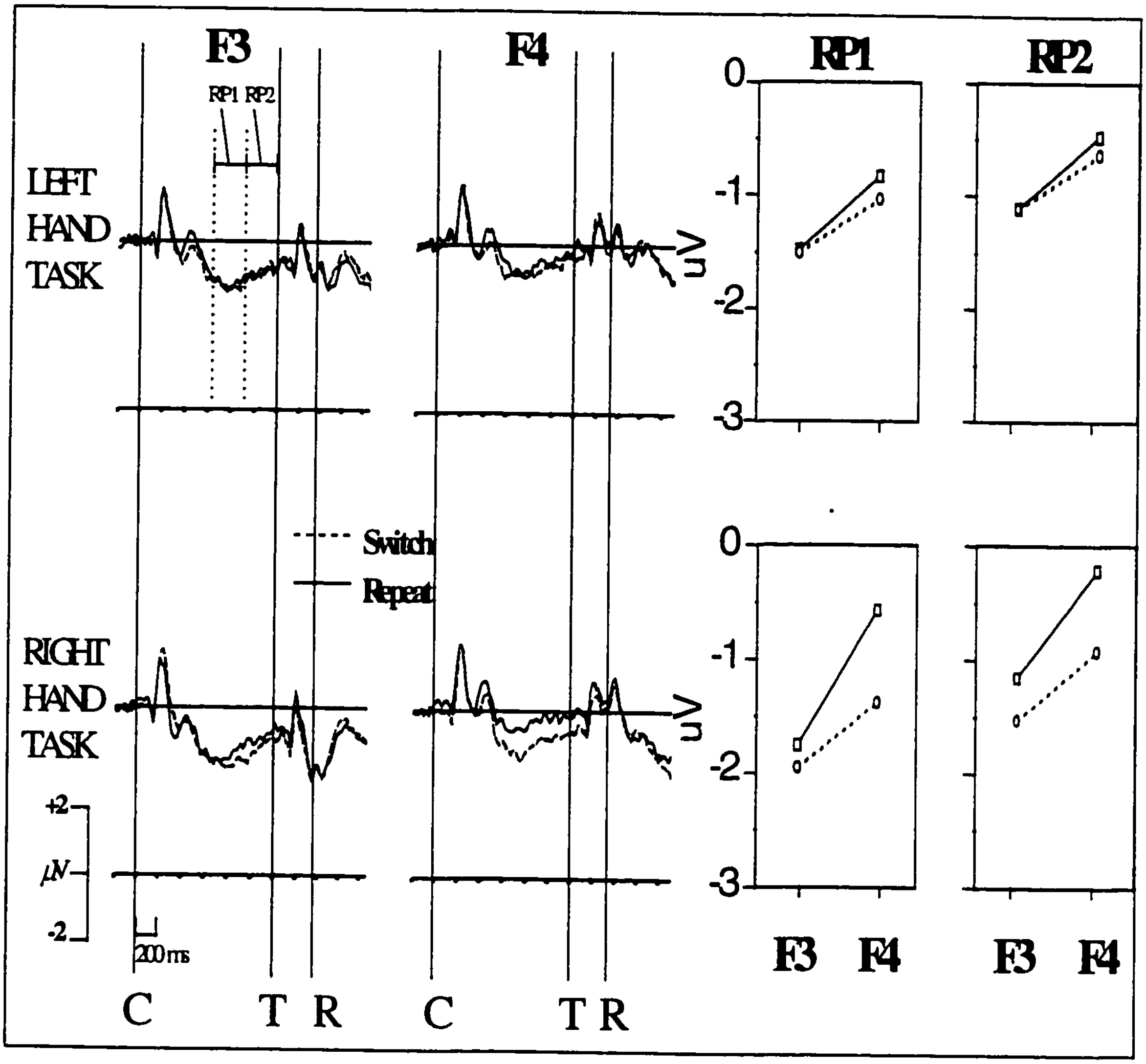

Figure 6:

Readiness Potential 600 to 300 ms (RP1) and 300 to 0 ms (RP2) prior to target onset at left (F3) and right (F4) mid-frontal electrodes. The figure highlights the greater negativity over the left mid-frontal region throughout the RP1 ($F(1,7) = 5.4$, $p = .05$) and RP2 ($F(1,7) = 11$, $p < .01$) epochs.

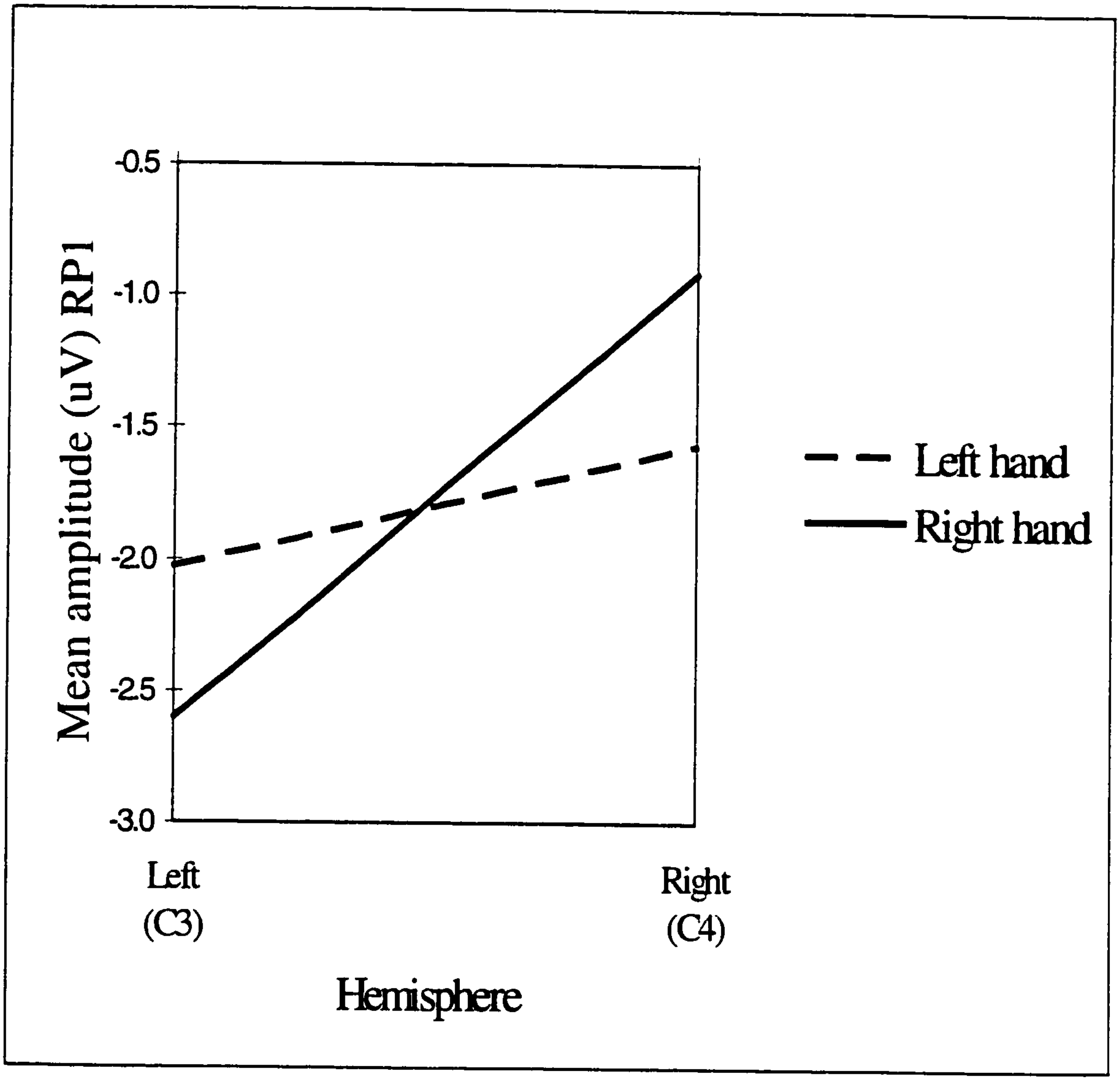

Figure 7:

Readiness Potential negativity largest over the central electrode site contralateral to the preparing response hand despite the underlying left hemisphere negative asymmetry.

Readiness Potential (RP): 1200 ms Cue-Target Interval

RP1 and RP2 at Central Electrodes:

The RP at the left (C3) and right (C4) central electrodes exhibited substantial hemispheric asymmetry during two pre-target average epochs. Significant hemisphere effects during the RP1, 600 to 300 ms pre-target ($F(1,7) = 19$, $p < .01$), and RP2, 300 ms pre-target to target onset ($F(1,7) = 7.7$, $p < .05$) epochs revealed that the average central RP was larger by approximately -1 μV over the left than the right central site. This asymmetry was clearly seen at the mid-frontal (F3, F4) electrode sites (see Figure 6) and was present both prior to and following the button press response. Despite this sustained left frontal negative asymmetry in the scalp topography, the hand x hemisphere RP interaction remained significant (Figure 7) during both the 600 to 300 ms ($F(1,7) = 67$, $p < .001$) and the 300 to 0 ms epoch ($F(1,7) = 15$, $p < .01$) revealing a greater negativity at the electrode site contralateral to the cued response hand. Thus, during the 600 to 300 ms epoch, the RP was larger over the left hemisphere during a right compared to a left hand response ($t(7) = -7.4$, $p < .001$), whereas there was greater negativity over the right hemisphere during a left than right hand response ($t(7) = -3.24$, $p = .01$).The hand x hemisphere interaction for the average RP between 300 ms pre-target to target onset was similar to the 600 to 300 ms interval ($F(1,7) = 15$, $p < .01$). However, during the 300 ms pre-target latency, the larger negativity over the left frontal region was only borderline ($F(1,7) = 5.6$, $p < .05$).

The hypothesized sequence x hand x hemisphere interaction was not significant at the central electrodes during either the 600 to 300 ms ($F(1,7) = 4.78$, $p = .06$) or the 300 to 0 ms pre-target epoch ($F(1,7) = 3.37$, $p > .05$). However, consistent with the stimulus-cued-completion hypothesis, a trend ($p = .06$) in the data did indicate that the RP exhibited a bilateral negativity during switch trials (see Figure 8) and an asymmetric, correctly lateralized topography during repeat trials (optimal response preparation?) (see Figure 9).

RP3 Combined over three Fronto-Central Electrodes:

The borderline three-way interaction of the RP at the central electrodes was investigated further by computing the average RP3 collapsed over three sets of left (C3, Fc1, Fc5) and right (C4, Fc2, Fc6) fronto-central electrodes during the 600 to 300 and 300 to 0 ms epochs prior to target onset (Figure 2 outlines the electrode combinations). For the 600 to 300 ms pre-target epoch significance was attained for hemisphere ($F(1,7) = 28$, $p < .001$), hand x hemisphere ($F(1,7) = 38$, $p < .001$), and sequence x hand x hemisphere ($F(1,7) = 7$, $p < .05$). Similarly, the hemisphere ($F(1,7) = 7.8$, $p < .05$) and hand x hemisphere ($F(1,7) = 10$, $p < .01$) interaction was significant during the 300 to 0 ms pre-target window, however during this epoch the three-way interaction was only borderline ($F(1,7) = 4.5$, $p < .07$).

Post-hoc analyses of the three-way interaction during the 600 to 300 ms pre-target epoch resulted in findings consistent with the bilateral central RP depicted in figure 8. During switch

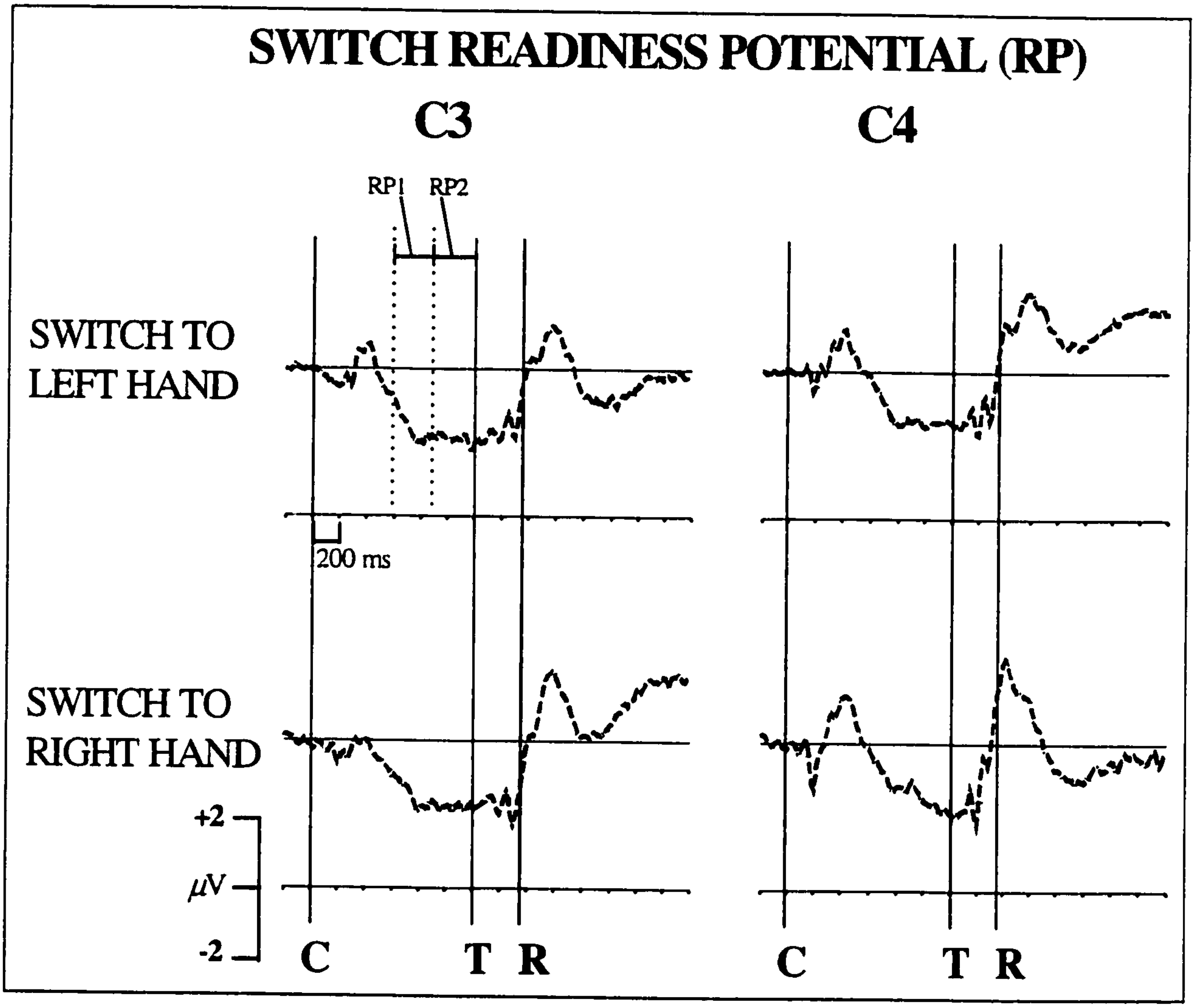

Figure 8:

Trend towards a bilateral RP during switch trials.

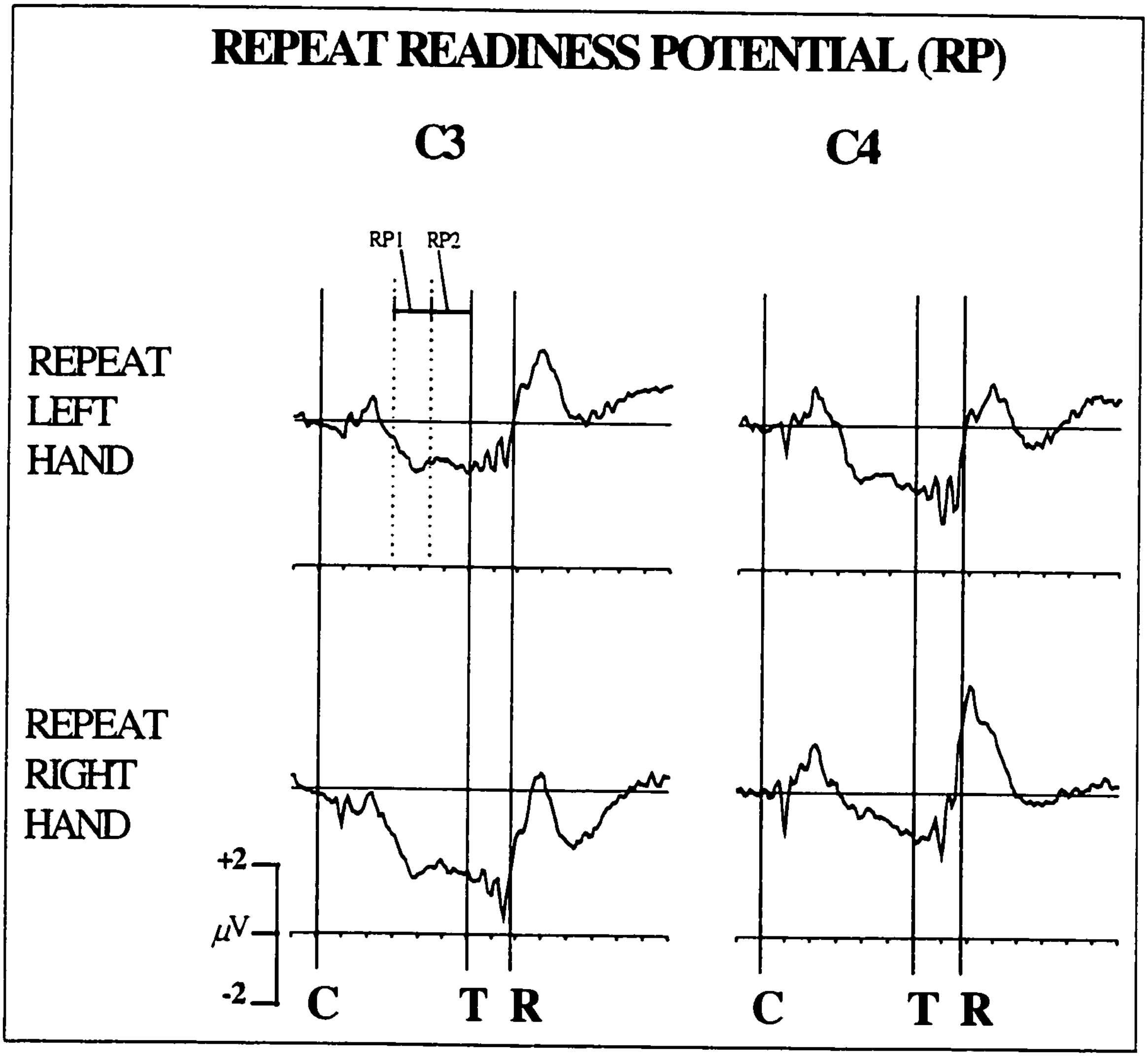

Figure 9:

RP during repeat trials shows greater negativity at the central site contralateral to the preparing response hand. This difference is especially marked for the right hand response. The less dramatic laterality difference during left hand trials might be due to the presence of a sustained negative slow wave over the left prefrontal region during all tasks (see Figure 7).

trials, the RP negativity was larger over the hemisphere of the hand that had responded on the preceding trial. Thus, the RP was larger over the left hemisphere ($t(7) = 3.6$, $p < .01$) on switch to the left hand (-2.1 μV) than repeat left hand (-1.5 μV) trials, and larger over the right hemisphere ($t(7) = 2.3$, $p = .05$) on switch to the right hand than repeat right hand trials - it is as though the wrong hand is being activated during switch trials.

Sustained Potentials: 200 ms Cue-Target Interval

The waveform was also analyzed for the 200 ms cue-target interval trials during the latency range of 900 to 1500 ms after the cue onset (i.e. approximately 440 to 1040 ms after the button press response) which is identical to the post-cue latency range analyzed for the 1200 ms cue-target interval trials. The ANOVA revealed a significant sequence effect ($F(1,7) = 29.4$, $p < .001$), task-hand x hemisphere ($F(1,7) = 6.2$, $p < .05$), as well as the sequence x task-hand x hemisphere interaction ($F(1,7) = 24.5$, $p < .005$). The 3-way interaction revealed that, during switch trials, an "RP-like" waveform was maximally recorded over the hemisphere ipsilateral to the correctly responding hand (i.e. contralateral to the hand that responded on the immediately preceding trial) (see Figure 10). Thus, the average amplitude at the left hemisphere electrode site (C3) was larger during switch (-1.21 uV) than repeat (0.23 uV) left hand trials ($p < .001$), whereas at the right central electrode (C4) the amplitude was largest during switch (-1.67 uV) than repeat (1.51 uV) right hand trials ($p < .001$). These two ipsilateral to the hand of response

"RP-like" ERPs are similar in latency and morphology to the bilateral RP recorded while subjects switched tasks during the 1200 ms cue-target interval trials (Figure 10).

Frontal Slow Waves

SPW and SNW:

Differential prefrontal activation was recorded during the cue-target delay at an inferior frontal electrode pair (F7, F8) during the latency range of 450 ms post-cue to 100 ms post-target. A significant hemisphere effect ($F(1,7) = 6.33$, $p < .05$) revealed a Sustained **P**ositive slow **W**ave (SPW) over the right (mean = + 1.6 μV) but not the left (mean = + 0.4) prefrontal site during the cue-target delay. This sustained positivity remained right frontal lateralized during both a left and right hand response (task-hand, $p > .05$) and for both switch and repeat trials (sequence, $p > .05$) and returned to baseline immediately after the button-press response (see Figure 11). No higher-order interaction approached significance ($p > 0.1$). That this waveform remained right frontal lateralized even while subjects were preparing either a right or left hand response suggests that this activity is not the inverse of the lateralized readiness potential. Nevertheless, a sustained left frontal negativity was simultaneously recorded at the left mid-frontal (F3) site (see Figure 6) during the latency range of 900 ms post-cue to target onset (i.e. SNW). Although the left frontal slow wave exhibited slightly different temporal properties than the right frontal positivity, it still remains difficult to determine whether this scalp electrophysiology shows a left-sided negativity, right-sided positivity, or some combination of the two.

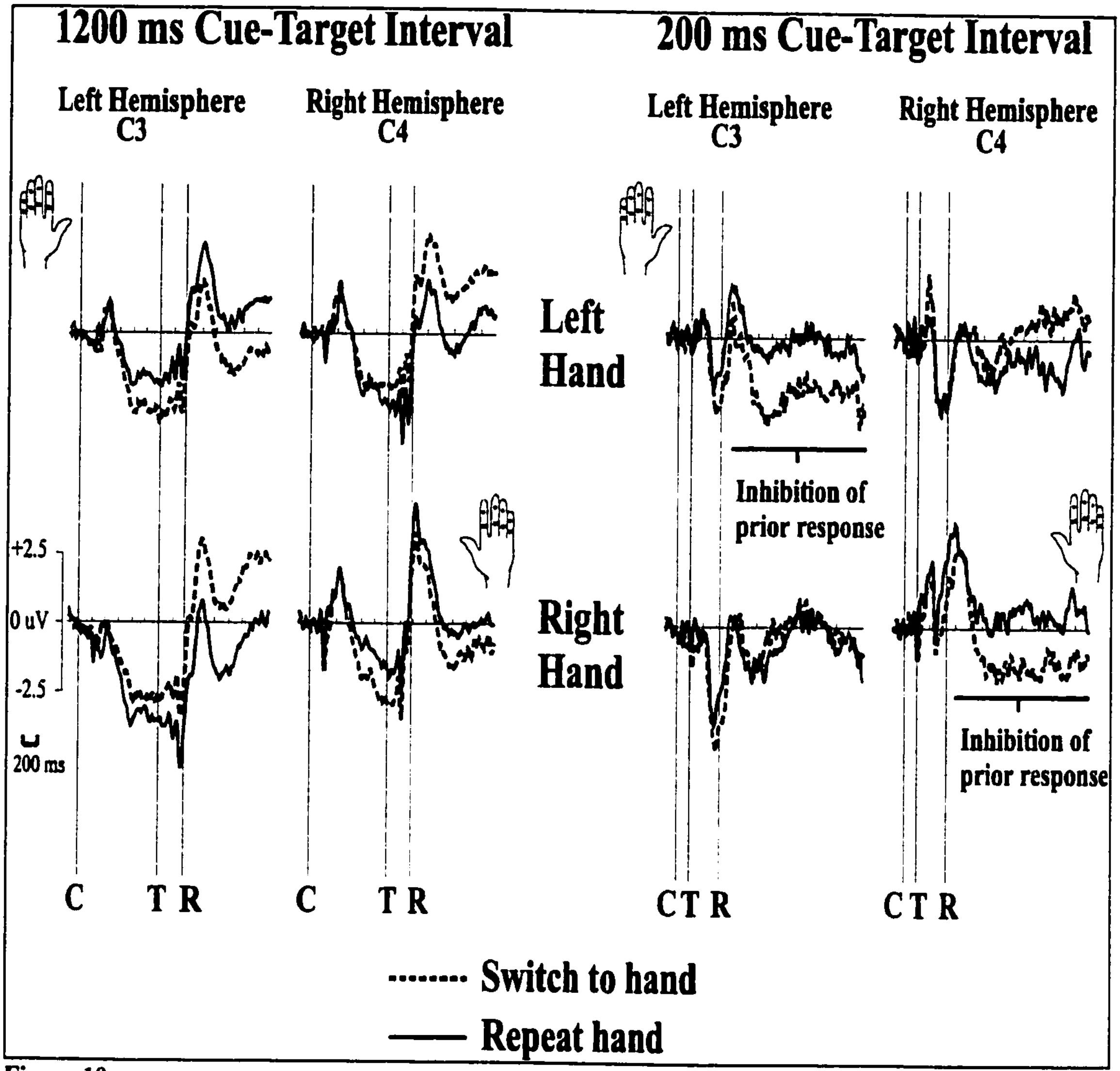

Figure 10:

Readiness potential (RP) during 1200 and 200 ms cue-target interval. The 200 ms switch trials exhibit a "RP-like" waveform that is maximally recorded over the hemisphere ipsilateral to the responding hand (i.e. contralateral to the hand that responded on the immediately preceding trial). That this waveform is only recorded after subjects have correctly responded to the switch task-hand trials suggests that this ERP may represent inhibition rather than the automatic activation of the hand that responded on the preceding trial.

