UNIVERSITY OF GRONINGEN

Thesis

Rate- and Pulse Coded Motor Preparation

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Hence the experienced soldier, once in motion, is never bewildered; once he has broken camp, he is never at a loss.

...

Rapidity is the essence of war: take advantage of the enemy's unreadiness, make your way by unexpected routes, and attack unguarded spots.

...

When it was to their advantage, they made a forward move; when otherwise, they stopped still.

...

Thus, what enables the wise sovereign and the good general to strike and conquer, and achieve things beyond the reach of ordinary men, is foreknowledge.

-The Art of War, Sun-Tzu

Military strategy has always been an important aspect of traditional chinese philosophy. So much so that a work of philosophy was considered incomplete if it did not contain some military advice. One explanation for this intimate relationship that is strange in western eyes is that strategy is a source of metaphors for life (Ames, R.T., 1993). Master Sun tells us to be prepared in any situation so we can take swift action. This basic thought lies at the heart of the paper you are about to read.

Acknowledgements

This thesis would not have been finished without the help of a lot of people. In the first place, I want to thank Ritske for giving me the freedom to make my own mistakes, listening to my ideas and for putting me back on track when I needed that. I want to thank Thomas for his patience in providing feedback, especially where it concerned the mathematic intricacies of the research and for the many conversations we had over the course of the last year. I want to thank both of you for your support when I faced the physical limitations imposed on me by two illnesses while working on this thesis. In this light I also want to thank some of my friends who typed parts of this text that were handwritten: Maysha, Joris, Harma and Ellen. Finally, I want to thank Dick Smid for his advice in setting up the experiment.

Contents

Abstract

The relationship between several measures of motor preparation was investigated in three tasks. The measures investigated were reaction times (RT), a behavioral measure, the contingent negative variation (CNV) and the lateralized readiness potential (LRP), two rate coded EEG measures and instantaneous amplitude (IA) and lateralized instantaneous amplitude (LIA), two pulse coded EEG measures. The tasks used were a Rogers and Monsell task switching paradigm, a Choice/go-nogo paradigm and a Sequence Element Cueing Task. The latter task was specifically designed to test a possible dissociation between rate- and pulse coded measures of motor preparation. This dissociation was not found, but each measure appears to be sensitive to task-specific processes of motor preparation. It is argued that the measures compliment each other.

1. Introduction

What is motor preparation? Preparing for action can be seen as a partial reaction to a stimulus in the future. The causal problem in this view was pointed out in an excellent overview chapter about 'Preparation for Action' by Requin (1991) who writes:

> "As an explanatory concept, 'motor preparation' has a teleological flavor because it insinuates that activity in the present is determined by events in the future. To prepare for future events implies an expectation of these events: an internal representation of what is going to happen. The teleological problem may be overcome by viewing expectations as the memory products of past experiences in similar contexts. Nevertheless, the role attributed to preparation in determining present behavior identifies a conspicuous cognitive facet of this concept. But preparation also has many tangible manifestations that render it responsive to experimental discussion."

Requin (1991) distinguishes tonic preparation and phasic preparation. Tonic preparation is an aspecific kind of preparation which occurs in situations marked by high uncertainty. In these situations most speed can be gained by preparing the whole body for fast reactions. Tonic preparation involves an increase in heart rate and hence blood flow to supply the striate muscles, which moves parts of the skeleton, with energy. During tonic preparation respiration is also increased to dispose of excess $CO2$, replenish the $O2$ and maintain the blood pH-level. Phasic preparation is preparation for a specific response. Preparation for a specific response usually occurs in well-known situations which results in low uncertainty about what will be an adequate response. As a result, the overall, tonic preparation is not necessary. The present study deals with phasic motor preparation and specifically what role the brain has in phasic motor preparation.

Reaction time studies show that if subjects are given increased opportunity to prepare for a coming action, their responses usually come faster and/or are more accurate. The question is how the brain does this: motor preparation as a neurophysiological process is not well understood. Possible ways to achieve preparation, which will be further explained below, are preprocessing of information, partial construction of motor programs, increasing sensitivity to input of several parts of the motor system and increasing the baseline output of the motor-cortex. All these kinds of phasic preparation occur largely in the motor cortex.

Preprocessing of information affects perceptual processes and/or information processing. If a cue provides part of the stimulus then that part of the stimulus does not have to be perceived anymore. The part of the stimulus given by a cue may also reduce the set of possible responses, affecting information processing at stimulus presentation: fewer parts of the stimulus may be necessary for discriminating between responses.

The motor programming perspective is based on observations that serial movements can be effectively made without feedback (Proctor and Dutta, 1995). High level plans, or motor programs guide movement instead (e.g. Keele, 1968). By providing a cue, part of a motor program may be produced and the additional information contained in the stimulus can be inserted into the program later, right before execution. By pregenerating a motor program, responses can be executed faster and more accurately. More recently, a coordination dynamics view on movement execution has become popular (Kelso, 1997). Coordination dynamics takes into account the inherent possibilities and restrictions of the human body and argues that some amount of feedback can be used during execution of movement.