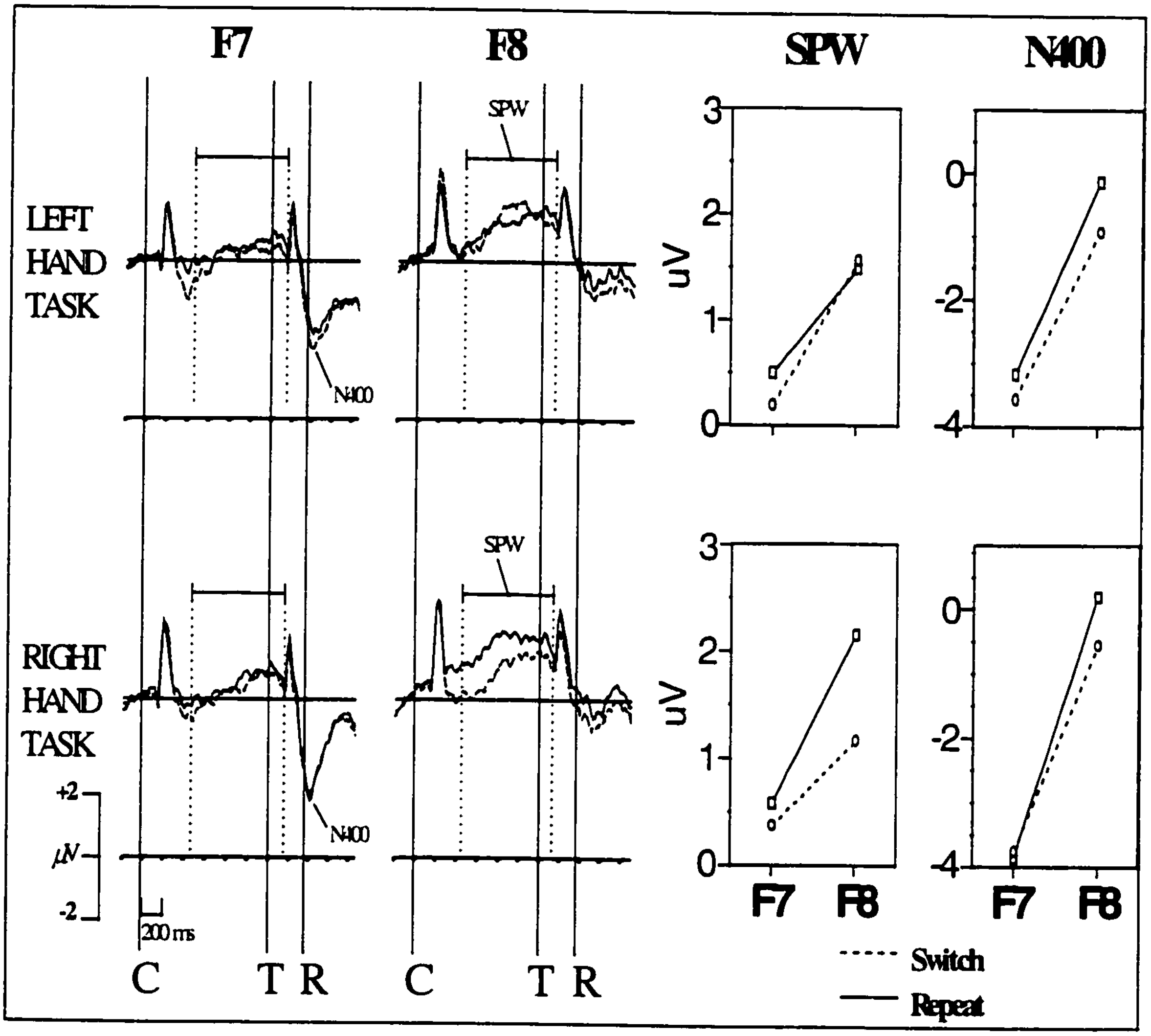

Figure 11:

Left (F7) and right (F8) lateral pre-frontal electrodes demonstrate a sustained positive slow (SPW) wave during the delay interval between perception of the cue and its associated target stimulus. A left frontal negative peak (N400T) was recorded only in association with the target stimuli and the button-press response.

Target Stimuli

N200T, P390T, Mid-frontal N430T:

Unlike the switch ERPs to cues, the identified ERP peaks to target stimuli did not exhibit significant amplitude variation across the sequence manipulation (see Figure 4). The amplitude of the occipital N200T, parietal P390T, and mid-frontal N430T components did not significantly differ between switch and repeat trials ($F(1,7) < 1$ for all comparisons). However, similar to the hemisphere asymmetry of the cue P390, the target P390 was significantly larger over the right (+6.4 µV) than the left (+4.5 µV) superior parietal recording site ($F(1,7) = 9.1$, $p < .05$) and was larger to target than cue stimuli (see Figure 5). The target N200T once again was symmetrical (hemisphere, $F(1,7) = .03$, $p > .05$).

Left Lateral Frontal Negative Peak: N400T

A large negative peak (N400T) was recorded at the left inferior-posterior frontal electrode (F7) between 300 and 500 ms after the target. This ERP was not significant ($p > .05$) for sequence, although a significant hemisphere effect ($F(1,7) = 14.1$, $p < .01$) revealed that this peak was -3.2 µV larger at the left than the right frontal electrode site. Interestingly, this left lateralized peak was not apparent after the cue arrows - it was only recorded after the target stimuli with an onset that preceded the button press (Figure 11). The ANOVA was not significant for the average peak latency (424 ms) of this component which was similar to that of the P390T latency recorded at the parietal electrode sites.

DISCUSSION

BEHAVIORAL

As predicted, the RT switch cost in the first experiment was largest during the short cue-target interval trials. This indicates that switching attention between tasks takes time (Meiran, 1996; Sudevan & Taylor, 1996). An alternative interpretation might be that there was interference between the processing of the cue and the processing of the target. This would have been greater in the short cue-target interval trials when the cues and targets were only 200 ms apart. We think this second explanation unlikely considering that processing in the primary visual pathways proceeds along multiple parallel rather than serial pathways (Goodale & Mishkin, 1995; Merzenich & Kaas, 1980; Van Essen & Maunsell, 1983).

The decline in the RT switch cost during the long cue-target interval trials indicates that subjects were using the cues to prepare for the upcoming task. An early switching stage was clearly present. However, contrary to previous reports in the task switching literature, and to our initial hypothesis, we did not obtain a residual RT cost (i.e. evidence for a late task-set switching stage). This may have resulted from the simple S-R mapping rules employed in our paradigm.

Studies that have obtained a residual RT switch cost have used more complex S-R mapping rules where subjects are forced to re-map response sets whenever they switch tasks (i.e. tasks share overlapping response sets) (Meiran, in press; Rogers & Monsell, 1995). In our experiment subjects did not have to re-map response sets during switch trials since the S-R associations for each task did not overlap, i.e. response sets were separately mapped to either the left or right hand. Another possible explanation is that the subjects were highly motivated and responded very rapidly. This is a reasonable interpretation since performance on the 200 ms catch trials was much better than chance (13% error rate), and quite fast (i.e. RTs of 440 to 480 ms) in comparison to the RTs recorded by other investigators (i.e 720 to 1200 ms) (Meiran, in press; Rogers & Monsell, 1995). It is possible that a highly motivated subject may complete all of the necessary switching prior to the target. Target-evoked completion of the switching may only occur when subjects are responding in a more relaxed manner.

CUE EVOKED ERPs

Consistent with the posterior-anterior attention switching dichotomy, two posterior (N200, P390), and one anterior (N430) ERP was associated with the attention switching trials and were active within the hypothesized 150 to 450 ms processing window.

The N200 wave was maximally recorded from the occipital scalp and occurred with opposite polarity over the frontal regions. It is probably generated in the extrastriate visual areas and the frontal negativity may reflect the opposite side of the dipole. Several negative waves in this latency range have been reported in association with the processing of visual stimuli. An N180 occurs with greater amplitude over the left occipital area when words are processed (Mangels, Picton & Craik, submitted; Compton, Grossenbacher, Posner & Tucker, 1991) and an N190 wave occurs with greater amplitude over the right temporoccipital regions when faces are perceived (Bentin, Allison, Puce Perez and McCarthy, 1996). These waves may be generated by activity in the inferior temporo-occipital cortex (Allison, Ginter, McCarthy, Nobre, Puce, Luby & Spencer, 1994). The N200 might be related to the disengagement of attention to location (Shedden, 1995) although in the present task this was not clearly a factor since attention to a particular location would not facilitate the task. Simson, Vaughan and Ritter (1977) reported a posterior N2 wave in association with the discrimination of visual targets, although the peak latency of this wave was 310 ms Other papers have reported earlier latencies such as approximately 250 ms (Luck & Hillyard, 1994) but these are significantly longer than the latency in the present experiment. Furthermore, the N2 wave is usually evoked by improbable targets and in the present experiment the two cue-stimuli were equally probable. A reasonable working hypothesis is that the N200 in this experiment is generated in the extrastriate visual cortex and indicates the perceptual processing of the information in the cue stimulus.

The P390 is very similar in scalp distribution and latency to the usual P300 wave recorded in response to a visual target (reviewed in Picton, 1992). The nomenclature, which provides the typical latency in a young adult making a simple discrimination, is based on the response to a target stimulus in the auditory modality and the wave peaks about 90 (Picton, Stuss, Champagne and Nelson, 1984) or 115 (Simson et al., 1977) ms later in the visual modality. The intracerebral generators of this wave are not clearly understood. Several regions of the brain, including the medial temporal lobes and the parietal association cortices probably contribute to the scalp-recorded activity (Picton, 1992: Halgren et al., 1995).

The P300 might relate to contextual updating of working memory (Donchin, 1981; Donchin & Coles, 1988), the extraction and utilization of relevant information contained within a cue (Deacon-Elliot & Campbell, 1987), the duration of stimulus categorization (Rugg et al., 1988), the transfer of information to consciousness (Picton, 1992; Picton, Donchin, Ford, Kahneman, & Norman, 1984), and/or perceptual or cognitive closure (i.e. erasure or resetting of perceptual analyzers) (Desmedt, 1980; Verleger, 1988). The data in the present experiment suggest that the closure argument is unlikely since the P390 was larger for switch trials. Switch trials would require less closure in the sense of dispensing with finished information, although they might entail more closure in the sense of resetting previous response rules. Since P300 seems more determined by stimulus factors than response factors, the larger waves on switch trials would argue against perceptual closure.

In the present experiment the peak latency of the parietal positive wave following the cue was between 0 and 100 ms earlier than the reaction time to the target. If one considers the visual difficulty of discriminating the cue and discriminating the target to be approximately equal, the peak of the P390 probably occurs at the time of perceptual discrimination. If one records the RT simultaneously with the P300, the RT occurs about 50 ms before the P300 peak in the simple oddball (Ritter, Simson, & Vaughan, 1972) as well as the omitted stimulus (Picton, Hillyard, & Galambos, 1976) paradigm. If a subject is instructed to emphasize response speed rather than accuracy the RT becomes faster although the P300 is invariant (Deacon-Elliott, 1988; Deacon-Elliott, Campbell, Suffield, & Proulx, 1987). The P300 is also unchanged when a behavioral response is not required by the task (Campbell, Suffield, & Deacon, 1990), and it is relatively insensitive to factors such as motor preparation and stimulus-response compatibility which affect RT by influencing response selection and execution (Magliero, Bashore, & Coles, 1984; McCarthy & Donchin, 1981). Thus, although RT is a composite measure of both stimulus evaluation and response production processes, the P300 appears to represent the time needed for stimulus evaluation.

The P390 recorded in the present experiment was larger over the right parietal scalp. The P300 wave is generally quite symmetrical (Picton, 1992) although some asymmetries occur in particular tasks depending upon the type of information being processed (Goodin, Waltz & Aminoff, 1990). In the present experiment the asymmetry may relate to the spatial nature of the stimuli (arrows) or to some involvement of the right parietal cortex in the actual switching of attention (Corbetta, Miezin, Shulman, & Petersen, 1993; Mesulam, 1981, 1990; Weintraub & Mesulam, 1987).

The P390 was smaller, particularly over the left hemisphere, during a top-bottom (right hand) task decision. We suspect that this effect was due to differences in the processing of the physical features of the cue arrows as they were located in the vertical or horizontal meridian of the visual fields rather than coding for the relevant response hand. This argument is based on the finding that the P300 is relatively insensitive to response selection factors (Magliero, Bashore, & Coles, 1984). In fact, despite the varied accounts of the meaning of the P300, a common underlying theme is that the P300 is more a function of stimulus evaluation processes (e.g. extract, classify, and recognize stimulus inputs) than it is of response production (e.g. anticipate, prepare, choose, and execute a response) (Picton, 1992).

In the present experiment the switch cue evoked a small negative wave that followed the P390 by about 40 ms and was recorded with maximal amplitude over the midline frontocentral scalp. This N430 is comparable to the frontal negative wave reported by Shedden (1995) and Harter and Anllo-Vento (1991) in their switching tasks. This process might be related to two ERP phenomena that are recorded in association with discriminative motor responses: the early Bereitschaftspotential and the error-related negativity.

The Bereitschaftspotential is the negative wave that precedes a motor response (Kornhuber & Deecke, 1965). The German word means "readiness potential". The later portion of this wave is lateralized over the cortex contralateral to the responding hand and will be discussed at greater length in the next section. The earlier part of the wave is maximally recorded from the vertex and mid-frontal regions of the scalp. Deecke and his colleagues (Deecke, 1987; Lang, Deecke, 1990; Cheyne, 1990) have suggested that this early part of the Bereitschaftspotential is generated in the supplementary motor area located on the medial surface of the frontal lobe. Physiological recordings in animals have demonstrated that this area is related to the planning and execution of complex motor movements (Tanji, 1994). Lang et al. (1990) recorded an enhanced negative wave at the vertex when a task became more complicated: musicians switched from a simple rhythm to one with different beats in each hand. They attributed this to the need for the supplementary motor area to supervise the response. Taylor (1978) reported a similar negativity in association with learning a complex motor response but did not attribute it specifically to the supplementary motor area. In the present experiment, it would be reasonable to propose that the supplementary motor area is briefly activated when the subject has to switch from one hand to the other.

When a subject mistakenly responds to a stimulus that should not have been responded to, an error-related negative wave can be recorded from the midline frontocentral regions (Falkenstein, Hohnsbein, Hoormann & Blanke, 1991; Gehring, Goss, Coles, Meyer & Donchin, 1993). Source analysis of this wave has suggested that it might be generated in the anterior cingulate cortex (Dehaene, Posner &Tucker, 1994). This area of the brain may be important in the online monitoring of task performance as part of the anterior attentional system (Posner & Peterson, 1990). In the present experiment the frontocentral negative wave was not associated with errors, but with the correct switching of response hand. The task does have some similarities to the NoGo tasks that are commonly used to elicit the error-related negativity, in that the previous active hand must be inhibited. The N430 in the present experiment probably respresents activity mainly in the supplementary motor area, but the anterior cingulate may also be involved.

The cue-evoked potentials suggest a sequence of events underlying the processing of the information in the cues. The N200 probably represents activity in the extrastriate visual cortex as the information in the cue is processed. The N430 likely represents activity in the supplementary motor area as the motor programs for a different set of responses are invoked. The nature of the P390 is not clear. It may represent further processing of the cue (for example, in relation to its meaning in this particular task) or it may represent some initiation of the switching process.

A major difficulty in relating these three waves to the process of switching is that the switch cue physically differed from the preceding cue as well informing the subject to switch. It is possible therefore that the switch-related amplitude enhancements of the N200, P390, and N430 in our experiment resulted from an exogenous switch in the physical features of the cue stimuli (i.e. horizontal to vertical arrows) rather than an endogenous switch of attention between tasks. The smaller ERPs during repeat than switch tasks may have resulted from a neuronal refractory period associated with stimulating the same cell assemblies during trials wherein the cue was the same as in the previous trial.

When stimuli are presented with short inter-stimulus intervals, the ERP responses are smaller than when the stimuli occur at long intervals. The classical example of this phenomenon is the auditory N1 response which decreases in amplitude as the inter-stimulus interval decreases from ten seconds to one second (reviewed in Näätänen and Picton, 1987). When the stimuli are different, the decrease in amplitude is less, presumably because there are neuronal assemblies that are specific to the different stimuli and therefore not previously activated. Although possible, this problem is unlikely in our experiment since the interval between the cues lasted several seconds and because other visual stimuli (the targets) intervened between the repeating or changing cues. The working hypothesis is therefore that the waves are indeed enhanced when the task-rules have to be switched.

MOTOR PREPARATION: READINESS POTENTIALS

Three RP laterality effects were obtained in experiment #1. First, the RP was largest contralateral to the preparing response hand on repeat trials and indicates correct motor preparation (Coles, 1989; Coles et al., 1995) Second, a bilateral RP was recorded during switch trials. This negativity over the hemisphere ipsilateral to the cued response hand may reflect either inhibition or automatic activation of the previous response set (hand) during switch trials. The automatic interpretation is more consistent with the target-evoked-completion hypothesis. Thus, both hands are activated (automatic activation prior to the target) but only one is allowed to respond to the target.

During the 200 ms cue-target interval switch trials, an "RP-like" waveform was maximally recorded over the hemisphere ipsilateral to the responding hand (i.e. contralateral to the hand that responded on the preceding trial). That this waveform was recorded after subjects had responded correctly on the switch task-hand trials could be argued as evidence in support of the automatic activation hypothesis The automatic (i.e. outside conscious control) activation of the previous response hand would occur prior to the target in the 1200 and 200 ms cue-target interval trials. Inhibition, on the other hand, would have to be conscious, and would be possible immediately after, and during, the response.

FRONTAL SLOW WAVES

Two other slow waves were measured in experiment # 1. First, irrespective of the preparing response hand, a sustained left dorsolateral prefrontal negativity was present throughout all trials (prior to and following the response). This may represent an executive monitoring process. A similar sustained left frontal negative wave has been recorded during several tasks involving memory (Duzel et al., submitted; Rösler, Heil, Glowalla, 1993; Rösler, Heil, Hennighausen, 1995a; 1995b). Stuss, Shallice, Alexander and Picton (1995) have suggested that the left dorsolateral frontal region may be involved in "setting attention" – the consistent mobilization of attentional schemata during a task.

Second, a sustained right pre-frontal positive slow wave was also recorded during both left and right hand trials. However, this waveform was only active during the delay interval between the visual evoked potential to the task-identifying cue stimulus and its associated response rule activating target. This time course is consistent with a working memory process that holds the cue information on-line until the target is presented and the appropriate response can be selected. Stuss and Picton (1978) reported a sustained right frontal positive wave during the processing of a visual stimulus in a task that involved changing stimulus-response rules. Functional magnetic resonance imaging of the human brain during working memory have indicated activity in the superior frontal sulcus bilaterally (Courtney, Ungerleider, Keil & Haxby, 1997; Courtney, Petit, Maisog, Ungerleider & Haxby, 1998). These results are compatible with the animal physiology showing activity in these areas of the frontal lobe during delayed tasks (Goldman-Rakic, 1987). Nevertheless, it remains difficult to determine whether scalp electrophysiology of the slow waves recorded in the present experiment reflects a left-sided negativity, right-sided positivity, or some combination of the two.

TARGET EVOKED ERPs

A left inferior frontal negative peak (N400T) was recorded only in association with the target stimulus and the execution of the button press response. This peak remained left frontal lateralized during both left and right hand responding. This unexpected finding may represent an electrical artifact, the negative pole of the right parietal P390T dipole to targets, or a left frontal dominance for selecting and activating the correct response rule.

SUMMARY

The behavioral results of the first experiment failed to replicate the finding reported in the literature of a residual RT switch cost when subjects are provided with adequate time to switch prior to the target. Our failure to replicate this result might be due to the relatively simple S-R mapping rules employed in our study. The present paradigm involved no overlap in the response rules. Different hands were used for the different tasks whereas the paradigms reported in the literature used the same fingers in both tasks. We will attempt to generate a residual RT switch cost in the second experiment by increasing the complexity of the S-R mapping rules associated with the switching task.

The first experiment yielded several ERPs that varied specifically with the cue to switch attention between tasks - a larger occipital N200, parietal P390, and mid-frontal N430. The P390 was also larger over the right than left parietal lobule. The increased amplitude of these ERP peaks during switch task trials may have resulted from endogenous mental operations involved in processing the need to switch attention, or from exogenous stimulus driven effects due to a switch in the physical features of the cue stimuli. The endogenous-exogenous hypothesis will be addressed in the second experiment by evaluating the peak ERPs when subjects switch cues, but do not switch tasks, and when subjects switch task, but do not switch cues. That the larger P390 over the right parietal recording site is due to a spatial evaluation of the cue stimuli will be evaluated in the second experiment by the inclusion of a second set of non-spatial (letter) cues presented at the center of fixation.

The RP was also found to vary with the cue to switch task-hands. The results indicated that, although the RP was correctly lateralized during repeat trials, a bilateral RP during task-hand switches revealed a larger negativity over the hemisphere of the hand that had responded on the immediately preceding trial. A similar asymmetry was observed during the infrequent 200 ms cue-target interval trials, however, during the short cue-target interval trials, this larger negativity over the hemisphere of the hand that had responded on the previous trial was generated even though subjects had already issued a correct response with the opposite hand.

The increased negativity ipsilateral to the response hand during switch trials may be due to the automatic activation or the inhibition of the response from the preceding trial. These interpretations will be evaluated in the second experiment by: 1) dropping the infrequent short cue-target interval catch trials and thereby removing any incentive (i.e. RT benefit) the subjects may have for automatically activating the immediately preceding hand during the upcoming trial; and 2) evaluating the amplitude of the correctly lateralized RP when subjects are forced to simultaneously inhibit the previous response, and prepare the current response, when both actions must be carried out on the same response hand during switch trials. This will be compared to the RP during switch trials wherein only the response preparation process is necessary for successful task performance.

One other peak and two slow wave effects were observed in experiment #1. First, a left lateral frontal negative peak was present only in response to the target stimuli. This may represent a frontal process involved in response selection, or an anterior inversion of the parietal P390 to targets. The response selection hypothesis will be evaluated in experiment #2 by attempting to dissociate the left frontal peak latency from that of the parietal P390 to target stimuli by increasing the complexity of the S-R mapping rules associated with the task. Finally, a left and right frontal sustained negative and positive waveform was recorded during the cue-target delay, and may represent executive monitoring, and working memory processes, respectively. These hypotheses will also be evaluated in the second experiment by comparing the amplitude of the respective ERPs across conditions of complex versus simple S-R mapping rules.

The results of this first experiment provide us with a sketch of what might be happening in the human brain when a human subject switches from one task to another. The information in the cue is analyzed and evaluated (N200 and P390) and, if the information indicates that switching is necessary the frontal regions of the brain set up the new stimulus-response rules (N430). These rules then prepare the appropriate hand for the response (RP) which is initiated when the target stimulus occurs. It is possible that the target may finalize the switching process. All of these processes appear to be under the supervision and monitoring of frontal processes which show up as sustained potentials during each trial. However, the sketch is ambiguous and several other interpretations of these results are possible. The second experiment will attempt to resolve some of these ambiguities.

EXPERIMENT #2

INTRODUCTION

The first experiment demonstrated ERP waves that are clearly associated with task-switching. First, the sequence of waves (N200, P390 and N430) that occur in response to the cue were significantly enhanced when the cue indicated that the task was to be switched. Second, the readiness potentials that developed prior to the anticipated movement were significantly different between switch and repeat trials. Third, large frontal sustained potentials occurred during the trials. These findings were exciting – they provided a clear physiological handle for what is going on in the brain during task-switching. However, the interpretation of what these ERP waves represent was not clear. Further experimental manipulations were necessary to define the cerebral processes indicated by the ERP stages.

One goal of the second study was to determine whether a residual RT switch cost was present when subjects switch between tasks having complex rather than simple S-R mapping rules. Such a finding would fit with the switch cost literature (i.e. the stimulus-evoked completion concept) and would support the original hypothesis of the first experiment that the residual RT switch cost reflects cognitive processes involved in the selection and activation of the response rules associated with task goals. The increased response rule complexity in the second experiment was achieved by cross-mapping the S-R rules for each task to a shared set of button press responses. In the first experiment, the S-R mapping across the "horizontal" and "vertical" tasks was completely independent - i.e. separate hands, separate response buttons. However, in experiment #2, the complexity of the response rules was increased by having the S-R rules across the two tasks share the same response mapping - i.e. same hand, same response buttons.

The original experiment confounded changes in the cue with changes in the task. This made it difficult to determine which of the ERP changes were stimulus-related and which were task-related. The enhanced N200 during switch trials might reflect exogenous stimulus (refractory period) effects, whereas the P390 and N430 might reflect endogenous cognitive mechanisms mediating a mental switch in task-set. This idea was tested by the addition of a second set of cue stimuli (symbolic - letters) which share the same task identifying characteristics as the spatial arrow cues but differed strikingly from the arrow cues in terms of their physical properties. Thus, in the second experiment, subjects could switch cues and/or switch tasks. The working hypothesis was that the N200 would be larger whenever subjects switch cues (for both switch and repeat task) whereas the amplitude of the P390 and N430 would only be larger when subjects switch tasks (for both switch and repeat cues). This double dissociation would support the interpretation that the P390 and N430 ERP effects in the first experiment arose from an internal switch in cognitive processing rather than an external switch in the physical features of the cue stimuli.

The right parietal distribution of the P390 could have been related to spatial processing rather than attention switching. This being true, then the P390 should not remain lateralized to the right parietal regions when subjects are prompted to switch attention based on verbal rather than spatial cues - both types of cues will be used in the second experiment.

The second experiment also attempted to replicate and expand upon the slow wave findings from experiment #1. Specifically, we attempted to increase the clarity of the slow wave components during the second experiment by increasing the number of scalp and facial recording electrodes to 46, by eliminating the short (200 ms) trials, and by increasing the number of subjects (to 14). The elimination of the catch trials also allowed the subjects to switch attention without trying to do this before an occasional early target. This could decrease the complexity of response preparation. Short (200 ms) trials were used in a control session at the end of the experiment to obtain baseline measurements of switch cost.

The bilateral readiness potential in the first experiment may represent automatic activation or inhibition of the previous response set (hand) on switch trials. Only the automatic activation interpretation is consistent with the stimulus-cued completion hypothesis. The second experiment will test the response inhibition interpretation. Specifically, if the larger RP negativity over the hemisphere of the previous response hand during switch trials represents inhibition of the previous response set, then the amplitude of the correctly lateralized RP should be larger when subjects switch between response sets involving the same response hand, than when switching occurs between hands. This hypothesis is based on the assumption that the magnitude of the scalp-recorded RP negativity during switch trials is additive over the contralateral scalp when subjects simultaneously activate inhibitory (of the previous response) and preparatory (of the current response) cognitive processes.

The other possible explanation for the bilateral RP in switch trials is that the previously responding hand may be automatically activated on every trial. The results of the 200 ms trials fit more easily with this explanation. The sustained negativity over the cortex contralateral to the non-responding hand may have been related to either inhibition or activation of the inappropriate hand. However, the inhibition would have to be consciously evoked following the perception of the switch cue. It would seem more reasonable that the brain would just activate the correct hand in these catch-trials and not consciously inhibit the response of the wrong hand after the correct one had responded. Activation could occur automatically and persist for a while.

HYPOTHESES

The following hypotheses were addressed in the second experiment:

1) Since subjects were able to use the task identifying cue stimuli prior to the targets during the simple and complex S-R mapping rule trials (cue-target interval = 1500 ms), the RT should have been longer for the control (cue-target interval = 200 ms) rather than the experimental

trials. This would indicate that subjects attended to and were processing the cue information prior to the targets during the experiment.

2) The other RT hypothesis was that a residual switch cost would be obtained for the complex and not the simple S-R mapping trials. This would support the notion of a late (response selection) switching stage (the stimulus-evoked completion hypothesis).

3) The ERP switch components (N200, P390, N430) should replicate in this second experiment. We suspected that the larger N200 amplitude during switch trials represented a refractory period (stimulus) effect due to the presentation of a different cue from the previous cue, whereas the larger parietal P390 and mid-frontal N430 during switch trials represented mental operations involved in programming the switch of attention between task-sets. The hypothesis was that the N200 amplitude would only be enhanced when there was a switch in cue stimuli, whereas the P390 and N430 would be enhanced only when there was a switch in task.

4) A further hypothesis concerned the right parietal maxima of the P390. If the right parietal focus of the P390 represents an endogenous attention switching stage rather than processing of the spatial arrow cues, then symbolic letter cues should also elicit a P390 with a right parietal scalp distribution.

5) The bilateral RP on switch trials may represent inhibition or automatic activation of the previous response hand. The hypothesis was that the bilateral switch RP would not replicate during the simple (2 hand) S-R mapping blocks since there were no catch trials and thus no

benefit for automatic activation of the previous response hand. If the bilateral RP was still present, then the inhibition hypothesis would be tested by comparing the amplitude of the RP contralateral to the preparing response hand during simple (2 hand) and complex (1 hand) S-R mapping switch trials. During the complex (1 hand) switch trials subjects must simultaneously inhibit the previous response and prepare the current response - both processes must be carried out on the same response hand which should increase the amplitude of the RP. Thus, the inhibition hypothesis would be supported if the RP contralateral to the cued response hand was larger during the complex (1 hand) than the simple (2 hand) task switch trials. The automatic activation hypothesis would be supported if the RP was unaffected by the complexity of the task.

6) The left frontal sustained negativity from the first experiment may represent a behavioral monitoring process and therefore should exhibit greater surface negativity during complex than simple S-R mapping tasks.

7) The right frontal slow positive wave was interpreted as indexing working memory and therefore should not vary in amplitude with complex and simple S-R tasks since the same number of S-R associations (2) must be held on-line during the cue-target interval for both tasks.

8) The first experiment also yielded a large left prefrontal negative peak (N400) only in association with the target stimuli and the selection-execution of the motor response. This component may represent an anterior inversion of the parietal P390. However, although a

parietal P390 was generated for both cue and target stimuli, the N400 was only recorded in association with the target (and response). Thus, it is possible that the N400 represents a distinct cognitive process associated with response generation rather than the anterior end of the P390 dipole. If the N400 is differentially associated with response selection processes, then its peak latency should dissociate from that of the P390 during the complex compared to the simple S-R mapping rule conditions in the second experiment. Thus, it was hypothesized that the P390 peak latency (goal identity?) would be constant across the simple and complex S-R tasks, whereas the target N400 peak latency (response rule activation?) would be significantly later for the complex than the simple S-R mapping task. This temporal dissociation would be consistent with a two-stage (parietal goal identity, frontal response rule selection) model of attention switching.

METHODS

SUBJECTS

Fourteen right-handed volunteers (3 female) with ages between 21and 39 (mean = 29) years participated in the experiment. All subjects were university graduates, with normal vision, and no history of neurological impairment. One subject's data was dropped from the ERP and RT analyses due to excessive slow wave artifacts and extremely variable RTs.

PARADIGM

In this second experiment the 2 x 2 grid was displayed continuously on a video monitor positioned 75 cm in front of the subject. The grid was a 6 cm square (4.5 degrees). The target was an 8 mm (0.6 degrees) diameter red circle that appeared in one of the four quadrants formed by the yellow grid. Once again the target stimulus could be responded to in two different ways - whether it was in the Left or Right half of the grid (Left-Right task) or whether it was in the Top or Bottom half of the grid (Top-Bottom task). The subject was provided a warning cue so that he or she could prepare to respond appropriately when the circle came on. During the experiment the cue to target interval was a constant 1500 ms. The inter-trial interval (between the response to the target and the next cue) varied randomly between 1300 and 1700 ms.

Two kinds of cue stimuli occurred. A spatial cue consisted of arrows either above and below the grid (Top-Bottom task) or to the left and right of the grid (Left-Right task). A symbolic cue consisted of a letter in the center of the grid with H representing a Horizontal (Left-Right task) decision and V representing a Vertical (Top-Bottom task) decision (see Figure 12). Thus, over a series of trials, subjects could switch tasks and repeat the cue modality (e.g. H to V, V to H, ⬄ to ⇳, or ⇳ to ⬄cues), or switch the cue modality but repeat the type of task (i.e. H to ⬄, ⬄ to H, ⇳ to V, or V to ⇳).

Experiment #1 had only one type of recording block involving simple S-R mapping rules where the response sets for the Left-Right and Top-Bottom task decisions were mapped to separate hands. Experiment #2 involved a replication of this simple (two hand) S-R mapping (Block 1) (Figure 13, Upper panel), as well as 2 separate blocks of complex (one hand) S-R mapping trials that forced subjects to re-map rather than simply enable the S-R mapping rules across the Left-Right and Top-Bottom tasks. Thus, during complex S-R trials, the target left and right as well as the target top and bottom stimulus position in the grid were all mapped to two button presses on either the left hand (Block 2) or the right hand (Block 3) (see Figure 13, Lower panel).

Separate left and right hand conditions were run in order to demonstrate that non-motor prefrontal slow wave asymmetries during the cue-target interval remain lateralized during either a right or left hand response during the complex S-R mapping rule trials and therefore are not artifacts related to the readiness potential.

Simple S-R Blocks

The blocks of Simple S-R mapping rule trials represent a repetition and extension of Experiment #1 as subjects were instructed to respond to the Left-Right and Top-Bottom tasks in the two-hand four-button press response mode. Thus, during a Left-Right task the subject is to respond with the left hand by pressing one button if the target is on the left (left middle finger) and another button if the target is on the right (left index finger). During the Top-Bottom task the right hand responds by pressing one button if the

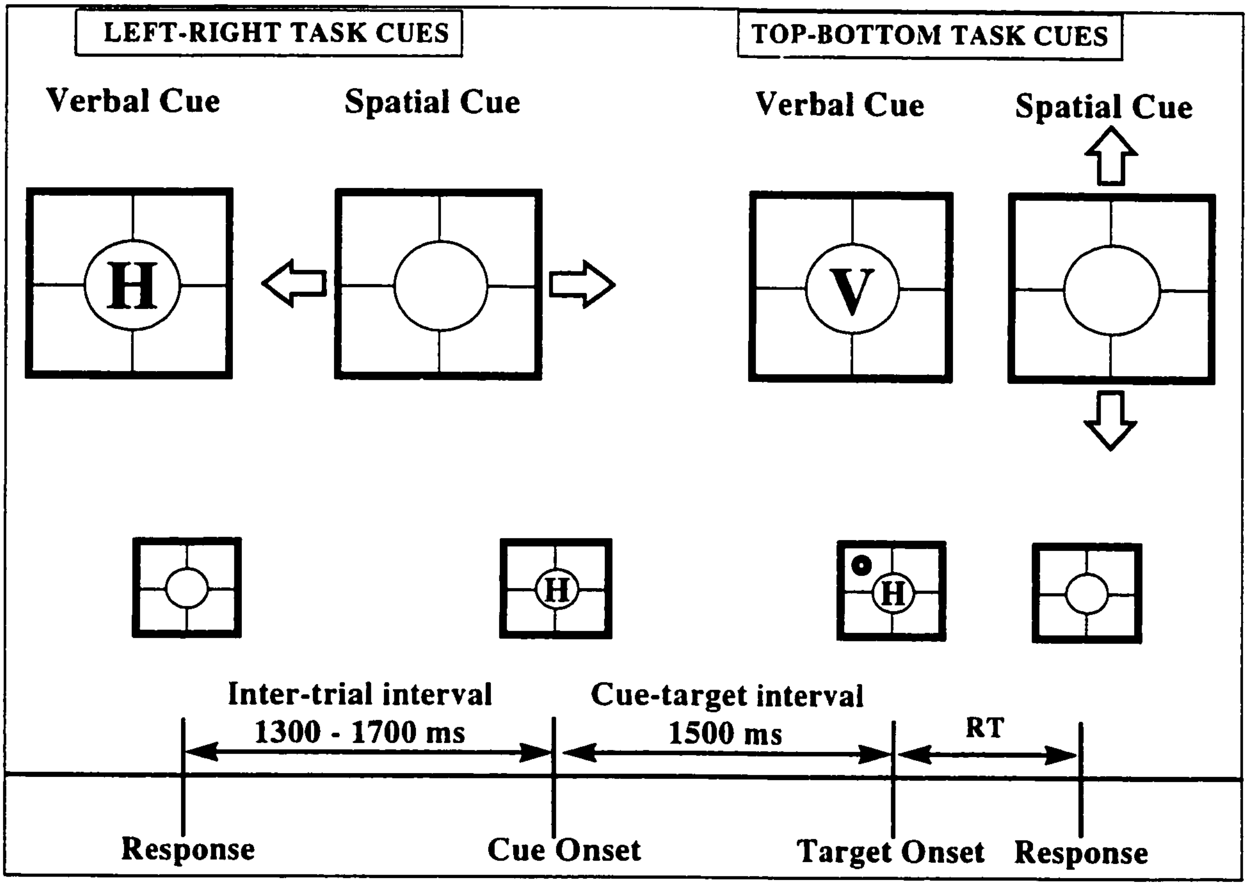

Figure 12:

Letter and spatial cues in the second experiment and stimulus onset-offset parameters.

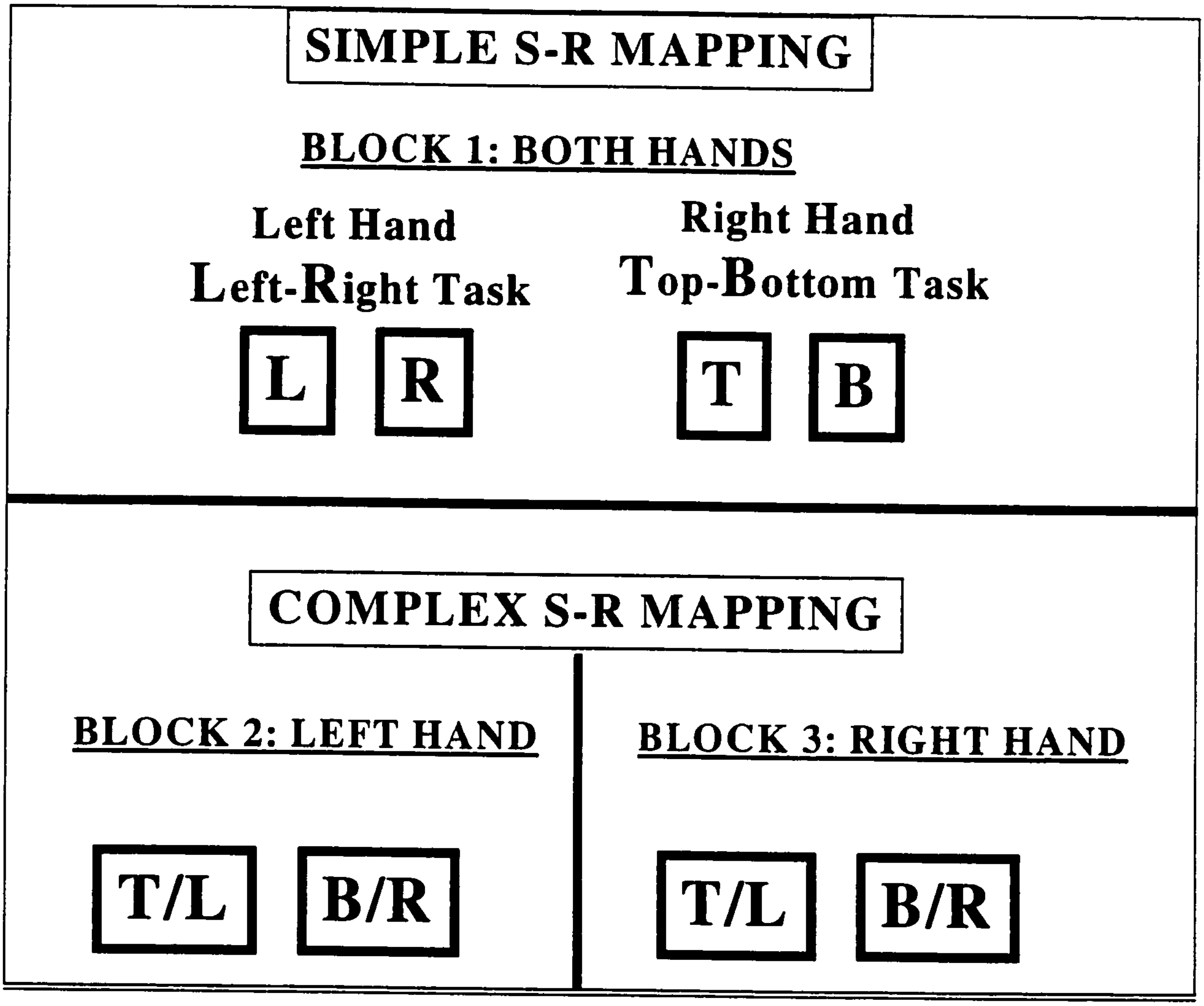

Figure 13:

Organization of button presses during the simple (two hand) and complex (one hand) S-R mapping tasks. The squares represent the buttons used for response (4 buttons in block 1, and 2 buttons in blocks 2 and 3). Letters within each square correspond to button press S-R mappings based on the position of the target in the grid during each task: Left-Right task, **L** = Left, **R** = Right; Top-Bottom task, **T** = Top, **B** = Bottom.

target is on the top (right middle finger) and another button if the target is on the bottom (right index finger) (see Figure 14, Upper panel). Switch versus repeat effects were obtained for Task-hand and Cue modality.

Task refers to whether subjects repeat or switch between a left-right or top-bottom analysis of the target location. The Hand variable, however, refers not only to the cued left or right hand response, but also to the physical features of the cue stimulus. Thus, in the simple S-R block, a Left hand trial also refers to an H or ⇔ cue, and a right hand trial also refers to a V or ⇕ cue.

Complex S-R Blocks

The complex S-R mapping rule trials were divided into two separate blocks where responses were coded to either the left or the right hand. Two key-presses represented all four possible responses. In block 2, for example, the target Top and target Left task decisions were both mapped to the middle finger of the left hand, while Bottom and Right positions were both mapped to the index finger (see Figure 13, Lower left panel). The response complexity of this set-up derives from the overlap of the S-R sets so that subjects must re-map the button-press responses whenever there is a switch in task. In contrast, during the simple S-R task, the S-R sets are completely independent (separate hands, separate response buttons) and subjects merely have to match the button press to the location of the target within the grid. Although the coding is simple in that there is no response-overlap, it is not one-to-one since two target stimuli are mapped to each button.

Control Blocks

Experiment #2 also differed from the first experiment in that there were no 200 ms (20% of trials) cue-target interval catch trials in the new design. Eliminating the infrequent catch trials removed any incentive (i.e. RT benefit) for automatically activating the immediately preceding response hand during the current trial (i.e. bilateral readiness potential on switch trials). Moreover, eliminating the catch trials increased the signal-to-noise ratio of the ERPs by increasing the number of experimental trials. However, the larger switch cost during the short (200 ms) than long (1200 ms) cue-target interval trials in the first experiment verified that subjects were actively using the cues to prepare for the upcoming target. Thus, as a check on subject preparation, RT was also recorded during five blocks of control trials immediately following the blocks of simple and complex S-R mapping rule trials. During the control blocks the cue and target onset asynchrony was 200 ms. This design prevented subjects from using the cue to prepare their response in advance of the target. The inter-trial interval (i.e. response to cue) during practice trials was 1300 ms more than during the experimental blocks in order to maintain the same rate of trial presentation.

BEHAVIORAL MEASURES

For each subject in each condition the median RT was measured for correct responses only. Separate across-subjects averages were computed for the simple (2 hand), complex (1 hand), and control trial blocks. A switch cost was calculated by subtracting the RT when subjects repeat a task (or cues) from the RT when subjects switch tasks (or cues). Variance inequalities in the data were further minimized by computing square root transformations of the average RTs.

ELECTROPHYSIOLICAL MEASURES

Data Recording

The EEG was recorded with recessed tin electrodes mounted in an electrode cap with 46 standard 10-10 scalp locations (Figure 14). All electrodes were referenced to the vertex (Cz) and converted to an average reference off-line prior to analyses. Inter-electrode impedance was maintained below 5 kOhms. EEG was recorded with a bandpass of 0.5 to 50 Hz at a rate of 250 samples/sec. Epochs were collapsed off-line to 180 points representing one sample every 16.67 ms over a 3 second sweep including a 200 ms pre-cue baseline. Rejection for movement artifact was set at ± 600 μVolts on any channel. As in the first experiment, ocular source components were used to remove ocular artifacts from each subjects averaged ERP data (Berg & Scherg, 1991; Lins, Picton, Berg, & Scherg, 1993a; Lins, Picton, Berg, & Scherg ,1993b).

RECORDING PROCEDURE

Prior to data recording, all subjects were allowed to familiarize themselves with the S-R mapping rules until they were able to make 15 consecutive correct responses for each type of trial block. ERPs and behavioral data were recorded while subjects completed 10 separate 50 trial blocks for each of the Simple, Complex (Left hand) and Complex (Right hand) S-R mapping conditions during the 1500 ms cue-target interval experimental trials. The cues and targets were randomly selected from the pairs of letter and spatial cues and the 4 target positions. At the end of the three experimental trials, behavioral data was recorded during 5 blocks each of 50 control trials wherein the cue and target onset asynchrony was 200 ms.

Subjects were instructed to maintain fixation at the center of the grid throughout the recording blocks, and to try not to make any unnecessary eye or muscle movements. Subjects were also repeatedly encouraged to use the cue stimuli to prepare their response in advance of the target in order to facilitate a faster RT.

ANALYSIS

In all analyses the electrophysiological data were collapsed according to whether the cue modality switched (e.g. arrow to letter, letter to arrow) or repeated, or the task switched (e.g. H or ⬄to V or ⇳ , V or ⇳ to H or ⬄) or repeated. The data was not re-averaged according to whether the cue stimulus itself repeated or switched since the change in the type of cue should cause as large an affect as a change in the specific cue and since measuring data according to the specific cue sequence would have resulted in an intractable set of data.

Independent variables were Cue sequence (repeat v. switch), Task sequence (repeat v. switch), Stimulus (letter v. arrow), Hemisphere (left v. right electrode), and S-R complexity (simple v. complex). The scalp distribution of the P390 was examined using a three way ANOVA using stimulus type as one variable, hemisphere as the second variable, and electrode

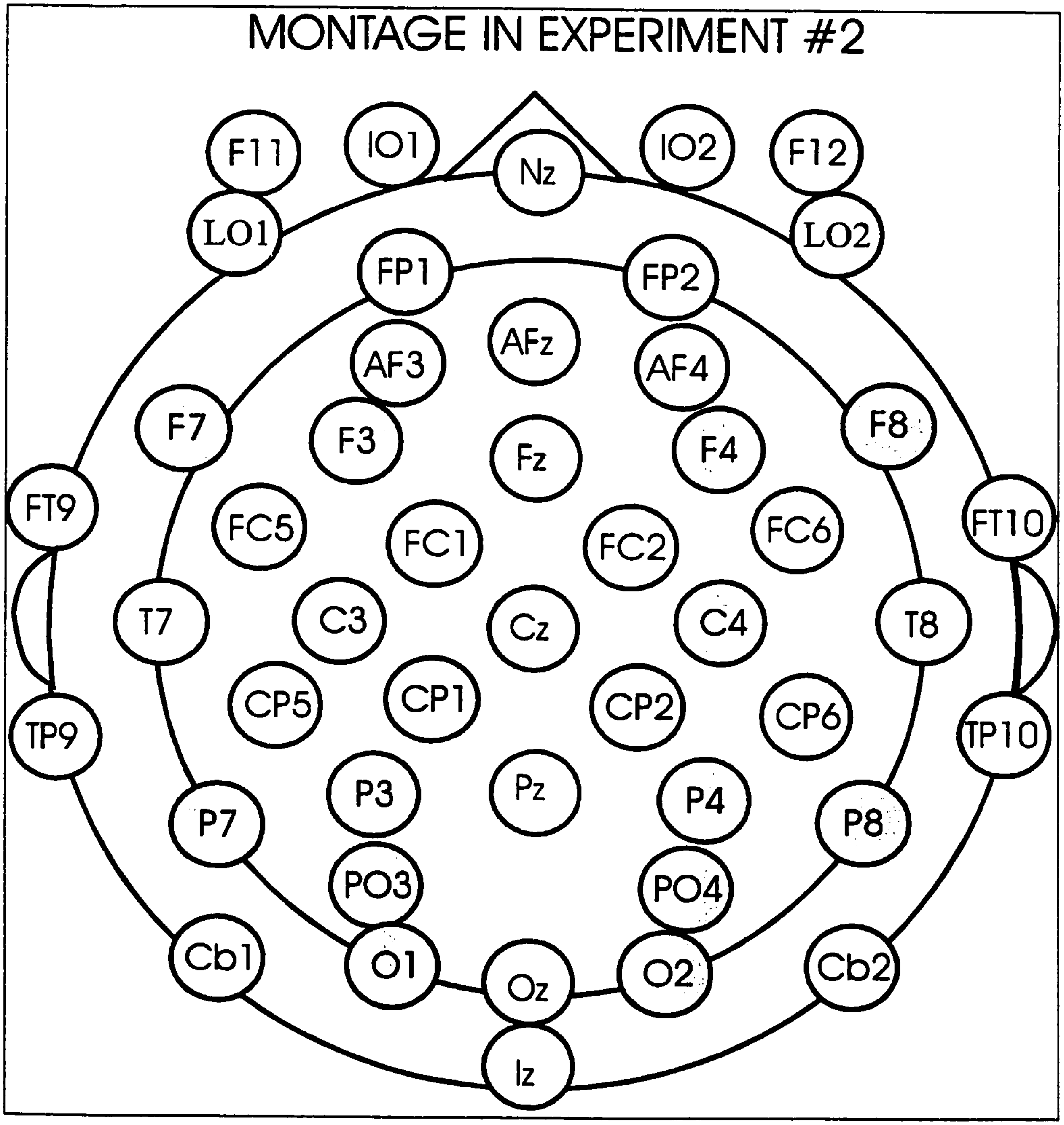

Figure 14:

Recording montage used in experiment #2. Shaded circles represent sites where ERPs were statistically analyzed for homologous pairs of electrodes location as the third variable [1) dorsal central-parietal (CP1,CP2), 2) parietal (P3, P4), and 3) ventral temporal-parietal (P7, P8)]. The P390 latency was evaluated using a 2 way ANOVA with stimulus type and electrode location variables. The RT switch costs from the simple and complex S-R mapping rule trials were compared to RTs obtained during the control trials when the cue-target interval was 200 ms. Behavioral and ERP data were analyzed with 2 separate repeated measures ANOVA for Repeat cue modality vs. Switch cue modality, and Repeat task vs. Switch task. ERP and statistical data from the complex S-R mapping rule trials are only presented as they relate to the hypotheses of interest.

ERP MEASUREMENTS

Peak and latency measurements were obtained from electrode sites where the component of interest was maximally recorded. The amplitude of ERP slow waveforms was quantified as the mean voltage within a specified latency range relative to the mean voltage 200 ms prior to the cue onset. The following ERPs were identified and measured:

Cue ERPs

(i) N200: maximum negative peak at O1 and O2, and PO3 and PO4 within the latency range of 70 to 300 ms post-cue.

(ii) P390: maximum positive peak at P3 and P4 within the latency range of 300 to 700 ms post-cue. Separate measurements were also made after identifying peaks at CP1 and CP2 within the latency range of 300 to 700 ms post-cue, and at ventral locations at P7 and P8 within the latency range of 300 to 700 ms post-cue.

(iii) Mid-Frontal Negative Wave: N740, maximum negative peak at Fz within the latency range of 300 to 1200 ms post-cue. In experiment #1, the N430 was selected as the largest negative peak between 300 and 700 ms after the cue. However, a visual inspection of the individual subject and grand average waveforms in experiment #2 indicated that the Fz peak during switch trials was delayed relative to the first experiment by approximately 300 ms. Indeed, there were no consistent negative peaks at Fz across subjects in the 300 to 700 ms time-window. Accordingly, in experiment #2, the N430 peak latency range was extended up to 1200 ms post-cue and was renamed the N740.

Readiness Potential

(iv) Readiness Potential: RP, mean area under the curve at C3 and C4 during the latency range 900 to 1500 ms post-cue (i.e. 600 ms pre-target to target onset).

Frontal Slow Waves

(vi) Sustained Positive Wave: SPW, mean area under the curve at F7 and F8 during the latency range 450 to 1600 ms post-cue (i.e. 1050 ms pre-target to 100 ms post-target).

(vii) Sustained Negative Wave: SNW, mean area under the curve at F3 and F4 during the latency range 900 to 1500 ms post-cue (i.e. 600 ms pre-target to target onset).

Target ERPs

(viii) N200T: maximum negative peak at O1 and O2 within latency range of 70 to 300 ms post-target.

(ix) P390T: maximum positive peak at P3 and P4 within latency range of 300 to 700 ms post-target.

(x) N400T: maximum negative peak at F7 and F8 within latency range 300 to 700 ms post-target.

RESULTS

BEHAVIORAL DATA

Control vs. Experimental

The RT switch costs were significantly longer during the control trials when the cue and target onset asynchrony was 200 ms compared to the experimental trials wherein the cue preceded the target by 1500 milliseconds. Overall median RT during the control trial (426 ms) was significantly delayed ($p < .001$) by 99 ms compared to the RT for complex trial blocks during both switch and repeat cue modality and switch and repeat tasks (all RTs approximately 327 ms). Similarly, the control trial RT was slower by 109 ms in comparison to the RT for simple trials which was approximately 317 ms for switching and repeating tasks or cues.