The primary motor cortex, the lateral premotor cortex and the supplementary motor area can facilitate or supress the information that reaches them via sensory relay nuclei (Kelly in Kandel et al (eds.), 1991). This way, these structures might increase their sensitivity to a selective set of inputs and decrease their sensitivity to other input. This selective sensitivity might speed up reactions to the selected part of inputs and decreases the speed of reactions to other inputs.

Finally, by increasing the baseline output of the cortical motor areas to the brain stem and the spinal cord, the regions controlling muscle activation might exceed their thresholds faster when the correct stimuli is identified, speeding up reactions.

These processes may all be involved but it is likely that situational demands and available information will favor one process over another. The object of this study is to find out whether and if so, under what conditions, these processes play a role.

There are several ways of measuring if and how subjects prepare for a coming action. First, behavioral measures will be discussed, specifically reaction times. Second, two kinds of ERP-measures, the Contingent Negative Variation (CNV) and the Lateralized Readiness Potential (LRP) will be discussed. Third, the relevance of Instantaneous Amplitude (IA) of EEG signals to motor preparation will be discussed.

1.1. Behavioral Measures of Motor Preparation: Reaction Times

If preparation has a behavioral advantage, this should be expressed in faster responses or more accurate responses or both. Several different kinds of experimental techniques rely on this assumption, e.g. response cueing and response priming. Rosenbaum and Kornblum discuss the advantages of response priming over response cueing designs (1982). Response cueing involves giving subjects trial-by-trial advance information about a set of responses which will be more likely to be demanded at stimulus presentation. In each trial of a response cueing task first a cue is presented, after a sufficiently long preparation interval the stimulus is presented and then the subject responds. The cue is supposed to give some, but not all information about the coming stimulus. For example, if the subject is to respond with the middle- or index finger of the right or left hand a cue might tell the subject either which hand to respond with or which finger to respond with. This effectively reduces the set of four possible responses to two. Rosenbaum and Kornblum identify two problems with response cueing. The first is that some cues may facilitate stimulus identification more than others. In the above example fingers might have been cued with an ‘M’ for middle finger or an

'I' for index finger and hands with an 'R' for right hand and an 'L' for left hand. So, if the finger were cued, the subject had to discriminate between the 'R' and 'L' which might be easier than discriminating between an 'M' and 'I'. This would result in different RT's even if motor preparation is the same for both cue types. The second problem Rosenbaum and Kornblum identify deals with the difference between the actions that remain possible after a cue is given. If, in the same example, a hand was cued, the subject would have to choose between two fingers of the same hand. On the other hand, if a finger was cued, the subject would have to choose between two prepared hands. Rejecting one hand and activating the other may be easier than rejecting a finger and activating another finger of the same hand. In other words, some cues may facilitate the preparation of a set of responses more readily distinguishable than others sets. This would result in different RT's for different cue types even if the level of preparation is the same for both cue types.

Rosenbaum and Kornblum claim response priming deals with these issues. Response priming involves making one of several responses more likely to be required, without the use of cues. This is done by increasing the likelihood of one stimulus over the others so that subjects prepare for that stimulus. For example, if subjects had to respond with the index- and middle finger of the left and right hand, the left index finger might be indicated by the stimulus 70% of the time and all other fingers 10% of the time. There are a few issues with response priming that should be kept in mind as well.

First, the state of readiness of subjects in a priming paradigm is a state that may not change much during an experiment or block of trials. The full preparation process is not repeated each trial so the preparation itself remains unmeasurable. The fast motor preparation required in a precueing paradigm may more accurately reflect an everyday environment where different people face different tasks at every moment. This may be seen as a tonic state of preparation.

Second, subjects may employ a response strategy based on the increased likelihood of the occurrence of the primed stimulus. If the presented stimulus is the primed stimulus, subjects give the favored response. If a presented stimulus is not the primed stimulus, an extra process has to be started to pick the appropriate response from the remaining alternatives. This extra process may result in increased differences in RT between primed and unprimed respsonses that does not reflect a difference in degree of motor preparation. This response strategy affects one trial at a time.

Third, on most trials the chance that a previous trial included a primed response is higher than that it included any other response. A sort of carry-over effect may take place: the previous response will usually still be a bit activated. When it has to be given again this is easier than giving a different response. An added effect may be that subjects might have to actively deprepare a residual activation when a non-primed response follows a primed response. These carry-over effects will result in differences in RT between primed and unprimed responses, independent of degree of preparation. This is like the tonic effect described first, but can only occur in specific sequences of trials. The residual activation of responses made in previous trials also plays a role in task switching paradigms. Task switching will be described later.