In the control blocks, a significant ($p < .01$) 22 ms cost for switching tasks exceeded a switch cost of -1.3 ms in the complex - 1 hand trials ($F(1,12) = 29.71$, $p < .001$), and -3.9 ms in the simple - 2 hand trials (Figure 15 upper graph). The negative sign in front of the RT indicates a small (but non-significant) benefit in the switch trials compared to the repeat trials. There was also a significant cost of switching cues on the control task ($F(1,12) = 21.2$, $p < .001$) but this was smaller than the effect of switching tasks (Figure 15 lower graph). A switch cost was not obtained for the switch versus repeat task RTs for either the complex (327 - 328 ms) or the simple (316 - 319 ms) S-R mapping rule blocks of trials ($F(1,12 = 0.1$ & $.07$, $p > .05$) (Figure 15 upper graph). In the cue sequence ANOVA, the RT costs associated with switching versus repeating cue modality for both the complex-1 hand (328 - 327 ms) and simple-2 hand (319 - 315 ms) trials were also non-significant ($p > .05$) (Figure 15 lower graph).

Simple vs. Complex

The hypothesis that a residual switch cost be present in the complex - 1 hand trials was not supported by either the median ($F(1,12 = 0.2$, $p >.05$) or the mean square root RTs during switch and repeat trials ($F(1,12 = 0.02$, $p >.05$). In fact, both the complex and simple trial blocks exhibited a small RT benefit of switching (Figure 15). Hence, there was no significant RT effect of S-R mapping complexity. The overall RT was significantly longer for the complex (329 ms) than simple (314 ms) trials for the task sequence ($F(1,12) = 8.4$, $p = .01$) analysis (Figure 15 upper graph). Similarly, the RT was an average of 15 ms longer for the complex than simple trials in the cue sequence ANOVA ($F(1,12) = 8.4$, $p = .01$) (Figure 15 lower graph).

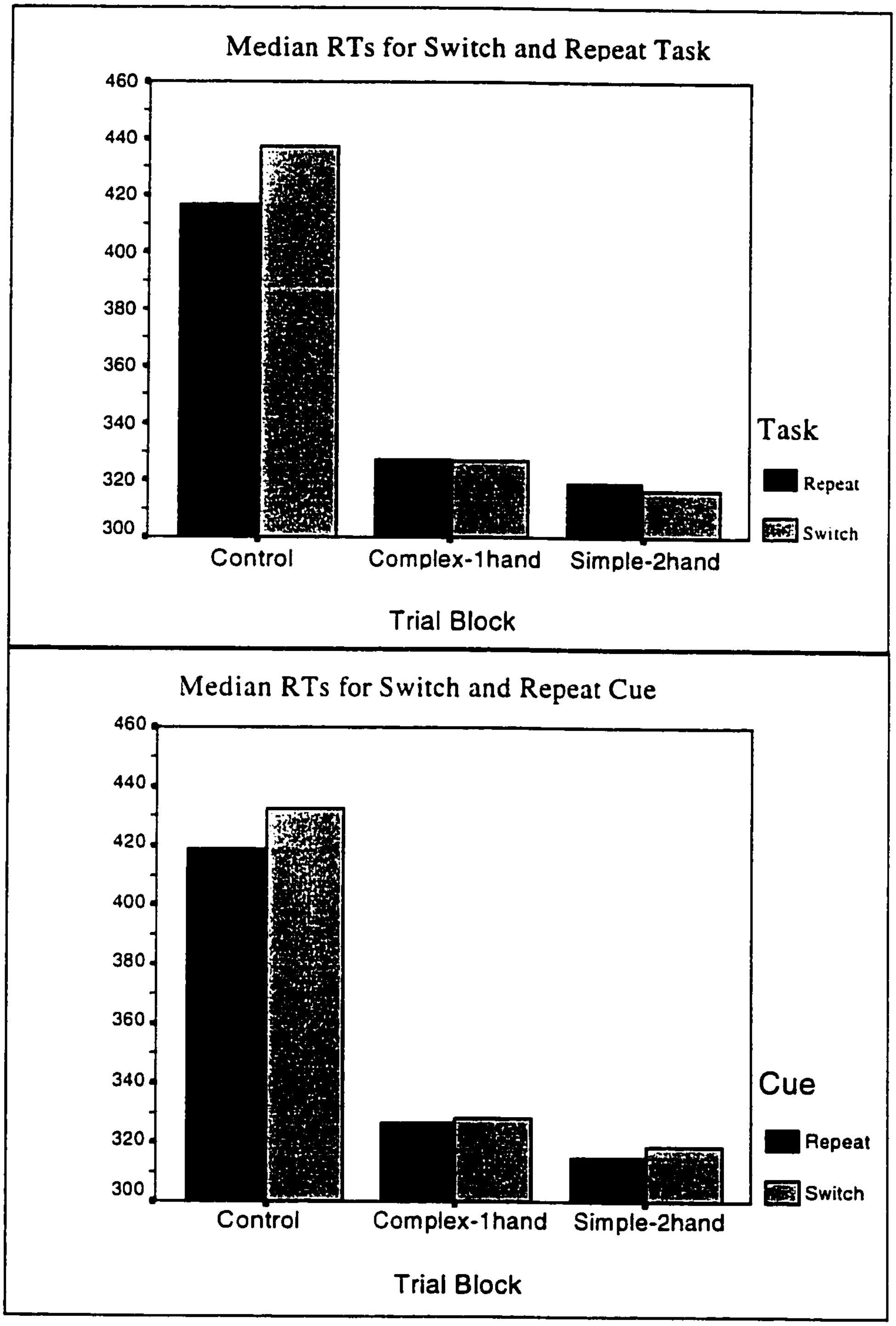

Figure 15:

RT during simple, complex, and practice trial blocks

ERP DATA

Simple (2 Hand - 4 button) S-R Blocks:

In the simple trial block, the left-right task was mapped to 2 buttons on the left hand, whereas the up-down task was mapped to 2 buttons on the right hand (Fig. 13, upper panel).

CUE STIMULI

N200

The N200 latency was significantly earlier for letter (152 ms) than arrow (185 ms) cues ($F(1,12) = 9.4$, $p <.01$) (Figure 24). There was no significant latency effect of switching/repeating for either cues or tasks ($p > .05$).

The N200 amplitude was measured at two separate pairs of electrode sites in experiment #2, O1 v. O2, PO3 v. PO4, and was symmetrical for all analyses (hemisphere, $p > .05$). There were no significant ($p > .05$). N200 amplitude effects during the Switch and Repeat (cue or task) ANOVAs. In particular, the N200 showed no significant effect of task sequence at either the occipital ($F(1,12) = 0.91$, $p > .05$) or parietal-occipital ($F(1,12) = 0.87$, $p >.05$) sites. The cue sequence effect also failed to reach significance at the O1 and O2 ($F(1,12) = 0.3$, $p > .05$), and PO3 and PO4 ($F(1,12) = 0.28$, $p > .05$) pairs of electrodes (Figure 16).

An unexpected finding at the O1, O2 site was a significant Task sequence x Hand interaction ($F(1,12) = 6.1$, $p < .05$). As shown in figures 17 and 18, this effect was due to the

N200 being larger ($p < .01$) during switch (-5.7 µV) than repeat (-4.7 µV) tasks during a cued right hand trial, whereas when the cue stimuli were configured for a left hand response the N200 did not differ significantly ($p > .05$) between switch (-5.1µV) and repeat (-5.4 µV) trials. Of note, task refers to whether subjects repeat or switch between a left-right or top-bottom analysis of the target location. The Hand variable, however, refers not only to the cued left or right hand response, but also to the physical features of the cue stimulus. Thus, a Left hand trial also refers to an H or ⇔ cue, and a right hand trial also refers to a V or ⇕ cue. It is therefore possible that the N200 hand effects are due to differences in the physical features of the cues assigned to the left and right hand.

The amplitude of the N200 at the parietal-occipital pair of electrodes was significant for the main effects of hand, stimulus, and the stimulus x electrode interaction in all analyses - only the statistics from the task sequence analysis are presented as these results are representative of all four ANOVAs. The hand main effect revealed that the N200 was larger for Left (left-right decision, H and ⇔ cues) than Right task-hand (top-bottom decision, V and ⇕ cues) conditions ($F(1,12) = 35$, $p < .001$) (Figure 17). In the stimulus x electrode interaction ($F(1,12) = 8.2$, $p = 0.1$) the N200 was larger for arrow than letter cues at the PO4 site, whereas the N200 to cue arrows and letters did not differ significantly at the PO3 site ($p > .05$) (see Figures 19 & 20).

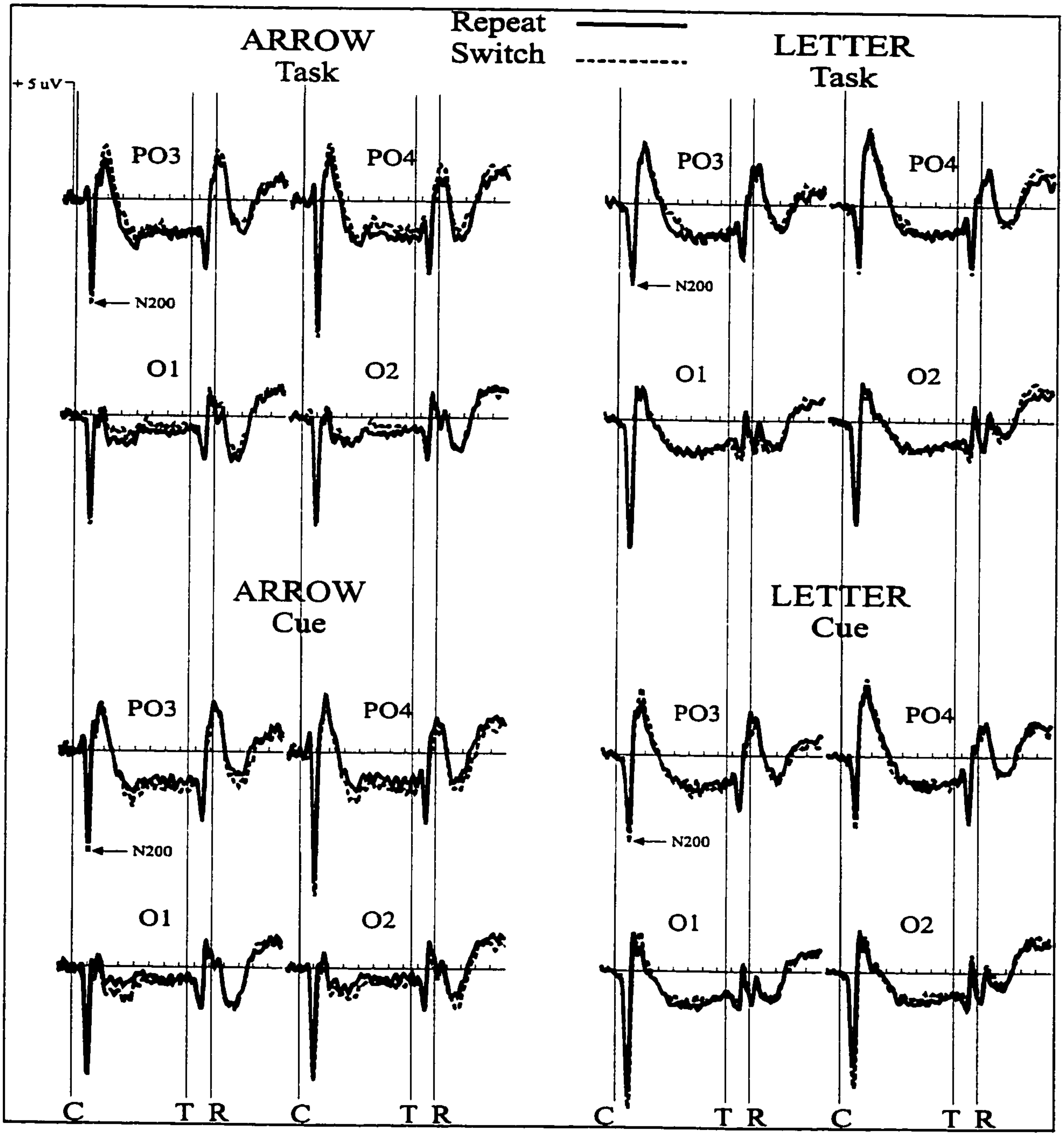

Figure 16:

N200 ERPs at occipital (O1, O2) and parieto-occipital (PO3, PO4) sites. The three vertical bars represent the Cue, Target, and Response. The cue stimulus occurs 200 ms after the onset of the sweep and the target 1500 ms after the cue. Switch trials (light dashed line) are superimposed on repeat trials (dark solid line). ERPs involving arrow cues are plotted at the left of the figure, letter cues are on the right. Task sequence ERPs are at the top of the figure, cue sequence on the bottom. Positivity is up. The waveforms demonstrate that the N200 amplitude was not affected by switching or repeating cues or tasks.

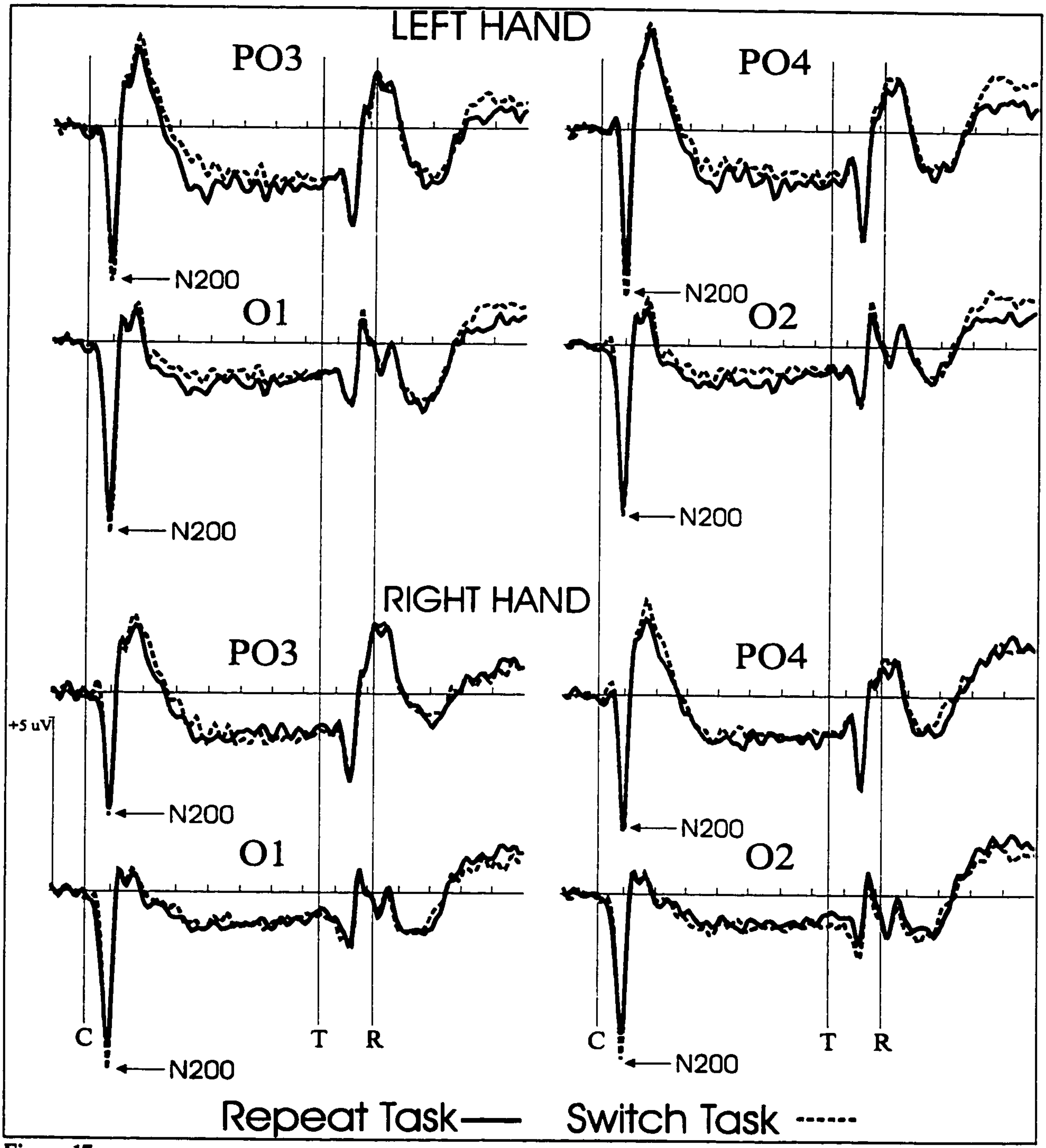

Figure 17:

N200 ERPs at parietal-occipital (PO3, PO4) and occipital (O1, O2) sites. ERPs are collapsed over arrow and letter stimuli for the task sequence condition. Switch task (dashed lines) is superimposed on repeat task (solid lines) for left hand (top of figure) and right hand (bottom of figure) trials. The occipital ERPs show that the N200 was larger for switch than repeat only during the right task-hand trials. At PO3 and PO4, the N200 was larger for Left (left-right decision, H and ⇔ cues) than Right task-hand (top-bottom decision, V and ⇕ cues) conditions.

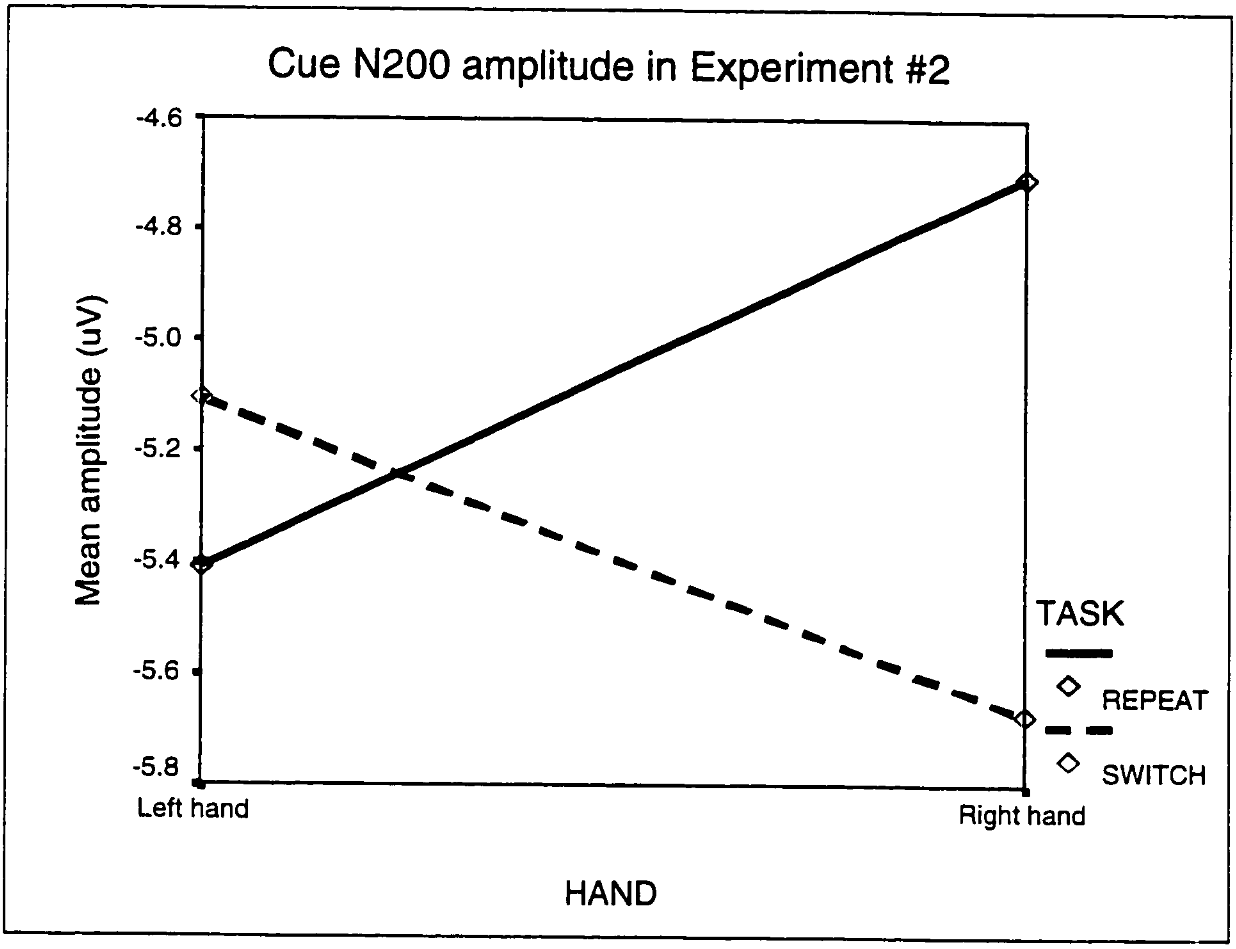

Figure 18:

N200 amplitude to cue stimuli at O1 and O2. The N200 amplitude was only larger during the switch than repeat task condition when the right hand was cued by the "V" and "⇕" cues and not when the left hand was cued by the "H" and "⇔" cues. Since it is extremely unlikely that the hand of response would be differentially encoded at this early latency, it follows that the larger N200 during the switch to the right task-hand condition is probably due to differences in the physical features of the cue stimuli between the left and right task-hand conditions.

The increased N200 amplitude to arrow rather than letter cues specifically over right posterior brain regions was also robustly demonstrated for the right temporal-parietal (P8) and right parietal (P4) electrodes (Figure 23). Figure 23 shows that the N200 differences were also quite strikingly present at CP1 and CP2 (see also Figures 21 and 22). Here the letter cues were recorded as a positive wave (denoted by a ★in both figures) whereas the arrow cues showed little if any deviation from baseline. The N200 scalp distribution was therefore quite strikingly different for arrows as opposed was slightly larger over the left parieto-occipital region and inverted over the centro-parietal scalp.

P390

The hypothesis that the larger parietal (P3, P4) P390 during switch trials in experiment #1 represents an endogenous "cognitive" switching process was not supported by the results of experiment #2. Contrary to our hypotheses, a Cue sequence effect was present indicating that the parietal P390 was significantly ($F(1,12) = 24.3$, $p < .001$) larger when subjects switched (4.2 μV) rather than repeated (3.4 μV) cue modalities (Figure 21), whereas the predicted Task sequence effect did not attain significance ($F(1,12) = 2.3$, $p > .05$) - the P390 amplitude was similar for switch (3.8 μV) and repeat (3.6 μV) task trials (Figure 22). The P390 amplitude was also

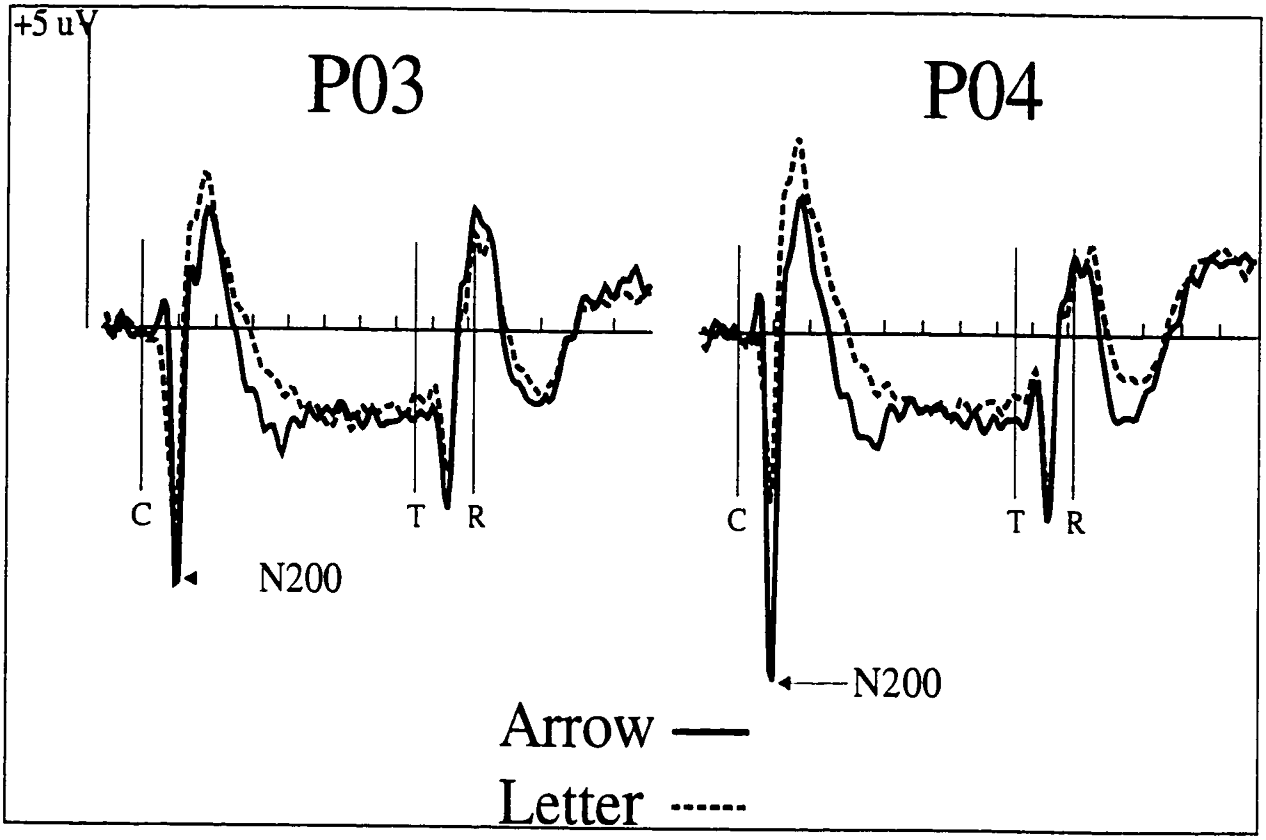

Figure 19:

N200 at parietal-occipital electrodes for arrow (solid lines) and letter (dashed lines) cues. ERPs are collapsed over the hand (left & right) and sequence variables for switch and repeat task and cue modality. The N200 is larger for arrow than letter cues only over right posterior electrodes (see also Figure 23). This indicates that the right parietal-occipital region is special in terms of processing the arrow cues. This unique role may be due to the spatial nature of the arrow cues, the peripheral location of the arrow cues relative to the ocular center of fixation, or a dominance of the right parietal-occipital hemisphere for processing stimuli in both ipsilateral and contralateral visual hemi-space. The N200 for letter cues exhibits a left-sided asymmetry.

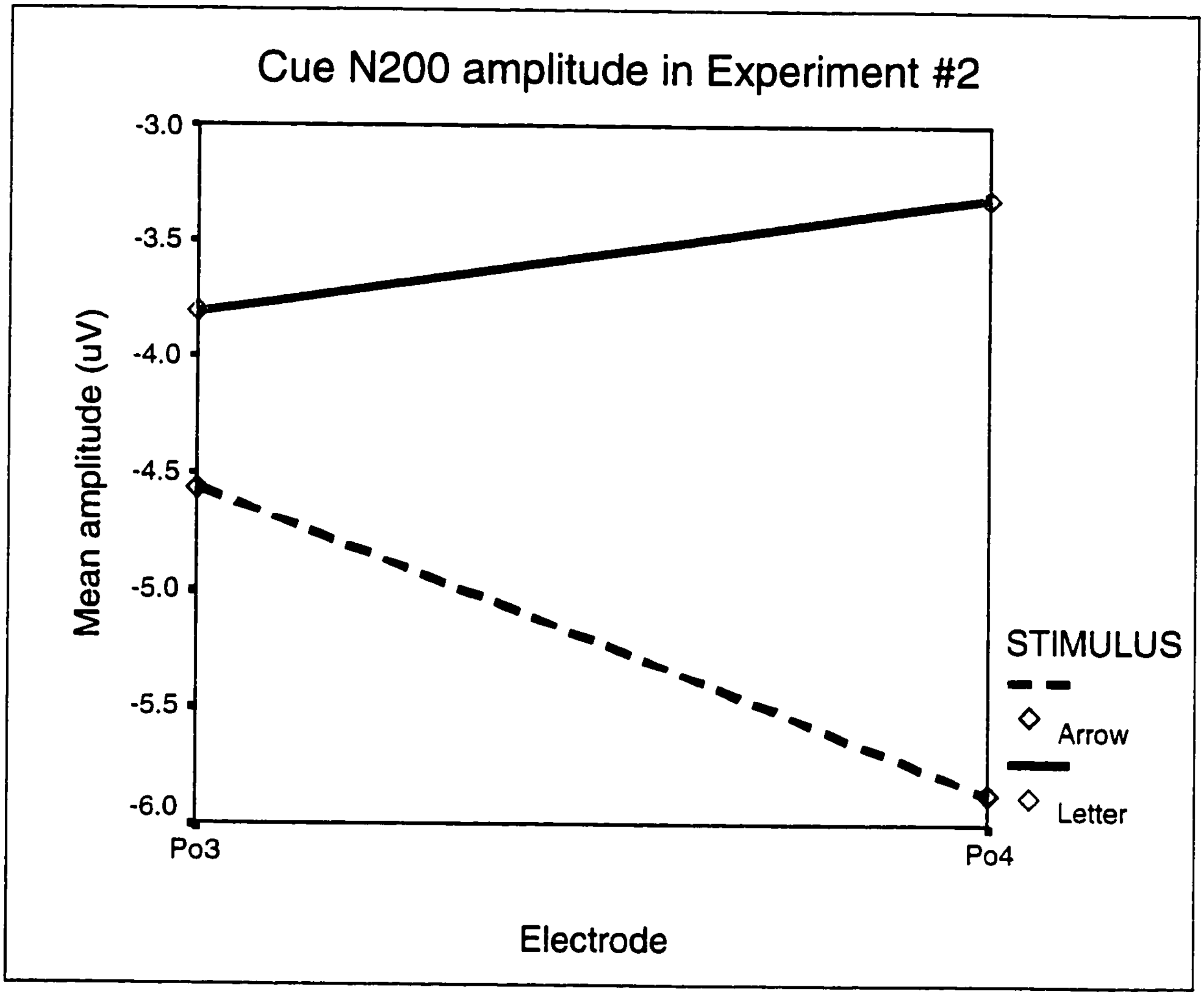

Figure 20:

N200 amplitude to cue stimuli at PO3 and PO4 sites during the Task sequence comparison shows a larger N200 to arrow than letter cues only at the PO4 site.

similar for the arrow (3.8 μV) and letter (3.9 μV) cues (F(1,12) = 0.4, p > .05). Curiously, the task x stimulus interaction was also non-significant (F(1,12) = 1.2, p > .05). This indicates that the P390 task switch effect from the first experiment failed to replicate in experiment #2, even though there was a clear trend in the waveforms (Figure 22) showing that the P390 was larger for task switches between the arrow rather than the letter cues. On the other hand, as in experiment #1, the P390 was maximally recorded over the right hemisphere. For example, the task sequence analysis, the P390 amplitude at P4 (4.3 μV) was approximately 1μV larger than P3 (3.4 μV) (Figure 22).

The amplitude of the P390 varied at a dorsal (CP1 and CP2) and ventral (P7 and P8) pair of electrodes relative to the type of cue stimulus. A subsequent analysis at the dorsal pair of electrodes was similar to the results at P3 and P4. The P390 was larger during switch (4.2 μV) than repeat (3.5μV) cue modality (F(1,12) = 21, p < .001), the task switch versus repeat (3.6 μV) effect remained non-significant (F(1,12) = 1.1, p > .05), and the hemisphere effect (F(1,12) = 11.2, p < .05) was once again larger at the right than the left parietal electrode (Figures 21 & 22). However, unlike the P3 P4 analysis, there was a robust cue stimulus effect at the central-parietal sites - the P390 was significantly (F(1,12) = 14.9, p < .001) larger for arrow than letter cues (Figure 23). At the ventral pair of electrodes, the stimulus effect was the only significant (F(1,12) = 6.3 to 8.9, p < .05) result, however, at this location, the P390 was larger for letter (2.9 μV)

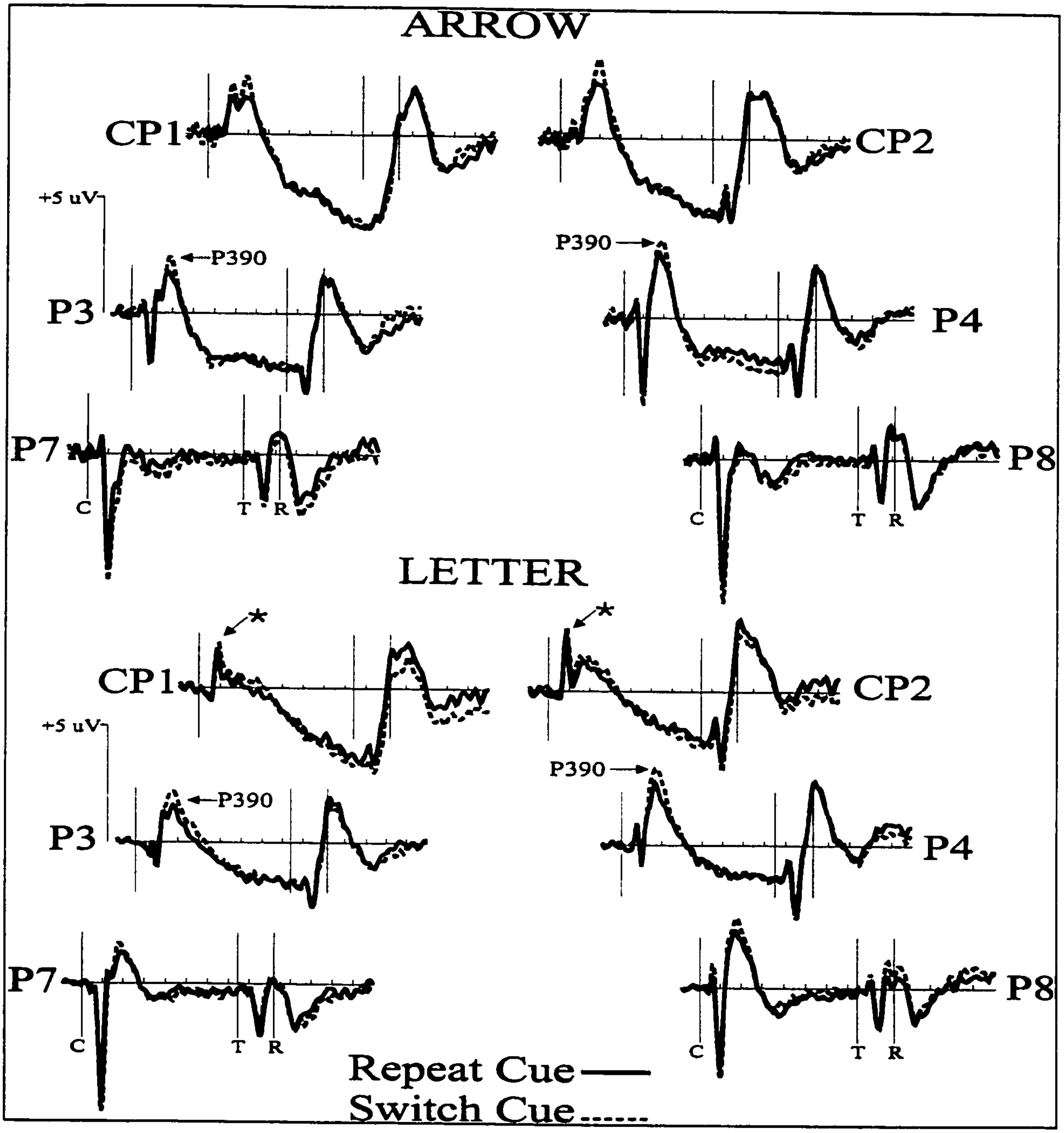

Figure 21:
P390 at parietal (P3, P4), central-parietal (CP1, CP2), and parietal-temporal (P7, P8) electrodes for repeat (solid lines) and switch (dashed lines) cue. Arrow cues are at the top of the figure, letter cues on the bottom. The parietal P390 (P3, P4) is larger during switching than repeating cue modality trials. This indicates that the larger P390 during switches is due to changes in the physical features of the cue stimulus (i.e. an exogenous switch effect). The P390 was maximally recorded from the right parietal (P4) electrode. An inversion of the N200 (marked with a ★) is recorded at CP1 and CP2 for letter, but not arrow cues.

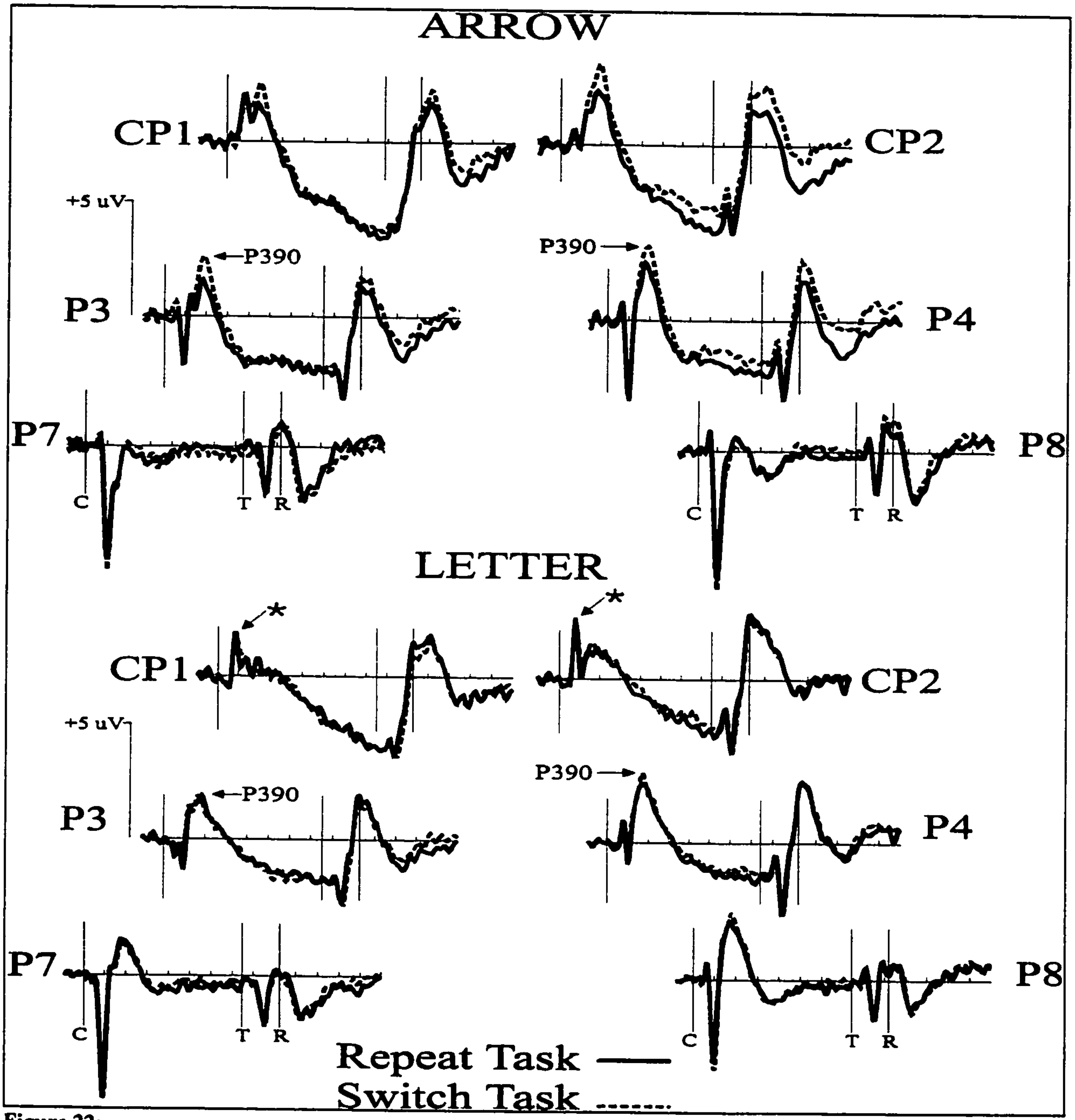

Figure 22:

P390 at parietal (P3, P4), central-parietal (CP1, CP2), and parietal-temporal (P7, P8) electrodes for repeat (solid lines) and switch (dashed lines) task. Arrow cues are at the top of the figure, letter cues on the bottom. The P390 is larger at the right (P4) than left (P3) parietal electrode. The P390 did not differ significantly between switching and repeating tasks, although a non-significant trend (task x stimulus) in the waveforms does suggest that the P390 at P3 and P4 might only be larger when switching occurs between peripherally located arrow cues rather than centrally located letters. An inversion of the N200 (marked with a ★) is recorded at CP1 and CP2 for letter, but not arrow cues.

rather than arrow (1.9 μV) cues .The scalp topography of the P390 was therefore markedly different for the arrow and letter cues (Figure 24).

A 28 ms "task switch cost" was recorded for the P390 peak as measured at the P3 and P4 electrodes. The P390 peak latency was significantly ($F(1,12) = 5.8$, $p < .05$) earlier for repeat (378 ms) than switch (406 ms) tasks. A hand x stimulus interaction was present in all analyses. In the Task sequence analysis, the P390 peak latency was significantly earlier for arrow (363 ms) than letter (418 ms) cues during the right hand task (Figure 25). Similarly, in the repeat vs. switch Cue ANOVA, the P390 peak latency was significantly ($F(1,12) = 16.6$, $p < .01$) earlier for arrow (363 ms) than letter (422 ms) cues during the right hand task, but did not differ significantly during a left hand task (390 v. 386 ms).

The latency of the P390 peak did not differ significantly ($p > .05$) between the measurements taken from the parietal verses the centro-parietal electrodes during the Cue (390 vs. 377 ms) and Task sequence (391 vs. 365 ms) analyses which indicates that these measurements likely reflect the same underlying cerebral event (Figure 23). However, in the task sequence analysis, the P390 latency was significantly earlier ($F(1,12) = 5.1$, $p < .05$) at the "dorsal" central-parietal compared to the "ventral" temporal-parietal electrodes (Figures 23 & 24). This demonstrates that at least two separate neurophysiological events contribute to the amplitude of the scalp recorded P390. Similarly, during the cue sequence ANOVA, the stimulus

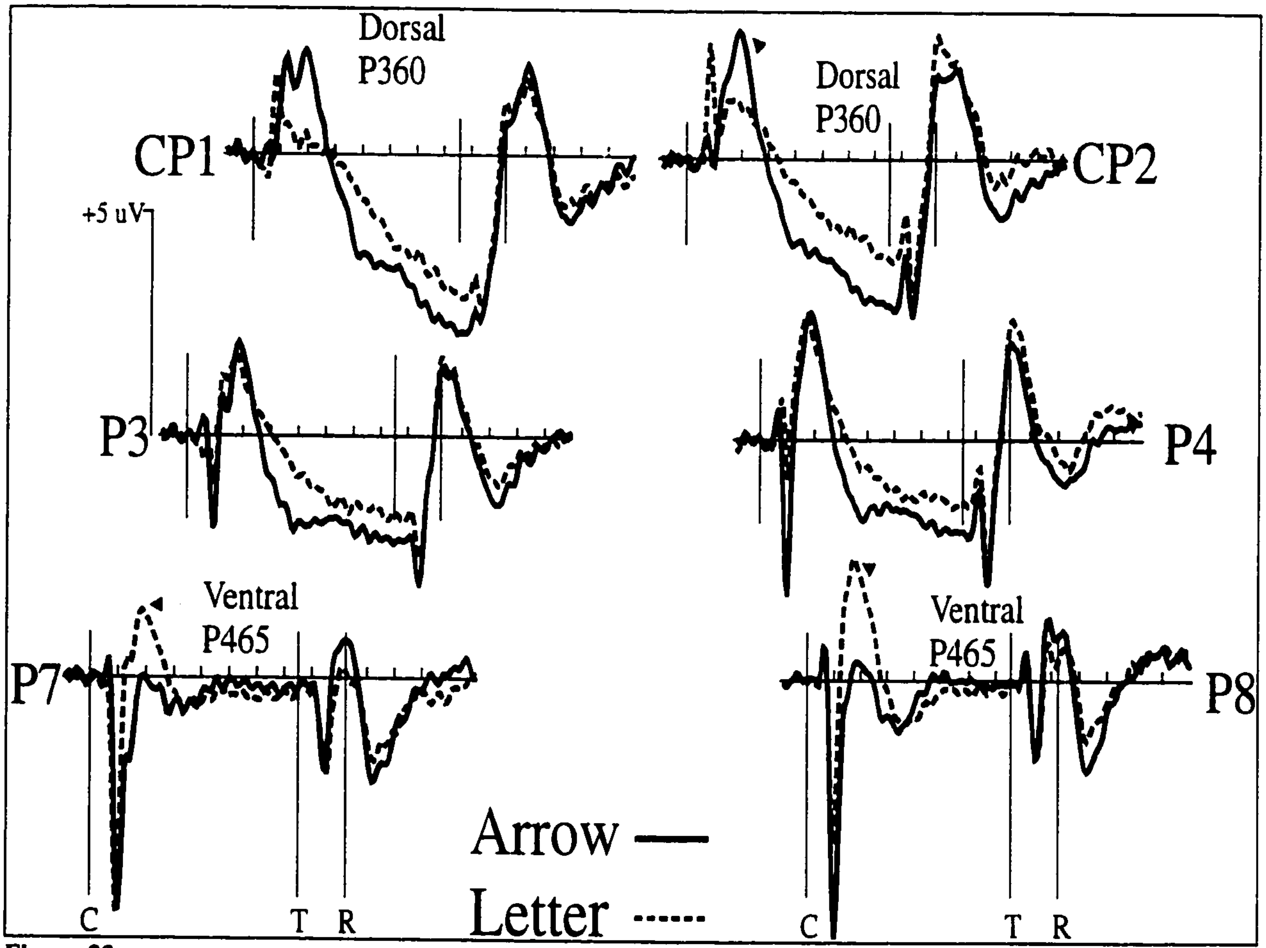

Figure 23:

P300 at dorsal central-parietal (CP1, CP2), parietal (P3, P4), and ventral temporal-parietal (P7, P8) electrodes for arrow (solid lines) and letter (dashed lines) cues. ERPs are collapsed over the hand (left & right) and sequence variables for switch and repeat task and cue modality. The P300 is larger for arrow than letter cues dorsally, larger for letter than arrow cues ventrally, and equivalent for arrow and letter cues at the parietal electrodes. P300 is also larger over the right hemisphere. P300 peak latency is 55 to 59 ms earlier at the dorsal than ventral pair of electrodes. P300 latency was similar for the parietal and central-parietal sites. An inversion of the N200 (marked with a ★) is recorded at CP1 and CP2 for letter, but not arrow cues.

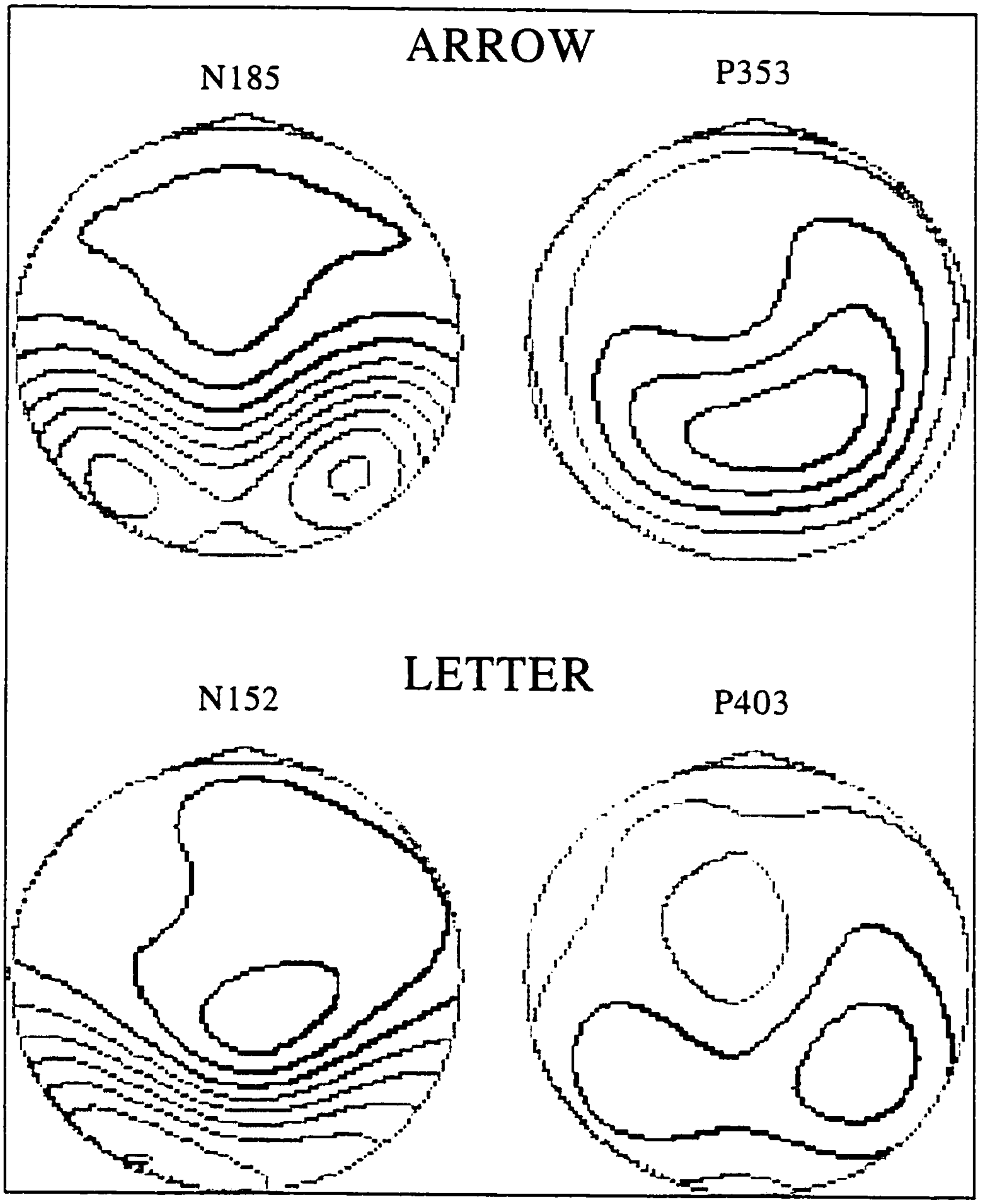

Figure 24:

Voltage maps of the N200 and P300 to arrow (top of figure) and letter (bottom of figure) cues. Data are for the grand mean waveforms where latencies are not as disparate as in the mean of individual waveforms. Contours represent areas of equipotential voltage (surface potentials) separated from adjacent areas by differences of ± 1μV. Light areas represent negative voltage (current sinks) and dark areas correspond to positive voltage (current sources). The N200 is earlier for letter than arrow cues, has a greater left sided distribution for letters, and greater right-sided distribution for arrows. P300 peak latency is earlier for arrow than letter cues, has a right hemisphere predominance, and is distributed dorsally for arrows, and ventrally for letter cues.

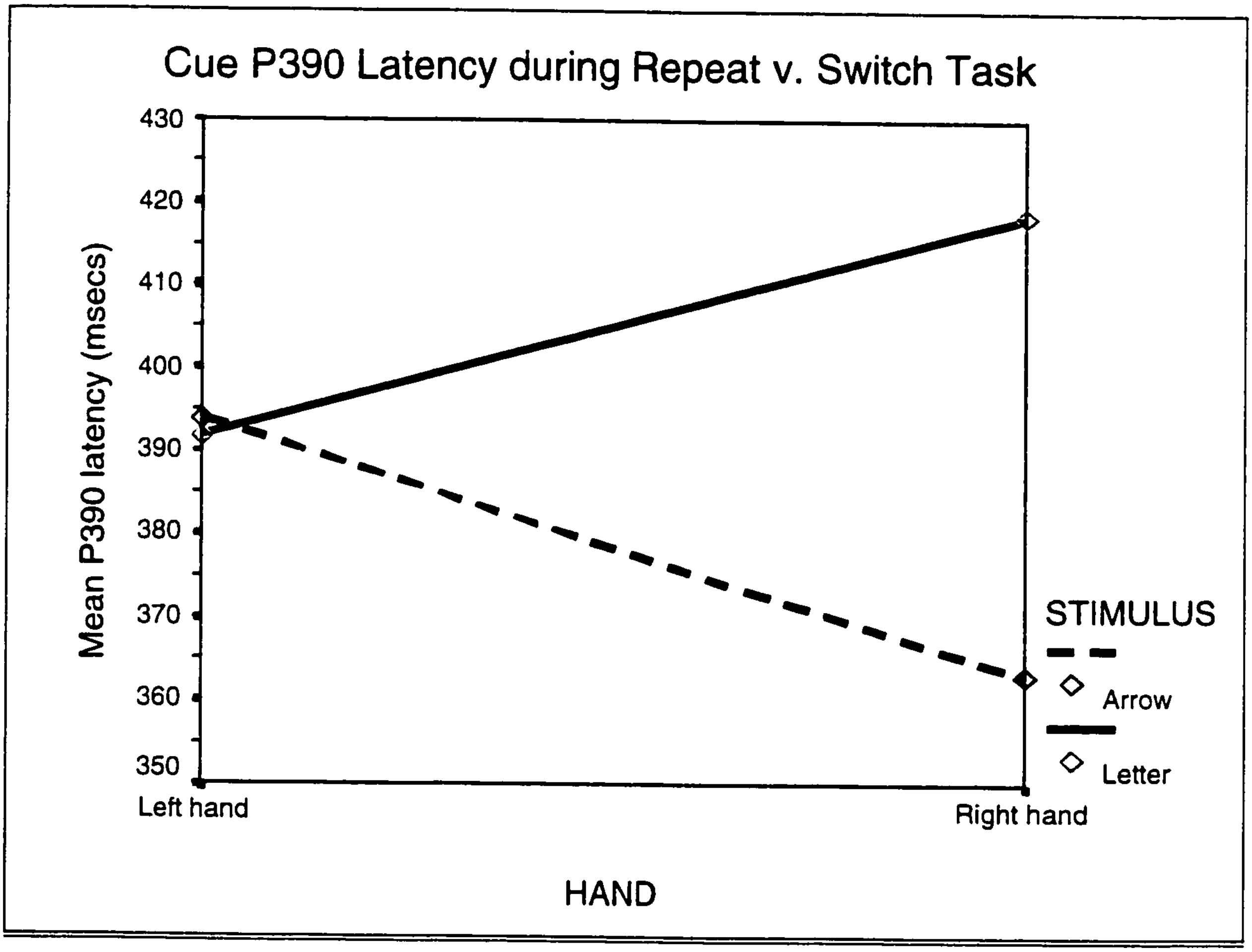

Figure 25:

P390 latency following cue stimuli is earlier for arrow than letter cues only during a right hand task (i.e. ⇕ and V cues, top-bottom target decision).

x electrode location (dorsal vs. ventral) interaction revealed that the P390 to arrow cues was significantly earlier (F(1,12) = 9.9, $p < .01$) at the dorsal central-parietal than ventral temporal-parietal pair of electrodes, while the P390 latency for letter cues was similar across the dorsal and ventral electrode locations.

N740: Frontal Negative Wave

The maximum negative peak at Fz in the 300 to 1200 ms post-cue latency occurred at 740 ms. The task sequence variable was the only effect to reach significance (F(1,12) = 5.25, $p < .05$) indicating that the N430 was larger for switch (-4.8 μV) than repeat (-4.2 μV) tasks, whereas the amplitude of the N430 did not significantly differ (F(1,12) = .001, $p > .05$) for switching between (-4.5 μV) or repeating (-4.4 μV) cue modalities (Figure 26).

READINESS POTENTIAL

Simple Trial Blocks

The RP was significantly ($p < .001$) larger at the left (C3: -2.8 μV) than the right central (C4: -1.6 μV) electrode site (these two means were collapsed across switching and repeating cues and tasks). Also similar to the results of the first experiment (re: see Figure 8), the RP was largest over the hemisphere contralateral to the cued response hand. This hand x electrode interaction was significant for both ANOVAs. For example, in the task sequence analysis, the RP was

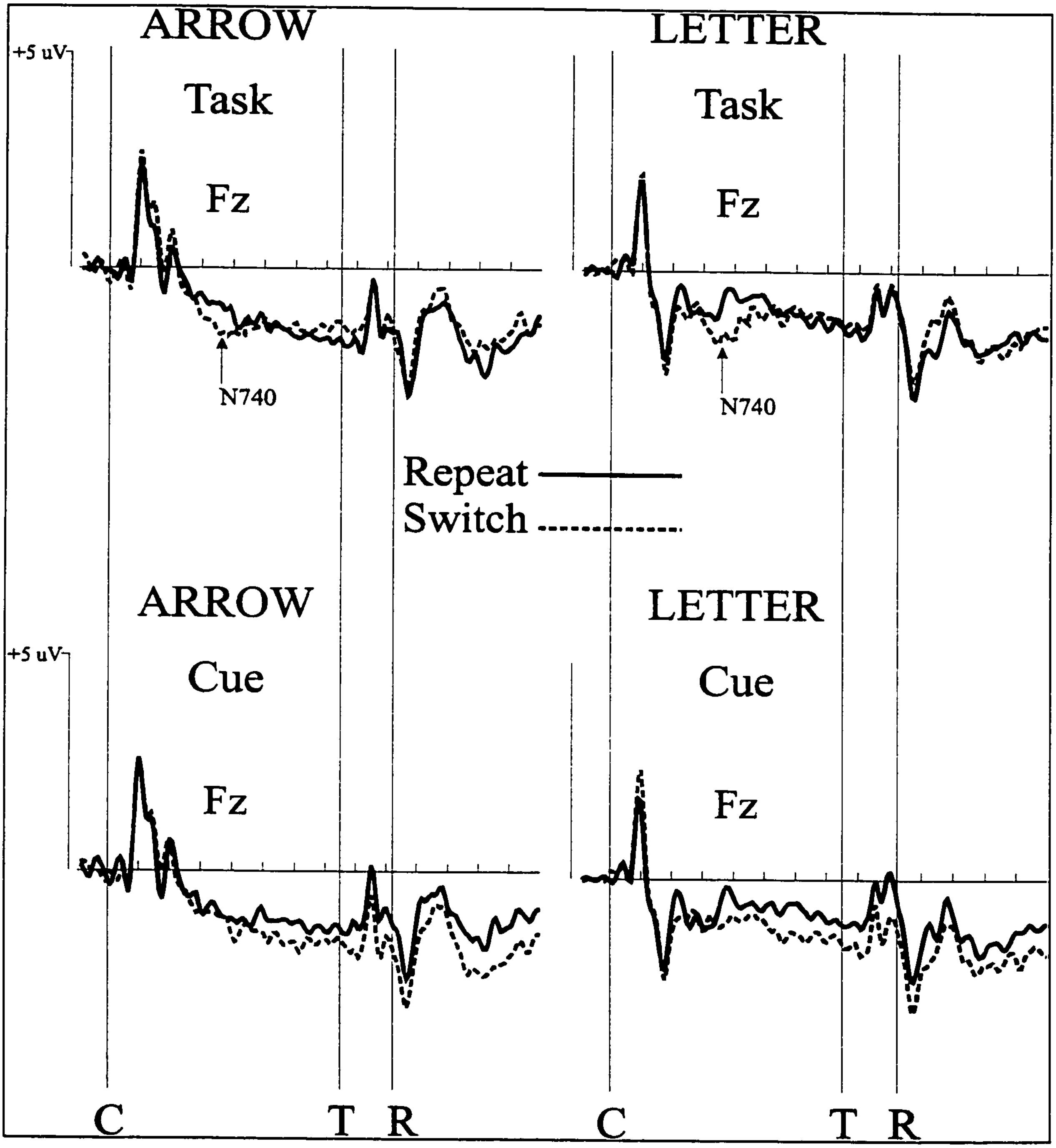

Figure 26

N740 peak at Fz is larger for switch than repeat tasks, but does not vary between switch verses repeat cue modality. This indicates that the mid-frontal switching negativity is specific for the processing of the task, rather than the cue stimuli.

significantly larger (i.e. more negative) ($F(1,12) = 18.3$, $p < .001$) over the right hemisphere (C4) during a left than a right hand response, and significantly larger ($F(1,12) = 9.4$, $p < .01$) over the left hemisphere when the right as opposed to the left hand was cued to prepare to respond (Figure 27).

The RP was not affected by switching or repeating the cue modality since the effects of cue, cue x hand, and cue x hand x electrode were all non-significant ($F(1,12) = 0.2, 0.1, \& 3.4$, $p > .05$). However, the RP was affected by switching or repeating task. The main effect of task ($F(1,12) = 7.7$, $p = .01$), and the task x hand x electrode interaction ($F(1,12) = 7.3$, $p < .01$) were both significant. The 3-way interaction showed that the bilateral RP during switch task-hand trials did not replicate in experiment #2, but that the RP was larger for switch than repeat tasks over the hemisphere contralateral to the responding hand. During a left hand response, the RP was significantly ($F(1,12) = 5.1$, $p < .05$) larger for switch ($-2.7\ \mu V$) than repeat ($-1.9\ \mu V$) tasks over the contralateral right hemisphere, but this effect was not significant ($F(1,12) = .06$, $p > .05$) over the left hemisphere ipsilateral to the responding left hand. Similarly, during a right hand response, the RP was significantly ($F(1,12) = 7.8$, $p < .01$) larger for switch ($-4.0\ \mu V$) than repeat ($-2.8\ \mu V$) tasks over the contralateral left hemisphere, but was not significantly ($F(1,12) = 1.0$, $p > .05$) different between switch ($-0.6\ \mu V$) and repeat ($-1.1\ \mu V$) tasks over the right hemisphere ipsilateral to the responding right hand. These results are graphed in figures 28 and 29 (effects are indicated with arrows), and in Figure 30.

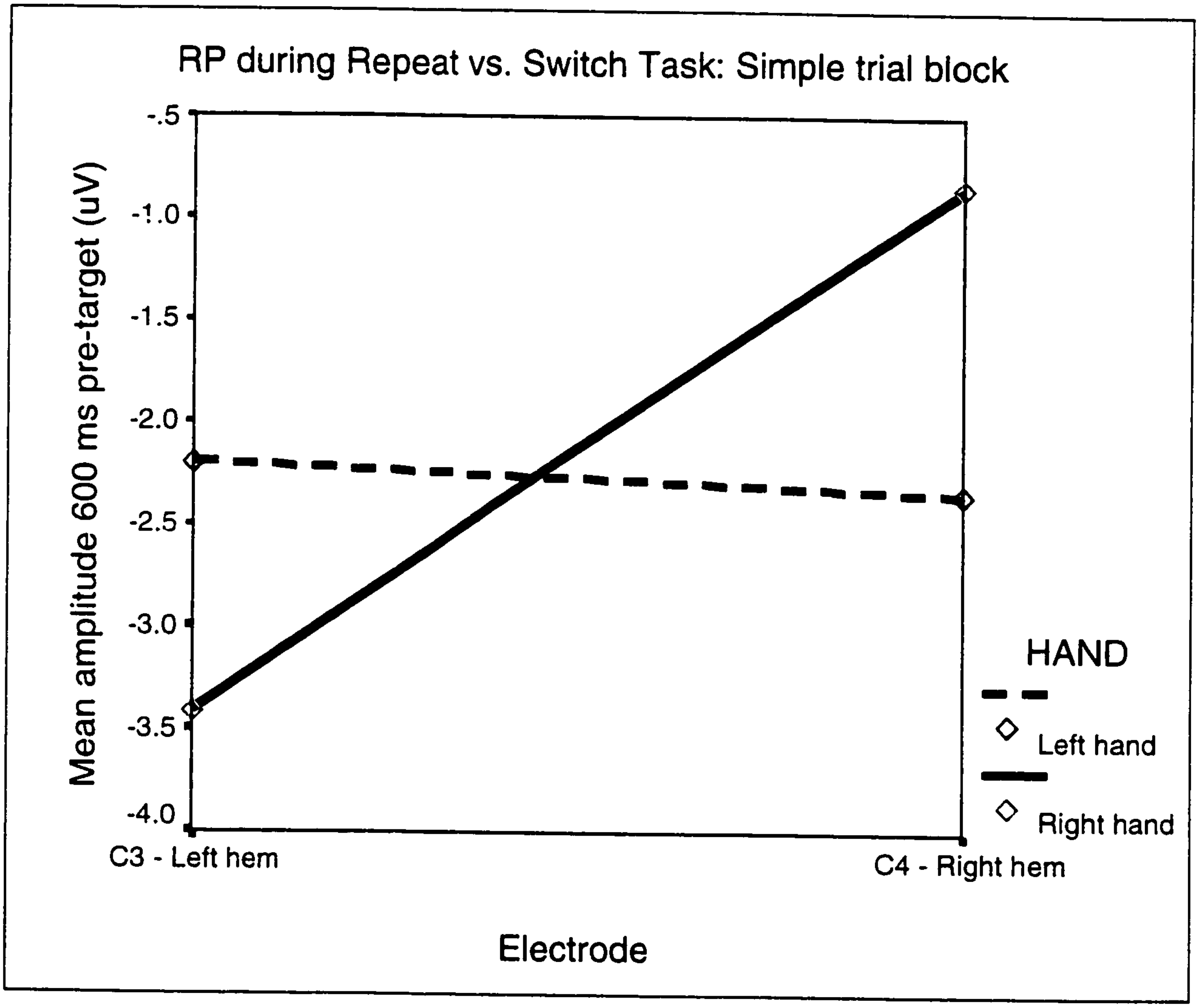

Figure 27:

Readiness potential (RP) during simple trial blocks in experiment #2. The RP is largest over the central electrode site contralateral to the preparing response hand as compared to the RP at the same site when the opposite hand responds.

Complex vs. Simple Trial Blocks

The RP at the central electrode site contralateral to the responding hand was analyzed during switch and repeat trials for the simple (2 hand) compared to the complex (1 hand) trial blocks. The RP was larger on switch trials during the simple rather than the complex blocks of trials. Thus, for a right hand response, the RP at C3 was significantly larger for simple than complex trials for both switching cue modality ($F(1,12) = 6.3$, $p < .05$) (-3.5 v. -2.7 μV) and switching task ($F(1,12) = 8.9$, $p = .01$) (- 4.0 v. -3.0 μV). Similarly, during a left hand response, the RP at C4 was significantly larger for simple than complex trials during the switch in cue modality ($F(1,12) = 17$, $p < .001$) (-2.4 v. -1.4 μV), and the switch in task ($F(1,12) = 16$, $p < .01$) (-2.7 v. -1.7 μV). There were no significant RP differences ($p > 0.2$) between the simple and complex blocks for the repeat cue or repeat task trials during either the right hand (C3) or the left hand (C4) responses.

FRONTAL SLOW WAVES

Simple Trial Blocks

Two frontal slow waves were analyzed at two sets of frontal electrodes in experiment #2. As in experiment #1, a Sustained left mid-frontal frontal Negative Wave (SNW), and a right lateral pre-frontal Positive (SPW) waveform were recorded during the cue-target delay.

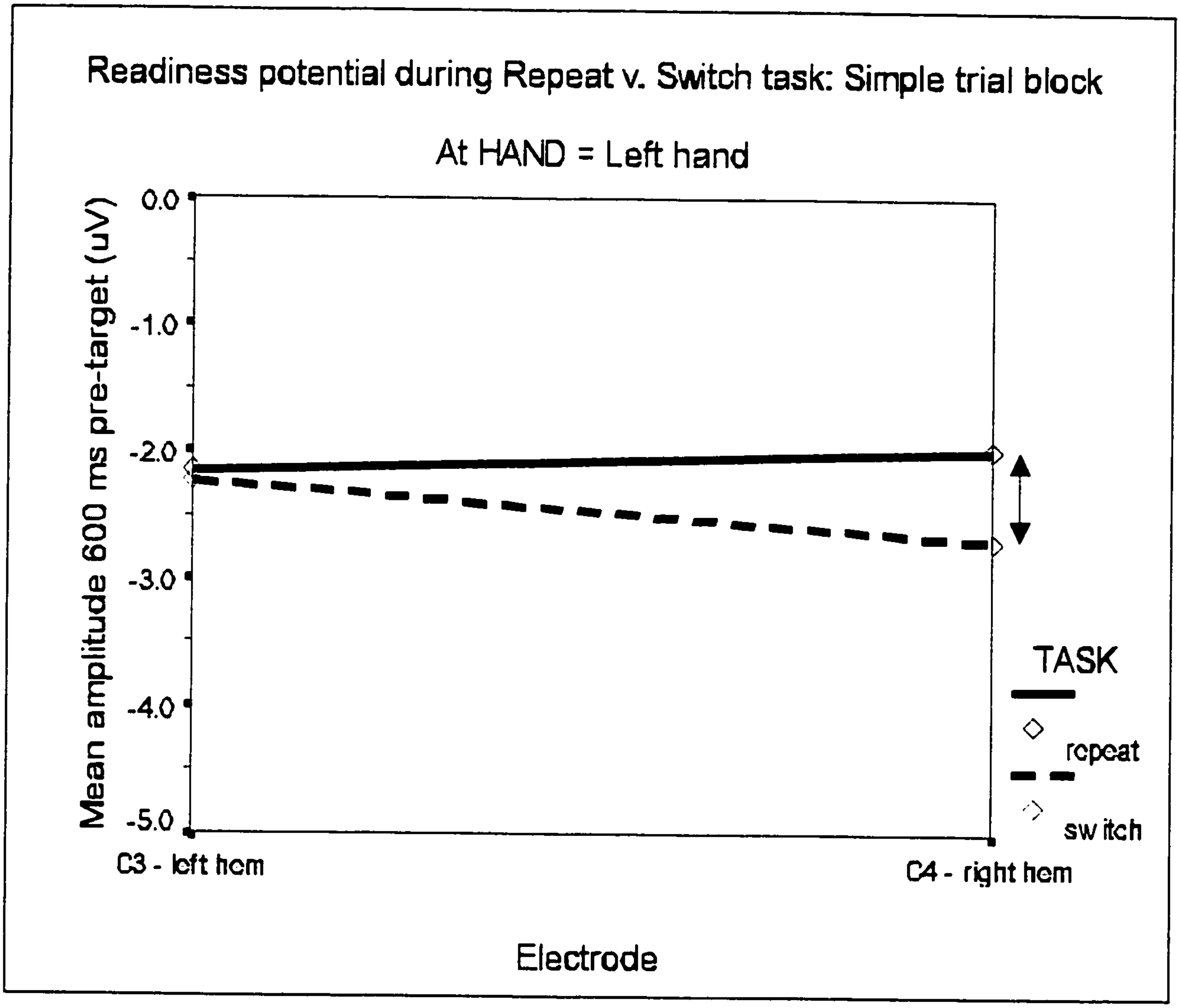

Figure 28:

Average readiness potential at C3 and C4 during 600 ms prior to target onset for a left hand response. The RP is larger over the hemisphere contralateral to the responding hand (C4) for switch compared to repeat task trials. A bilateral RP was not present since the switch and repeat tasks were not significantly different over the hemisphere ipsilateral to the cued response hand (C3).

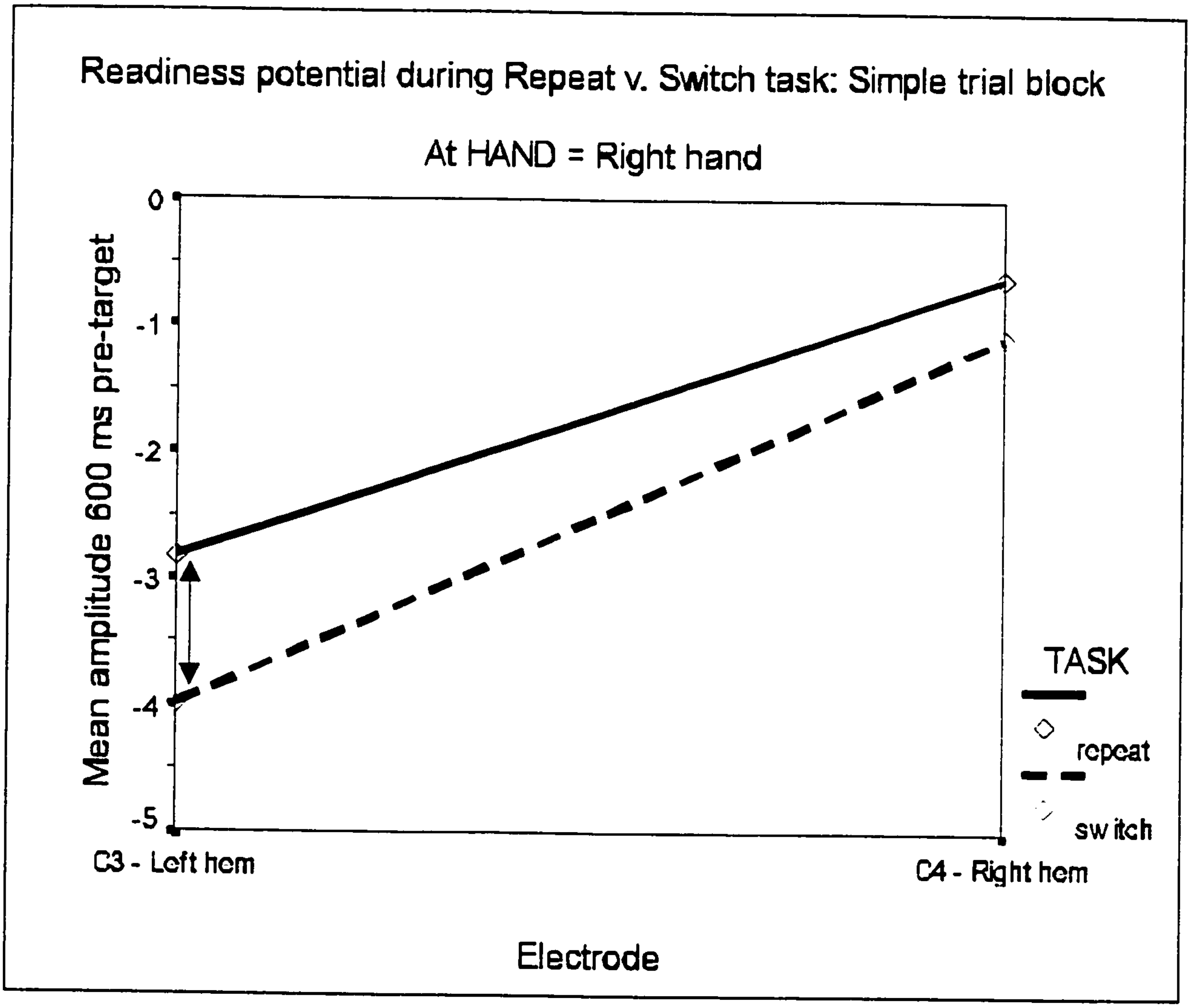

Figure 29:

Average readiness potential at C3 and C4 during 600 ms prior to target onset for a right hand response. The RP is larger over the hemisphere contralateral to the responding hand (C3) for switch compared to repeat task trials. A bilateral RP was not present since the switch and repeat tasks were not significantly different over the hemisphere ipsilateral to the cued response hand (C4).

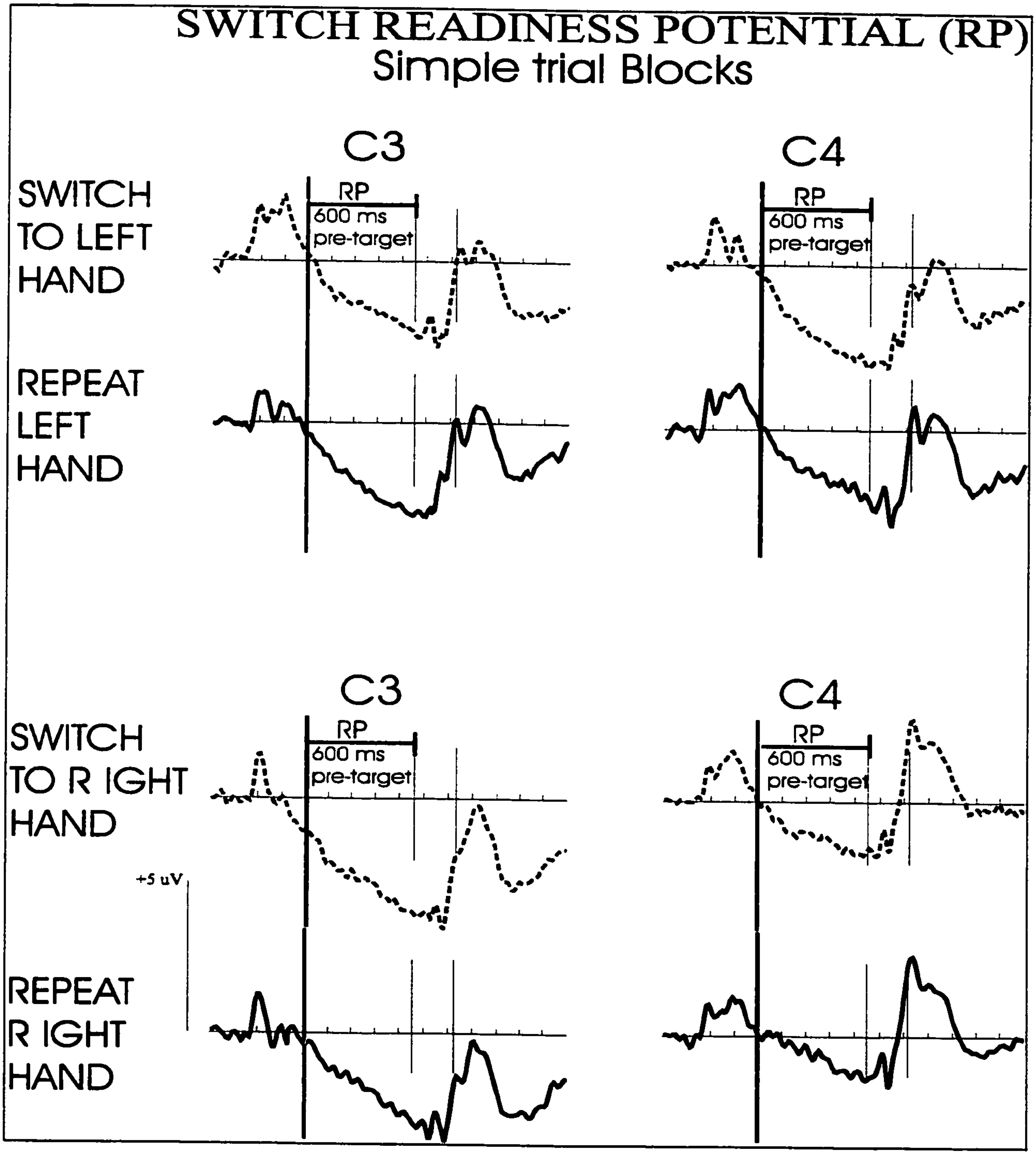

Figure 30
RP during simple trial blocks for switch and repeat task over left (C3) and right (C4) central electrodes.

The SNW was significant for hemisphere ($F(1,12) = 9.5$, $p < .01$), and hand x hemisphere in all ANOVAs. No other main effect or interaction reached significance. Only the results from the task sequence analysis are presented. The hand x hemisphere interaction ($F(1,12) = 8.6$, $p = .01$) revealed that although the SNW was larger ($F(1,12) = 15.3$, $p < .01$) over the left (-1.8 μV) than the right (-0.3 μV) hemisphere during a right hand response, it remained left frontal lateralized regardless of whether subjects responded with their left or right hand ($F(1,12 = 0.9$, $p > .05$) (Figure 31).

The SPW was significant for the main effects of hemisphere and stimulus in all analyses with the exception of the stimulus effect during the repeat vs. switch cue analysis which was only borderline ($p = .08$). The hemisphere effect showed greater positivity at the right than left lateral frontal electrode for the cue sequence ($F(1,12) = 21$, $p < .001$), task sequence ($F(1,12) = 22$, $p < .001$), switch ($F(1,12) = 22$, $p < .001$), and repeat ($F(1,12) = 14.5$, $p < .01$) analyses. The stimulus effect demonstrated that the SPW was also larger for arrow than letter cues during the cue sequence ($F(1,12) = 8.3$, $p < .01$), task sequence ($F(1,12) = 5.2$, $p < .05$), and switch ($F(1,12) = 4.9$, $p < .05$) ANOVAs (Figure 31).

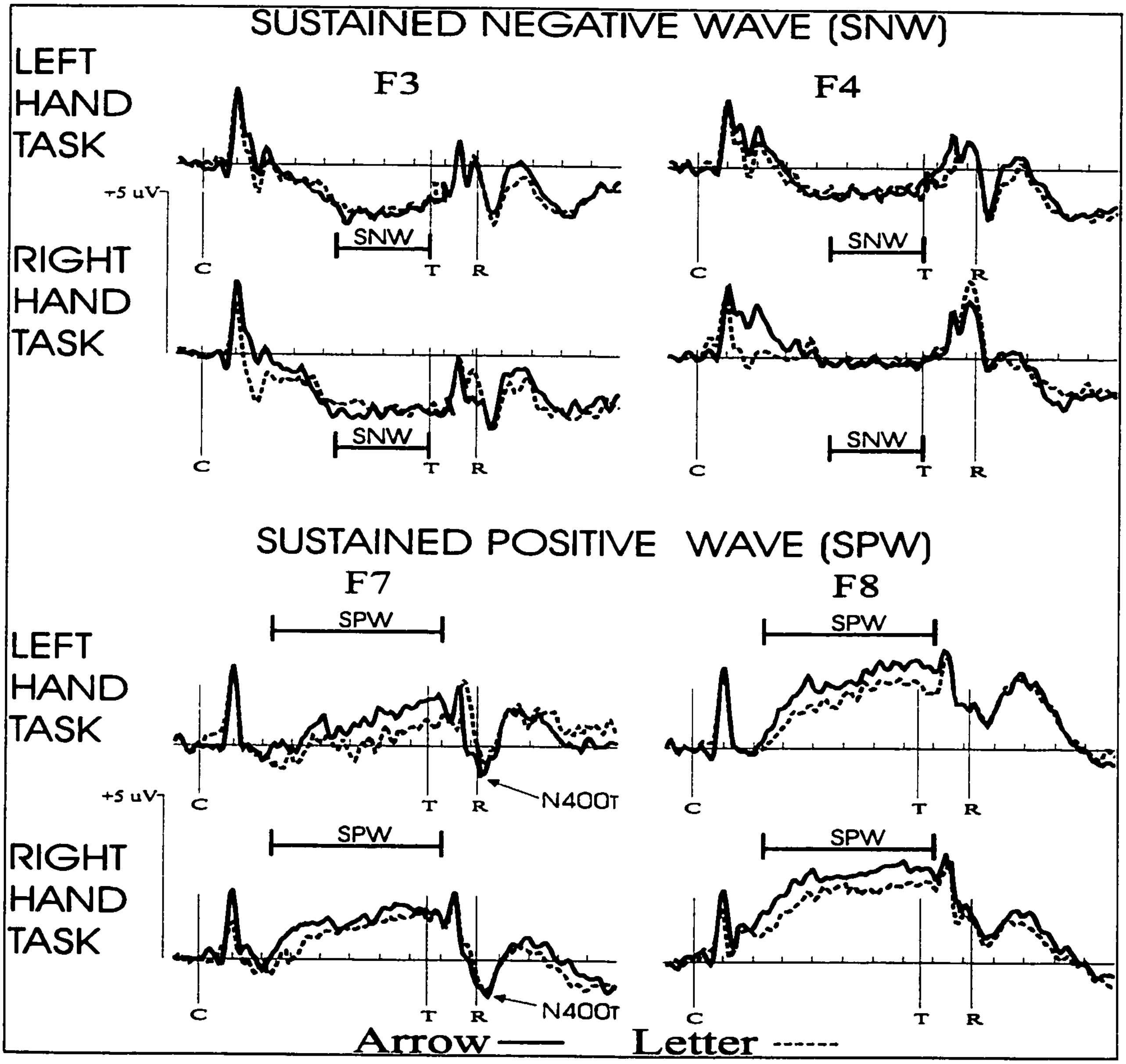

Figure 31:

Frontal slow waves: Left frontal (F3) Sustained Negative Wave (SNW) and right frontal (F8) Sustained Positive Wave (SPW) during the cue target delay for the simple (2 hand) task. ERPs have been collapsed over switching and repeating task. Although the SNW is larger over the left than right hemisphere during right hand trials, it remains left frontal lateralized regardless of whether the left or the right hand is preparing to respond. The SPW remains right frontal lateralized during both left and right hand responses, and is larger for arrow than letter stimuli. A left frontal (F7) negative peak (N400T) is recorded only after the targets. The N400T appears to be an anterior inversion of the target P390T.

Complex vs. Simple Trial Blocks

The frontal slow waves dissociated from one another across the two S-R mapping rule conditions. The SNW at F3 and F4 was larger during the simple (2 hand) than complex (1 hand) trials, whereas the SPW at F7 and F8 was larger during the complex (1 hand) than simple (2 hand) S-R mapping rule trials. These effects were present in all ANOVAs. For example, during the task sequence analysis, the SNW during the simple trial blocks was significantly larger ($F(1,12) = 24$, $p < .001$) than during the complex trials, whereas the SPW during the complex trial blocks was significantly ($F(1,12) = 9.8$, $p < .01$) larger than that recorded during simple S-R mapping rule trials.

TARGET STIMULI

N200T, P390T, N740T peaks

The N200T, P390T, and N740T were also measured in response to the target stimuli. The N200T, at both the occipital (O1, O2) and parietal-occipital (PO3, PO4) electrodes, and the N740T at Fz did not give rise to any significant effects ($p > .05$. However, similar to the hemisphere asymmetry of the cue P390, and to the results of experiment #1, the P390T to target stimuli was significantly ($F(1,12) = 10.6$, $p < .01$) larger over the right (P4) than the left (P3) hemisphere for the task sequence analysis. This effect was also present for the cue sequence ANOVA.

The peak latency of the P390T at the P4 and P3 electrodes was also analyzed for complex and simple trials. A consistent finding across all ANOVAs was that the latency of the P390T did not vary significantly between the complex and simple trial blocks. For example, the peak latency of the P390T for complex (1 hand) compared to simple (2 hand) S-R mapping rule trials was not significantly different for the task sequence ($F(1,12) = 0.3$, $p > .05$; 420 v. 427 ms), the cue sequence ($F(1,12) = .03$ $p > .05$; 438 v. 434 ms), the switch ($F(1,12) = 0.9$, $p > .05$), or the repeat ($F(1,12) = 0.6$ $p > .05$) main effects. No other main effects or higher order interactions approached significance.

F7 Target Peak - N400t

The N400T was selected as the maximum negative peak between 300 to 600 ms after the target at F7 and F8. As in experiment #1, a prominent left frontal (F7) peak was recorded only in association with the target stimuli and the button press response (Figure 28). The main effect of electrode (F7 > F8) was the only significant term, and this effect was present in all four ANOVAs - the results from the task sequence analysis are presented. The N400T was not significant ($p > .05$) for task, hand, stimulus, or any higher-order interaction ($p > .05$), however, a significant hemisphere effect ($F(1,12) = 7.6$, $p = .01$) revealed that this peak was -1.7 μV larger at the left than the right frontal electrode site. Interestingly, as in experiment #1, this left frontal peak was not prominent after the cue arrows - it was only recorded after the target stimuli with an onset that preceded the button press (Figure 31).

The hypothesis that the peak latency of the N400T would be delayed for the complex compared to the simple trial blocks was not supported by the results of the second experiment. The peak latency of the N400T for complex (1 hand) compared to simple (2 hand) S-R mapping rule trials was not significantly different for the task sequence (F(1,12) = 1.1, p > .05) or the cue sequence (F(1,12) = .02 p > .05).

The latency of the left frontal N400T was subsequently compared to the latency of the parietal P390T in order to determine if these peaks were temporally distinct. The N400T was, on average, 30 ms later than the P390T. However, they were statistically indistinguishable since their peak latencies did not differ significantly during either the task sequence (F(1,12) = 2.6, p > .05; 463 v. 424 ms) or cue sequence (F(1,12) = 0.5 p > .05; 458 v. 436 ms) ANOVAs. Logarithmic (base 10) transformation of the data did not appreciably change the results, and no higher order interaction approached significance (p > .05).

DISCUSSION

BEHAVIORAL

In experiment #1 a RT switch cost of 40 ms was significant during the short (200 ms) but not during the long (1200 ms) cue-target interval trials. This indicated that subjects were using the cue stimuli to prepare in advance of the targets and that this switching takes longer than 200 ms and less than 1200 ms. In experiment #2, a significant RT switch cost of 22 ms was obtained during control trials when the cue and target onset asynchrony was 200 ms, and there was no cost of switching during the experimental trials when the cue preceded the target by 1500 ms. This switch cost indicates that subjects were also actively processing the cues prior to the targets in experiment #2. The reaction times were on average slightly faster in the second experiment - 330 ms for the 1500 ms interval compared to the first experiment 380 ms for the 1200 ms interval. This difference may have been related to the brighter stimuli in the second experiment, the longer cue-target interval, the greater time certainty (all hands within a block used the same cue-target interval), or subject differences (the subjects were younger in experiment #2). The fast RT again indicates that subjects were very highly motivated.

The larger switch cost during the 200 ms cue-target interval trials in experiment #1, compared to the 200 ms cue-target asynchrony control trials in experiment #2 may have arisen in part from the faster overall RTs during the control (426 ms) than experiment #1 catch trials (462 ms). The faster RTs during the control blocks probably resulted from the added knowledge of when the stimulus would occur since subjects knew that every trial within the block would have a short cue-target interval. Furthermore, in the second experiment the 200 ms control trials occurred at the end of the experiment. The subjects were by this time highly practiced. This order had been chosen purposefully since any switch effect could then clearly indicate the time necessary to switch when this could not be anticipated prior to the target. It was also important that the subjects initially only have the experience of the longer interval, so that they would not automatically anticipate the 200 ms interval.

There was no RT cost of switching between cues or tasks in the simple (2 hand) S-R mapping trials. This replicates the results of experiment #1. However, contrary to our hypothesis, and to the switch-cost published in the literature, we did not obtain a significant switch-cost during the complex stimulus-response rule trials. This indicates that subjects can complete all the mental operations involved in switching prior to the target stimulus when there was a complex overlap of stimulus response maps. Our subjects were highly motivated and they were repeatedly encouraged to use the cue stimuli to prepare to respond in advance of the onset of the imperative target stimulus as this would facilitate a faster RT. Our RT results do not support the necessity of the stimulus-evoked-completion hypothesis (Rogers and Monsell, 1995), or the two-stage (goal-identity vs. response-rule activation) task-set switching model proposed by Rubenstein et al. (1994) and elaborated by Lauber et al. (submitted). It is possible that two stages may be used by some subjects under certain experimental conditions. However, our results clearly show that this is not necessary and all switching may occur prior to the imperative stimulus.

Allport et al. (1994) claimed that all RT task switching effects can be explained in terms of proactive interference from the previous task's mental set onto the current task, and that this "interference" effect can be avoided provided that the response to cue interval across trials is not too short (i.e. our experiments had a 1500 ms inter-trial interval). However, although Meiran (in press) demonstrated that RT switch cost decreased as the inter-trial interval increases, a residual RT switch cost of 10 to 15 ms remained even when the inter-trial interval reached 3000 ms. The results in both of our experiments indicate that this residual RT can be eliminated if subjects are highly motivated and/or practiced.

When recording ERPs more trials are generally used than when measuring RT. Without ERPs. For example, Meiran (1996; in press) usually used between 100 and 350 trials whereas our subjects completed 750 experimental trials in experiment #2 and 1000 trials in experiment #1. This leads to two effects. The subjects become highly practiced, and they are highly motivated to respond quickly (in order to finish sooner). Meiran (1996, experiment 4) studied RTs over four blocks of 150 trials and found a significant decrease in switch cost (on short cue-target trials) over the four blocks. Interestingly there was no significant change in the residual switch cost (i.e. on long cue-target trials).

Motivational and practice differences between our subjects and those in the literature are evident in the RT results. In our simple and complex S-R mapping trials, the average RT of 328 ms during both repeat and switch tasks (and cues) is substantially faster than switch versus repeat task RTs reported by Meiran (in press) in both elderly (1127 v. 979 ms) and young subjects (720 v. 667 ms), by Rogers and Monsell (1995) in their identical and separate response sets conditions (790 to 1200 ms switch v. 600 to 750 ms repeat), and by Rubenstein et al. (1994) in their low and high-complexity matching rules and tasks (1904 to 2299 v. 1354 to 1719 ms). Reaction times are difficult to compare across laboratories because of differences in stimulus presentation and response timing. Nevertheless, these differences are large enough to be considered significant. Thus, it is reasonable to conclude that RT switch costs arise from motivational and experimental confounds rather than discrete task switching stages.

The fact that the switch in the type of cue caused a significant switch independently of any change in the task was unexpected. The cue selected switch-cost was much less than the task-selected switch cost but we had predicted that there would be no such cue effect. The actual results indicate that the 200 ms interval between cue and target is probably borderline for interference in the processing of the two stimuli and that when the cue changed, the increased time needed to process the new type of cue interfered with processing the target. Certainly this effect indicates that changing the type of cue stimulus significantly disrupted the processing of the cue.

Finally, the complex task was associated with significantly longer RT than the simple task. This result confirms our manipulation of task complexity.

N200

The cue-evoked N200 findings did not fit with our hypotheses. Rather than disconfirming the predictions, they indicated a different pattern of controlling variables. In the first experiment the N200 was larger for task-switching trials than for task-repeating trials. We had hypothesized that this might have been due to a confounding of task-switching with stimulus-switching, since a change in task was indicated by a change in cue. In the second experiment there were no significant effects of switching the type of stimulus (arrows and letters). This is indeed not the same as the stimulus-change in the first experiment (particularly from the point of view of the repeating stimulus which could have been either exactly the same or just of the same type). Nevertheless, it is clear that the N200 is controlled differently than we had suspected. The results of experiment #2 indicate that the N200 is quite different in latency and scalp distribution between arrows and letters. The N200 was not affected by the switch-repeat manipulation. These results indicate more clearly than the results of experiment #1 that the N200 depends upon the physical characteristics of the stimulus and not upon the meaning of the stimulus to the task.

The N200 latency was generally earlier than in the first experiment. Indeed the N200 nomenclature is not completely appropriate since the latencies were significantly less than 200 ms. This may have been due to the brightness of the stimuli in the second experiment. The most significant latency effect involved the difference between the letters (152 ms) and the arrows (185 ms). This is probably most likely due to the fact that the letters were presented foveally and the arrows occurred parafoveally.

The scalp distributions of the N200 varied significantly for letter and arrow cues. The meaning of these scalp distributions will only be clearly understood after source analysis. However, the scalp-topographies suggest that the letters activate a dipole in the left parieto-occipital area that is oriented vertically such that the opposite polarity occurs in the centoparietal area, and that the arrows activate radially oriented dipoles in the parieto-occipiatl regions maximal on the right.

The N200 also showed an unexpected effect of hand in the simple task. The N200 was larger for switch than repeat task for right hand responses but not for left hand responses. It is highly unlikely that this effect could have been due to the brain processing the response requirement at this early latency. More likely it was due to physical differences between the stimuli that denoted which hand to respond with. In particular, the midline vertically oriented arrows may have evoked a larger response than the horizontally directed arrows.

P390

The hypothesis that the larger P390 during switch task trials in experiment #1 represented an endogenous switch in attention between task-sets was not supported by several results from experiment #2. First, the larger P390 during switches in cue modality rather than task switches indicates that the amplitude of the P390 is enhanced by changes in the physical properties (e.g.

location, orientation, feature analysis) of the cue stimuli - an exogenous effect. Second, the P390 task switch effect from the first experiment failed to replicate in experiment #2. The only difference between these two studies was that the task switch analysis in the second experiment included task switches based on letters in addition to the arrow cues. It is therefore possible that the letter cues prevented the P390 from being amplitude modulated during task switches in experiment #2. This interpretation is consistent with the non-significant trend in Figure 22 which shows a larger P390 for switch than repeat tasks for the arrow, but not the letter stimuli. Corbetta et al. (1993) have shown that the superior parietal cortex is more active when attention switches to peripheral locations than when maintained at a central fixation point.

One of the differences between the letter and arrow cues in the second experiment was that the letter cues were presented at the center of fixation, whereas the arrow cues were located in the periphery of the visual fields. Thus, it is possible that the P390 switch effects in experiment #1 were entirely due to switches in the location of visual attention (i.e. between vertical and horizontal meridians) (Shedden, 1995) rather than switching between different tasks. Moreover, the larger P390 over the right hemisphere in both experiment #1 and #2 might also be explained by the PET findings of Corbetta et al. (1993) indicating that the right parietal lobe is involved in attention shifts in both visual fields, whereas the left parietal lobe is only active during rightward shifts in the location of visual attention. It is possible that switching based solely on changes in the location of the arrow cues in the visual fields elicited a larger P390 in experiment #1, whereas, in experiment #2, the significance of this switch effect was masked by the addition of the letter cues at the center of fixation (re: Figure 22). For example, the letters did not require any shifts in the location of visual attention when the letter stimuli cued a switch in task, but not a switch in cue modality (e.g. H to V, or V to H cue).

Topographical Dissociation of the P390: Dorsal and Ventral Generators

Two related results further indicate that the P390 is affected by the physical properties of the cue stimuli, rather than an endogenous switch between task-sets. The observation that the P390 was significantly larger for arrow than letter cues at the dorsal pair of electrodes (CP1, CP2) supports the interpretation that the P390 amplitude is sensitive to changes in the physical properties of the cue stimuli. Moreover, the sensitivity of the P390 to differences in the physical features of the cue stimuli was further demonstrated by the P390 being larger for letter than arrow cues at the ventral (P7, P8) pair of electrodes. The robust differences in scalp topography indicate clearly different generators for each type of stimulus. These data clearly indicate that the P390 can be generated by different regions of the brain. The current understanding of the P300 is that it does not represent a unitary cerebral process but is the result of multiple intracerebral generators (Picton, 1992; Halgren et al., 1995).

The dorsal (arrow cue) and ventral (letter cue) P390 peak amplitude dissociation in experiment #2 may correspond to the dorsal (object location - where) and ventral (object identity - what) visual pathways which was first proposed by Ungerleider & Mishkin, (1982) to explain their anatomical and behavioral findings in monkeys (Maunsell & Newsome, 1987). Ungerleider and Mishkin's (1982) model identifies two parallel neural streams: one specialized for the perception of visual space and motion, the other concerned with the shape or form of objects. The "spatial" stream follows a dorsal route from primary visual cortex towards the posterior parietal region, while the "object identity" pathway takes a ventral course leading to the inferior temporal cortex (see also Milner and Goodale, 1995, p. 20-24).

Dorsal "Where" and Ventral "What" pathways

As initially conceived by Ungerleider and Mishkin (1982), the dorsal "what" and ventral "where" streams emanating from the striate cortex were depicted as two anatomically, and functionally independent pathways. In a much more detailed hypothesis, Livingstone and Hubel (1988), further interpreted the ventral and dorsal streams as a continuation of the lateral geniculate parvocellular and magnocellular layers, respectively. The segregation of these pathways was traced both proximally (up to the level of specific retinal ganglion cells) and distally from the primary visual cortex. In this view, the magnocellular channel traverses a course from the eye through the striate to the posterior parietal cortex and is critical to the spatial localization of objects in the visual field, while the parvocellular travels independently along its own course through primary visual cortex and on to the inferotemporal cortex, and plays an essential role in object identification.

It has become clear that there is greater cross-talk between the two systems than was initially thought. For example, direct recording from neurons in the primary visual cortex (V1) after selective blocking at the level of the lateral geniculate nuclei, show that more than a third of the neurons in V1 are affected by blocking the pathways emanating from either the magno or parvo layers (Nealey & Maunsell, 1994). Despite this functional overlap, the distinction between an occipito-temporal or "ventral" pathway involved in processing the identity of objects, and a "dorsal" or occipito-parietal pathway involved in processing the location of objects has been repeatedly confirmed (Morel & Bullier, 1990; Baizer et al., 1991; Felleman & Van Essen, 1991; Young, 1992).

Most recently, the Ungerleider and Mishkin (1982) model has been investigated by functional brain imaging techniques such as PET (Positron emission tomography) (Ungerleider, 1995; for a general review of PET studies and cognition, see Cabeza & Nyberg, 1997). The object identity pathway has been imaged by comparing perception of faces with perception of objects (Sergent, Ohta, & MacDonald, 1992), and both object identity and object location pathways have been studied with face-matching and location-matching tasks (Grady et al., 1992, 1994; Haxby et al., 1991, 1994), and by having subjects decide whether three common objects in each of two simultaneously presented displays are in the same location (object-location) in both displays, or if the displays contain the same objects (object-identity) (Köhler et al., 1995).

The PET results have been consistent across the groups of investigators. In the Köhler et al. (1995) study, when the object-identity was subtracted from the object location condition, increased activity in parietal regions was observed, when the object-location was subtracted from the object-identity condition, increased activity in the temporal regions was found. Thus, the PET studies are also in accord with Ungerleider and Mishkin's (1982) distinction between a dorsal occipito-parietal pathway for spatial/location processing, and a ventral occipito-temporal pathway for object processing.

Milner & Goodale's (1995) review has distinguished the streams further on the basis of the networks of cells in the dorsal stream performing the computations and transformations required for visually guided actions, while networks in the ventral stream permit the formation of perceptual and cognitive representations of the enduring characteristics of objects and their relations. That is, the basic premise of Milner and Goodales (1995) account of the division of labor in cortical visual systems is based on a distinction between the requirements for action and perception, and that this division cuts across any distinction between spatial and object visual processing

Magnocellular and Parvocellular Streams: Processing speed

Livingstone and Hubel's (1988) description of the "magnocellular system", or dorsal-where pathway as described by Underleider and Mishkin (1982), was that it is concerned with: "deciding which visual elements, such as edges and discontinuities, belong to and define individual objects in the scene, as well as determining the overall three-dimensional organization of the scene and the positions of objects in space...". On the other hand, the parvocellular (or ventral what) system, was held to be more "important for analyzing the scene in much greater and more leisurely detail" (p. 748). The greater analysis in the parvo system is for details of form, to some degree color, orientation of edges, and because a great deal of information about shape is derived from borders, this system is important for the perception of shape and surface properties of objects (De Yoe & Van Essen, 1988; Kandel, 1991, p. 447). Moreover, by integrating multiple visual attributes of an object the parvo system could identify the object and help establish its relations to other objects and events impinging upon the organism.

The notion of a "leisurely" or slower processing mode for the ventral parvocellular system emerged from the detailed analyses of the response characteristics of ganglion cells, initially in the cat (Enroth-Cugell & Robson, 1966). Two classes of cells, X and Y cells can be differentiated. The X cells exhibit large receptive fields (i.e. sensitivity to high spatial frequencies) and medium axonal conduction velocities, whereas the Y cells have rapidly conducting axons, and relatively small receptive fields (i.e. poor sensitivity to spatial variability) (for reviews, see Lennie, 1980 and Schiller, 1986). Retinal ganglion cells with identical conducting characteristics have since been identified in the primate visual system - faster Pα and slower Pβ cells (Hubel & Livingstone, 1987; Merigan & Maunsell, 1993). The physio-anatomical distinctiveness of the channels formed by these cells is preserved at the level of the primate lateral geniculate bodies (Dreher et al., 1976; Hendry & Yoshioka, 1994).

According to the Livingstone and Hubel (1988) proposal, the faster Pα ganglion cells project from the lateral geniculate to the four parvocellular layers (and on to the ventral "what" stream and temporo-parietal lobule), whereas the slower Pβ cells project to the two magnocellular layers (and on to the dorsal "where" stream and parietal lobule) (Levethal et al., 1981).

Unfortunately, the segregation between the dorsal and ventral projections to the striate cortex, and beyond, is far from complete. There is a large degree of overlap in the range of stimuli that elicit electrophysiological activity in both pathways (Neally & Maunsell, 1994), and the degree of temporal and spatial frequency of a stimulus determines whether or not a deficit in contrast sensitivity will manifest itself following lesions to the parvo and magno pathways (Schiller, Logothetis, and Charles, 1990; Merigan Byrne, & Maunsell, 1991; Merigan Katz, Byrne, & Maunsell, 1991), Accordingly, the processing preferences of the parvo and magno pathways are best understood as a trade-off between the different requirements of spatial, temporal, and wavelength (luminance contrast) processing (Schiller and Logothetis, 1990; Merigan & Maunsell, 1993).

In summary, the initial proposal of a one-to-one correspondence between the dorsal-ventral and parvocellular-magnocellular streams is clearly incorrect. It is accepted, however, that: 1) the inputs to each stream are heavily intermingled; 2) the parvocellular system conveys information about form and color primarily to the inferior temporal cortex, the area identified by Ungerleider and Mishkin (1982) as being important in the recognition of form; 3) the location of an object in space is the task, in large part, of the magnocellular system, a pathway that terminates primarily in the posterior parietal cortex, the area identified by Ungerleider and Mishkin (1982) as important for spatial organization; 4) PET studies firmly support the dorsal-ventral pathway distinction in the intact human brain; and 4) axonal transmission of the various properties of a visual stimulus occurs faster along the parvocellular than magnocellular pathway (Livingstone & Hubel, 1988; for a review, see Kandel, 1991, & Mason & Kandel, 1991). These different conducting speeds along the pathways further implies that certain features of a visual stimulus will be processed at the cortex earlier than others - depending on the pathway taken, the distance traveled, and perhaps the clarity of the object presented.

Temporal Dissociation of the P390 and the Dorsal-Ventral Stream

Consistent with our dorsal-ventral stream interpretation of the P390 was the finding that the dorsal "arrow location" ERP preceded the ventral "letter identity" ERP by 55 and 59 ms in the task sequence and cue sequence ANOVAs, respectively. This demonstrates two points. First, that the scalp P390 is a composite of at least two distinct neuronal processes, one possibly originating in the superior parietal lobule(s), the other from the inferior, temporo-parietal cortex. Second, that the visual pathways taken by the arrow and letter cues might be different. The arrow cues may be processed along the faster magnocellular pathway, preferentially to the dorsal parietal lobule(s) for spatial analysis and a "where is it" decision, whereas the letter cues may proceed along the parvocellular pathway, preferentially to the temporo-parietal cortex, for form analysis and a "what is it" decision.

The temporal delay between the dorsal "spatial location" and ventral P390 "letter identity" is also comparable to the ERP results of Hillyard and Munte (1984) who found that ERP effects of sustained spatial attention preceded the effects related to attention to a secondary stimulus feature (color) by about 50 ms at lateral parietal-occipital electrode locations. Similarly, in an ERP study of transient attention to the spatial and color features of a target preceding cue stimulus, Eimer (1995) observed that parietal and temporal-occipital ERP modulations due to selectively attending to location features of the cue stimulus preceded the effects due to selectively attending to stimulus color by as much as 60 ms. This primacy of spatial over non-spatial attention appears to have been present in the dorsal and ventral ERP findings in our experiment #2. However, the ERP effects of attending to spatial location and color found by Hillyard and Munte (1984), and Eimer (1995) are much earlier (by 150-250 ms) than in our second experiment. The fact that subjects had to attend to 8 possible combinations of 2 distinct cue stimulus features (arrow location and letter identity) on each trial may have delayed the onset of the feature-specific attention effects in the second experiment, even though the earlier ERP effects of spatial compared to non-spatial attention were retained.

Further ERP evidence for the primacy of processing spatial location features, particularly in dorsal parietal brain regions, and stimulus identity in ventral regions, comes from a series of studies by Rusell Harter and colleagues. The studies involved recording ERPs in response to the same visual stimuli, when they were attended and when they were ignored. Each study focused on a different feature of the stimulus: color and meaning (Aine & Harter, 1986), integration of multiple stimulus features (Previc & Harter, 1982), orientation (Harter & Guido, 1980), spatial frequency (Harter & Previc, 1978), and spatial location (Eason, Harter, & White, 1969; Harter, Aine, & Schroeder, 1982). Difference waveforms were calculated by subtracting the averaged ERP when a particular feature was ignored from the averaged ERP to that same stimulus when the same feature was attended. A "selection negativity" deflection in the difference waveforms was found to vary in onset latency and scalp distribution in relation to the type of stimulus feature being attended (Harter & Aine, 1984). The onset latencies of the selection negativities evoked by the various features revealed that the spatial location of the stimulus was the first feature to be processed. Moreover, the negativity associated with the selection of the relevant location tended to have its maximum amplitude over dorsal central and parietal scalp sites. In contrast, the selection negativities evoked by attending to the color, orientation, and spatial frequency of the stimulus had longer latencies, and scalp topographies that were maximal over the ventral parieto-occipital sites. The variations observed in the onset latency, and scalp distribution of the selection negativity across studies was interpreted as reflecting variations in the initial activation of the neural channels that were selectively activated by the attended feature(s) of the stimulus (Harter & Aine, 1984, 1986) in either the dorsal (spatial location) or ventral (stimulus form and shape) projection systems as outlined by Ungerleider & Mishkin (1982).

How can the dorsal-ventral stream model of the P390 from our second experiment account for the similar scalp topography of the P300 during both auditory and visual oddball paradigms (see Picton, 1992) in adults? The answer may be that processing associated with visual and auditory spatial (and non-spatial) attention is not entirely modality specific but may partially depend upon common supramodal mechanisms (Eimer & Schroger, 1998). Such mechanisms might be located in multi-sensory neurons found in parietal (location discrimination) and temporo-parietal (object identity) association cortices. For example, objects that capture our attention both visually and acoustically almost always share the same location in extrapersonal space. In such situations there has to be a common mechanism for coordinating spatial attention across modalities - i.e. an integrated retinotopic and tonotopic mapping of visual and auditory space. It is an accepted general principle of sensory processing that neurons that are involved in the processing of related information tend to be clustered together (Kuffler, Nicholls, & Martin, 1984). It may be that some clusters are based on the location and identity, rather than the modality of the salient stimulus.

The notion that there may be cross-modal links in spatial attention, served by a common supramodal neuronal system, is supported by both lesion (Farah, Wong, Monheit, & Morrow, 1989) and RT (Spence and Driver, 1996, 1997) studies. First, that patients with parietal lesions have difficulties in disengaging attention from the ipsilesional hemispace in response to both visual and auditory cues suggests that the disengage deficit arises from damage to a shared, modality non-specific brain region (Farah et al., 1990). Second, RT to auditory and visual targets is facilitated by location identifying cues presented in the opposite modality. For example, Spence and Driver (1996) used centrally located arrow cues to indicate the likely location of target stimuli of one modality. Target stimuli of the other modality were presented less frequently (25% of trials) and were more likely to be presented at the uncued side. The results indicated a supramodal link between auditory and visual spatial attention. Thus, when the cue indicated the likely location of visual targets, auditory discrimination was faster when auditory targets were presented at cued locations. When the location of auditory targets was cued, visual discrimination was faster at cued than uncued locations.

If the P300 is generated in object location and object identity supra-modal regions in the parietal and temporo-parietal cortices, then the scalp topography of the P300 would be expected to be similar whether the P300 is generated by auditory or visual stimuli. When stimuli provide both spatial (location) and object identity (e.g. pitch, loudness, timbre; shape, color, orientation...) information the scalp P300 will represent a composite of both analyses. However, our experiment #2 demonstrated that a "common" parietal (P3 and P4) P300 will be generated whether or not stimuli are processed in terms of spatial location or identity attributes. It is only when the P300 is analyzed topographically (dorsal vs. ventral electrodes) and temporally in relation to stimulus location and stimulus identity processing, that it becomes clear that the scalp P300 is the product of at least two physio-anatomically distinct neuronal clusters, activated simultaneously, or nearly so.

That the P300 is related to the coordinated activity of various, feature specific perceptual analyzers, rather than the processing of stimuli as a gestalt as in the "context updating" of working memory hypothesis (Donchin 1981; Donchin & Coles, 1988), is supported by studies where consciousness is dissociated from behavior. P300 waves have been recorded in patients with blindsight who are not conscious of visual stimuli, yet can guess, at better than chance levels, the identity or location of stimuli in parts of their visual field that correspond to their scotomata (Shefrin, Goodin, & Aminoff, 1988). In a patient with prosopagnosia, although the P300 differentiated between familiar and unfamiliar faces, these distinctions were not recognized by the patient (Renault, et al., 1989). Finally, normal subjects may sometimes show a P300 for somatosensory stimuli that are below the threshold for conscious awareness (Barrett Neshige, & Shibasaki, 1987).

Studies wherein the P300 is dissociated from behavior have demonstrated that specific features of the to-be-identified stimuli are associated with the generation of the P300, rather than some global, holistic "contextual updating" following perceptual analysis. A P300 would be generated as long as some distinctive perceptual features are processed, irrespective of the brains ability to categorize these features in terms of "context updating" or conscious awareness.

P300 and Feature Analysis?

Our feature analysis model of the P300 might also account for why a P300 is generated when an expected stimulus is not presented, and for the observation that the RT often precedes the P300.

The omission of a stimulus in a train of stimuli (Simson, 1976, 1977a) would be expected to generate a P300 since the omitted stimulus could only be classified as distinct provided that the unique features of the expected stimulus have been processed to a point to allow an identification of their absence. RT typically precedes the P300 by 50 ms (Ritter, Simson, & Vaughan, 1972). Some volitional control is possible since earlier RTs relative to the P300 peak are possible when subjects are instructed to emphasize response speed rather than accuracy (Kutas, 1977; Deacon-Elliott, 1988; Deacon-Elliott, Campbell, Suffield, & Proulx, 1987) although more errors are made by responding early. These results suggest that when responding as quickly as possible, subjects initiate their response before the stimulus is fully evaluated. Under speed instructions, subjects might risk being wrong and respond prior to a full evaluation of the stimulus.

If the scalp recorded P300 represents the collective analysis of stimuli in terms of their defining features, and as we have demonstrated in experiment #2, certain features are processed before others, then it is reasonable to expect that that an accurate, and early response (i.e. button press RT) could be executed based only on a partial analysis of key features of the presented stimulus. Although the decision to respond would precede the full perceptual analysis and categorization of a stimulus (i.e. the P300), a correct response could nevertheless be executed. Perhaps this is why the response and movement time of extroverted and neurotic subjects is negatively related to P300 latency (Stelmack, Houlihan, McGarry-Roberts, 1992) - such personalities may be more willing to proceed based on a less than complete analysis of the available information.

The main point is that the peak latency of the P300 may not be a true representation of the time needed to categorize a stimulus, rather it appears to represent an interpolation at the scalp of temporally overlapping intracerebral potentials which are generated when new key features of a stimulus have been identified. Some stimulus features will have been processed prior to the P300 peak. Since the P300 appears to be an interpolation of positive scalp potentials with different temporal properties, its peak latency will be delayed as a function of the temporal span between the peaks of the underlying feature analysis waveforms. In certain circumstances, the early feature analysis may be all that is required in order to respond correctly, and a response (RT) will therefore precede the P300 peak. Being able to respond to a sudden sound or shadow prior to a full perceptual analysis certainly confers a survival advantage. Although any unexpected noise or image may be benign, it may well signify food to a predator and death to its potential prey. Under these circumstances, it would be advantageous if the organism could "shoot first", and ask questions later. Perhaps the P300 is the sensory system's way of pushing new news onto the neurophysiological front page. However, the news (feature analysis), and ability to respond, may precede the headlines (full stimulus categorization).

FRONTAL NEGATIVE WAVE: N740

The hypothesis that the N430 in experiment #1 represents an endogenous switch in attention between task sets rather than an exogenous stimulus effect was supported by the ANOVA results in experiment #2. The amplitude of the "N740" in experiment #2 was larger for switch than repeat tasks, but did not vary with switching between or repeating the cue modality. This indicates that the mid-frontal switching negativity goes specifically with the processing of the task. The N740 wave in the second experiment is almost certainly the same wave as the N430 in the first experiment. The latency difference may be related to the greater urgency for switching in the first experiment where the cue-target interval was either 1200 or 200 ms compared to the second experiment where the cue-target interval was always 1500 ms. The N430 and N740 task switching peaks in our two experiments are comparable to Shedden's (1995) N2 (250 to 450 ms) negative slow difference wave (switch - fixed spatial attention) over central anterior electrode sites, and to Harter and Anllo-Vento's (1991) anterior switching negativity (200 to 500 ms).

Shedden (1995) interpreted her anterior switching negativity as the disengagement of attention to location, whereas Harter and Anllo-Vento's (1991) interpretation was that of the selective recruitment of cognitive processes involved with directing attention in space. However, the results of our second experiment indicate that this mid-frontal switching negativity is not specific to spatial-location attention switching. It is generated whether subjects are cued to switch attention between tasks based on either the spatial location, or a secondary feature such as the identity (i.e. different letters) of the eliciting cue stimulus. The intracerebral source(s) for this potential may be the supplementary motor area, anterior cingulate, or a combination of activity from both of these regions.

Recall that the early part of the Bereitschaftspotential has a mid-frontal scalp distribution. Deecke and his colleagues (Deecke, 1987; Lang, Deecke, 1990; Cheyne, 1990) have suggested that this early part of the Bereitschaftspotential is generated in the supplementary motor area located on the medial surface of the frontal lobe - an area involved in planning and execution of complex motor sequences (Lang et al., 1990; Tanji, 1994). In the present experiment, it would be reasonable to propose that the supplementary motor area is briefly activated when the subject has to switch between tasks since the task switch also forced subjects to select a new set of response rules.

On the other hand, Posner and colleagues (Posner, 1980; Posner, Petersen, Fox, & Raichle, 1988; Posner & Petersen, 1990; Posner & Raichle, 1994) have emphasized the role of an anterior mid-line attentional system (cingulate) that is involved with high-level selection of information, targets, and cognitive procedures for output. For example, PET studies have demonstrated no change in the blood flow in the anterior cingulate during the simple reading of visually presented words, but robust activation of the anterior cingulate occurs when the words are more complexly processed during semantic monitoring and verb generation tasks, or under conditions of Stroop interference (Pardo, Pardo, Janer, & Raichle, 1990; Petersen et al., 1988b, 1989; Posner et al., 1988b; see also Janer & Pardo, 1991). Moreover, the degree of blood flow in the anterior cingulate increases as the number of targets in a detection task increases (Posner et al., 1988b). Thus, the mid-frontal negative wave in our two experiments may have arisen from the anterior cingulate being activated when subjects were required to select a new mode of interpreting and responding to the cue stimuli during task switch trials.

READINESS POTENTIAL

Simple Trial block

As in experiment #1, the RP was larger over the hemisphere contralateral to the hand of response. For example, the RP was larger over the right hemisphere during a left than a right hand response, and larger over left hemisphere during a right than a left hand response.

Although the RP was larger at the central electrode site contralateral to the preparing response hand during switch task trials, the bilateral RP during switch trials in the first experiment did not replicate in experiment #2. Thus, the RP was not larger for switch than repeat task trials at the central electrode site ipsilateral to the preparing response hand (i.e. contralateral to the hand that responded on the immediately preceding trial). Since the fast 200 ms cue-target interval catch trials were not included in the experiment #2, it is possible that the subject's incentive, in terms of achieving a faster RT, for automatically activating the hand that responded on the previous trial was removed. Thus, one possible interpretation is that the bilateral switch RP in experiment #1 was due to the automatic activation of the hand that responded on the previous trial. In experiment #2 it is possible that, without the urgency of the occasional catch trials, subjects did not set up to activate the preceding hand automatically. Rather, they may have just activated the cortex for the appropriate hand and done so to a greater degree on switch trials which were otherwise more likely to lead to errors.

Complex (1 hand) vs. Simple (2 hand) Trial Blocks

We hypothesized that the inhibition hypothesis would be supported if the RP contralateral to the cued response hand was larger during the complex than simple task switch trials. This hypothesis was based on the assumption that during complex task switch trials subjects must simultaneously inhibit the previous response and prepare the current response. Since both processes must be carried out on the same response hand, then this should increase the amplitude of the RP during the complex trials - provided that the hypothesized response inhibition and response preparation negativity's are additive at the scalp. Thus the inhibition hypothesis would be supported if the RP contralateral to the preparing response hand was larger during the complex (1 hand) than the simple (2 hand) task switch trials.

Completely opposite to the hypothesis, the RP contralateral to the preparing left and right hand on task switch trials was found to be larger during the simple rather than the complex blocks of trials. One possible explanation may be that an inhibition negativity might occur only when there is a switch in hands and not when there is simply a switch in fingers. We are aware that this interpretation of the functional significance of the RP at the present time remains speculative and will require further experiments to allow a more precise or valid explanation.

F7 TARGET PEAK - N400T

As in the first experiment, a large left prefrontal negative peak (N400T) was recorded only in association with the target stimuli and the execution of the button press response. In experiment #1 it was unclear whether this ERP represented a distinct cognitive process associated with response selection or the anterior end of the parietal P390T dipole to the targets. Accordingly, we speculated that if the N400T represents a distinct neurophysiological event, independent of the P390T, and specific to response selection, then its peak latency should be significantly later for the complex than simple S-R mapping task, whereas the P390T peak latency should be constant across the simple and complex S-R tasks. On the other hand, it was recognized that if this effect was absent, and if the peak latency of the N400T was found to be statistically equivalent to that of the P390T, then the hypothesis that the N400T represents an anterior inversion of the parietal P390T would be inescapable.

The task complexity manipulation failed to dissociate the N400T from the P390T since the peak latencies for both ERPs were not significantly different between the complex and simple S-R mapping rule trials. The N400T also failed to dissociate from the P390T in the direct analysis since both peaks were found to share a common latency. It must therefore be concluded that the left frontal N400T represents nothing more than an anterior inversion of the parietal P390T to the target stimuli. Since the N400T is only present after the target stimuli, whereas the P390T is present for both cues and targets, it is reasonable to speculate that the configuration for the neuronal generators of the cue P390 and target P390T are different - another indication that the scalp topography of the P390 is sensitive to the physical properties of the eliciting stimuli. These data also indicate that the P390T to targets must have an intra-cerebral generator whose physiological dipole points negatively towards the left inferior frontal site, and positively to the superior (right) parietal scalp.

FRONTAL SLOW WAVES

SPW and SNW

The sustained left frontal negativity, and right frontal positivity effects recorded in experiment #1 replicated in the second experiment. In experiment #1 it was unclear whether the negative left frontal (F3) and positive right (F8) frontal slow waves during the cue-target interval represented opposite poles of a common source dipole, or two separate source generators each representing a distinct cognitive process (e.g. monitoring and/or working memory). Two results from experiment #2 support the hypothesis of two simultaneously active, and independent, cognitive processes. First, the right frontal positive slow wave was larger during arrow than letter cue stimuli, whereas the left frontal negativity was invariant with respect to the modality of the cue stimulus. Second, a task complexity dissociation was observed. The right frontal positivity was largest during the complex (1 hand) than the simple (2 hand) S-R mapping rule trials, whereas the left frontal negativity showed an opposite effect being largest during the simple than complex S-R mapping rule trials. It is also clear that the left frontal negativity represents a cerebral process independent from the right hand (left hemisphere) readiness potential. The readiness potential at C3 during a right hand response was significantly larger during the simple than complex S-R mapping rule trials when subjects switched rather than repeated cues and tasks, whereas, while the left frontal negativity at F3 was also significantly larger during the simple than complex trials, it was statistically invariant during switching and repeating both cues and tasks.

A slowly increasing positive frontal pre-movement potential has been recorded in addition to the central-parietal CNV during simple and choice RT paradigms (Bötzel, Mayer, Oertel, & Paulus, 1995). In our second experiment, this positive slow wave was right frontal lateralized, and was larger during the complex than simple S-R mapping rule trials. However, Bötzel et al. (1995) observed that the steepness of their frontal positivity actually decreased with the complexity of the task (simple vs. choice RT) in young healthy controls. One interpretation for the discrepancy between the two studies is that subjects may not have experienced our complex (1hand) manipulation task as complex at all. However, the behavioral data did show that the complex trials were experienced as difficult by the subjects in terms of longer RTs. Thus, we remain uncertain as to how to interpret the variation in our frontal sustained potentials. Future experimental manipulations are required before a firm interpretation can be rendered.

GENERAL DISCUSSION

The purposes for conducting the experiments reported in this manuscript were three-fold. First, we wanted to see if the ERPs could provide evidence for the hypothesized posterior (goal identity) and anterior (response rule selection) attention switching dichotomy. Second, we set out to test the stimulus-cued completion hypothesis that the mental set could not be completely reconfigured until the arrival of the imperative (target) stimulus. This was investigated electrophysiologically by an analysis of the readiness potential, and behaviorally through the RTs. We sought to replicate the RT reports of previous task-set switching studies that had demonstrated the presence of both an early, and a late switching stage. The existence of these stages would be supported by a partial decline in RT switch cost between the short and long cue-target-interval trials, and by a residual switch cost even though subjects were provided with ample time to complete the switch in mental set. The ERPs would support the stimulus-cued completion hypothesis provided that the readiness potential demonstrated less than optimal response preparation prior to the imperative target stimulus. Third, assuming that a residual RT switch cost would be present, we hoped to identify an ERP that corresponded, in time, to the switch cost latency range.

Task-set switching studies have demonstrated that RT increases as the difficulty of discriminating between stimuli increases - although the switch cost remains constant (Allport &

Styles, 1990; Allport, Styles, & Hsieh, 1994; Rubenstein, Meyer, & Evans, 1994). This has been interpreted as indicating that the executive control of switching is central to the process of stimulus evaluation. Our study has demonstrated that posterior and anterior ERPs are associated with the switching attention between tasks. The occipital N200 may represent orientation to a salient visual stimulus, the P390 appears to represent stimulus evaluation in terms of temporally overlapping analyses of specific features of visual stimuli, and a mid-frontal negative wave which goes specifically with processing the need to switch from one mode of action to another. Although this spatio-temporal sequence of ERPs makes intuitive sense, we recognize that the mid-frontal N430 and N740 in our experiments must be interpreted with caution since the size of the effect, in microvolts, was small, and the statistical significance was only borderline ($p < .05$).

The RP results were very complex. They varied from the first experiment to the second and it is difficult to determine with any certainty what caused the variance. An added factor complicating the RP results is that they ride on an underlying left negative sustained potential that lasts throughout the trial. A working hypothesis is that the lateralized RP does indeed respond with the contralateral hand and that this is increased during switch trials. This would be compatible with the results of the second experiment. If the response is urgent (as in the first experiment) it is possible that the brain automatically activates the previously responding hand just in case it is needed again. This would lead to the bilateral RP recorded on switch trials in the first experiment.

The manipulation of task complexity in the second experiment showed that there is probably no additional cerebral processing associated with inhibition of previous response patterns. The RP therefore most likely represents an activation process.

Large frontal sustained potentials that occurred during task performance were essentially the same as in the previous experiment. There were no clear effects of task complexity or task hand on these results. These sustained potentials may represent frontal processes of working memory and task-supervision. Their exact nature will only be determined when they can be experimentally manipulated.

Our experiments demonstrate that electrical measurements can show the millisecond-to-millisecond sequence of cerebral activity during a complex cognitive paradigm. The ERP results suggest that successful switching between tasks in the present paradigm included a sequential activation of posterior (extrastriate, dorsal parietal, ventral temporal-parietal) and anterior (mid-frontal) cognitive processes. This distribution is consistent with kinds of task-set switching deficits patients exhibit on the Wisconsin Card Sorting Test following either an anterior (Milner, 1967) or a posterior (Drewe, 1974) brain lesion.

The hypothesis that the attention switching system is configured in separate posterior and anterior brain regions is consistent with clinical observations of patients with switching deficits. While performing a sorting task that requires a switch between sorting principles, some frontal patients continue to make perseverative sorting errors even while verbalizing the correct strategy or verbally identifying a response error (i.e. pathological inertia) (see Stuss & Benson, 1984). Luria (1973) repeatedly called attention to these deficits and considered them hallmarks of frontal lobe dysfunction - it is as though an intact posterior perceptual system (feature analysis?) has been uncoupled from the frontal controls responsible for applying the new task rules (response rule activation? working memory? monitoring?)

Our results are also fit quite nicely with recent neurocognitive theories that have differentiated an anterior attentional system (i.e. high level selection of processing for output) in the frontal lobes, a posterior attentional system (i.e. spatial allocation of attention) in the parietal lobes (Mesulam, 1985; Posner 1988, 1994; Posner & Petersen, 1990; Posner & Raichle, 1994; Stuss et al., 1995). Finally, the scalp distribution of the ERPs in our second experiment are in accord with the dorsal "where" and ventral "what" processing streams as initially proposed by Ungerleider & Mishkin (1982), and most recently confirmed through the use of functional brain imaging technology (Köhler et al., 1995).

Our experiments also illustrate some of the difficulties in trying to decipher what is going on in the human brain as it performs relatively simple tasks. Many of the results did not so much disconfirm hypotheses as indicate that the hypotheses were set up incorrectly. In retrospect, the results make sense and we are left with a much richer view of cerebral function than was available in simplistic working hypotheses. The N200 does not simply represent the processing of the stimulus but varies strikingly in its scalp distribution with the nature of the stimulus being processed. Science mixes the logic of hypothesis testing with the luck of serendipitous findings. Sometimes the hypotheses do not fit with the data because the brain has many more options available to it than evaluated by simple dichotomous tests. When preparing to respond, the brain can choose its timing and can choose to prepare responses without knowing whether they will be needed or not. This large range of subject options probably explains the complexity of the RP results.

Despite the complexity of the brain and the simplicity of our ideas of how it might function, the thesis has nevertheless led to some clear insights into how the brain uses the information in a cue to switch from one task to another. The posterior N200 and P390 waves indicate that the cerebral processing of stimulus information occurs in cerebral areas that are distinctly related to different types of stimuli. More clearly than any other available data the differences in the scalp topography of the P390 with the different stimulus types indicate that this late positive wave can derive from multiple generators. The frontocentral negative wave is clearly related to the cerebral process of switching tasks. This indicates the cerebral process that may be disturbed in frontal lobe lesioned patients who have difficulties with switching.

Science is never complete. There is always something that needs further understanding. In the results of this thesis, the sustained frontal waves stand out as requiring further evaluation. They likely represent cerebral processes underlying working memory or task-supervision. They will only be understood when we can show how they change with experimental manipulations.

GENERAL CONCLUSION

This research has shown that the cognitive processes involved in switching attention between different tasks can all be completed in advance of an imperative target stimulus. This conclusion is based on our failure to obtain a residual RT switch cost, in either experiment during the long cue-target interval trials. Remarkably, even when the stimulus-response mapping rules were made very complex, the data still failed to yield a residual RT cost. If subjects were less motivated, the final preparation or completion of the response-set might occur after the target and this may explain our discrepancy with the residual RT switch cost literature. Our results, both behaviorally and electrophysiologically, did not support the target-evoked completion hypothesis.

Our ERP data did succeed at breaking down the cognitive process of task-switching into a logical sequence of steps that appear to involve both posterior and anterior cerebral events. The occipital N200 may represent the processing of a salient visual stimulus ("What is this stimulus?"). This is followed by the parietal P390 wherein the precise meaning of the stimulus in relation to the task is extracted ("What does it mean?"). This information extraction appears to be in the form of a feature analysis wherein dorsal parietal regions decipher salient spatial features of the visual stimuli, whereas ventral temporo-parietal regions process significant physical attributes (e.g. color, form). The next step in the switching process emerges as the mid-frontal N430 and N740. These anterior ERPs might represent the cerebral process that connects the output from the earlier feature analysis processing stages with the new response mode ("What do I do now?"). Finally, the readiness potential is the last step in the task-switching sequence and it represents preparation of the appropriate response hand. Clearly, both posterior and anterior brain regions are involved in switching, and each region carries out a distinct set of cognitive operations. This multi-stage model of attention-switching likely explains the complexity of the clinical reports of both diffuse and focal brain-injuries being associated with attention-switching deficits on such standardized tests such as the WCST.

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