Priming and cueing both manipulate the event uncertainty of an experimental task, or the question of what to do. Requin (1991) also distinguishes time uncertainty: when to act? Requin et al (1991) reported the finding of Alegria (1974) that it is not possible to maintain a constant state of preparation for a completely specified action. Subjects first prepare for about 150 ms, then deprepare for another 250 ms and reprepare during another 750 ms. Maximum readiness occurred at about 150 ms and 1150 ms after a cue. Earlier research by Alegria and Bertelson (1970) and Holender and Bertelson (1974) suggests that even longer Stimulus Onset Asynchronies (SOA's) of 5 seconds further increase time uncertainty and decrease task-performance as measured by RT and errors. As the time between cue and stimulus increases it appears subjects are less able to estimate when the stimulus will occur and their preparation for the stimulus suffers as a result. This is called the ageing foreperiod effect.

The task switching paradigm described by Rogers and Monsell (1995) is used to investigate the process of changing and maintaining task sets. As will be explained below, a manipulation of time uncertainty is inherent to a typical Rogers and Monsell task switching setup. The Rogers and Monsell task switching paradigm presents two tasks to subjects in an AABBAABB… sequence by clockwise presentation of stimuli in a four by four matrix. Usually the pairs of the upper two and lower two squares of the matrix are each assigned a task (as opposed to the left or right two squares of the matrix). As soon as subjects respond, a preparation interval starts followed by the next stimulus. The preparation interval is randomly chosen from a set of intervals ranging between 0 ms for no preparation to 1000 ms or more for optimum preparation. Rogers and Monsell (1995) found that switch costs decrease if subjects have more time and this effect reached a maximum after about 500 ms Rogers and Monsell used inter-trial intervals (ITI) of 150, 300, 450, 600 and 1200 ms but they did not find an effect of ageing foreperiod, although their maximum ITI might still have been too short for an ageing foreperiod effect to occur. Alternatively, the effects of task switching may have masked or altered an ageing foreperiod effect and/or vice versa.

From both the comparison of response cueing with response priming and the comparison of task switching with the ageing foreperiod effect it can be concluded that it is difficult to draw straightforward conclusions from behavioral data, such as RT and error rates, about the organization and mechanisms of the brain. But behavioral data only reflect the effects of preparation: the 'what' of brain functions. So, even if straightforward conclusions could be drawn from RT data, measurements of the brain in action, such as electroencephalogram (EEG), functional magnetic resonance imaging (fMRI) and positron emission tomography (PET) provide a peek into the 'how' of brain functions. Combining these neuroimaging techniques and behavioral data with knowledge of neuroanatomy allows building a more complete picture of what is going on in the brain. In the next sections, various analyses of EEG data will be discussed.

1.2. EEG Measures of Motor Preparation: Event Related Potentials

ERP-based measures used to study preparation are the Contingent Negative Variation (CNV; Walter et al, 1964) and the Lateralized Readiness Potential (LRP; Coles et al, 1988; De Jong et al, 1988). Both these measures are used in this study and will be discussed here, starting with the CNV. But first, sources of EEG will be briefly described to provide a frame of reference to interpret the CNV and LRP and other EEG measures. The focus in this description will be on motor systems.

1.2.1. Sources of EEG

EEG signals primarily reflect summated currents through the extracellular space caused by excitation and inhibition of pyramidal cells in the cortex. Although action potentials are the largest signals generated by neurons, they contribute little to the EEG (Martin in Kandel et al (eds.), 1991).

When a postsynaptic neuron receives an excitatory postsynaptic potential (EPSP) or an inhibitory postsynaptic potential (IPSP), a short flow of ions between the inside and outside of the neuron is started (see Figure 1.1.). This ion-flow disturbs the equilibrium of the resting potential of the neuron locally. By various processes the resting potential will gradually be restored and sometimes the neuron produces an action potential. But the incoming signal has also generated a potential within and outside the cell because suddenly ions within the cell are unevenly distributed as are the ions outside the cell. This causes ions inside the cell and outside the cell to flow so that they are evenly distributed again. For example, if an EPSP is generated at the end of a dendrite (far from the soma), the number of positive Na^+ ions outside the cell around the synapse drops in comparison to the number of positive ions around the rest of the cell. Positive ions will now move from the rest of the cell to the location of the synapse. In effect, the location of the synapse becomes the negative end of an equivalent dipole. The same process occurs within the cell, causing a current with reversed polarity. The current within the cell however is not picked up by electrodes outside the cell. If a cell receives an EPSP close to the soma, the negative end of the dipole is still located near the synapse generating the EPSP but the positive pole may now be located at the far end of the dendrite. IPSP's cause the same processes but with reversed polarity (K^+ ions leave the neuron). The currents caused by EPSP's and IPSP's received by one cell are too small to pick up at the scalp. Because pyramidal cells in the cortex all have their apical dendrites oriented parallel to one another and perpendicular to the surface of the cortex, simultaneous stimulation of a large group of pyramidal cells can be measured outside the scalp (Martin in Kandel et al (eds.), 1991).

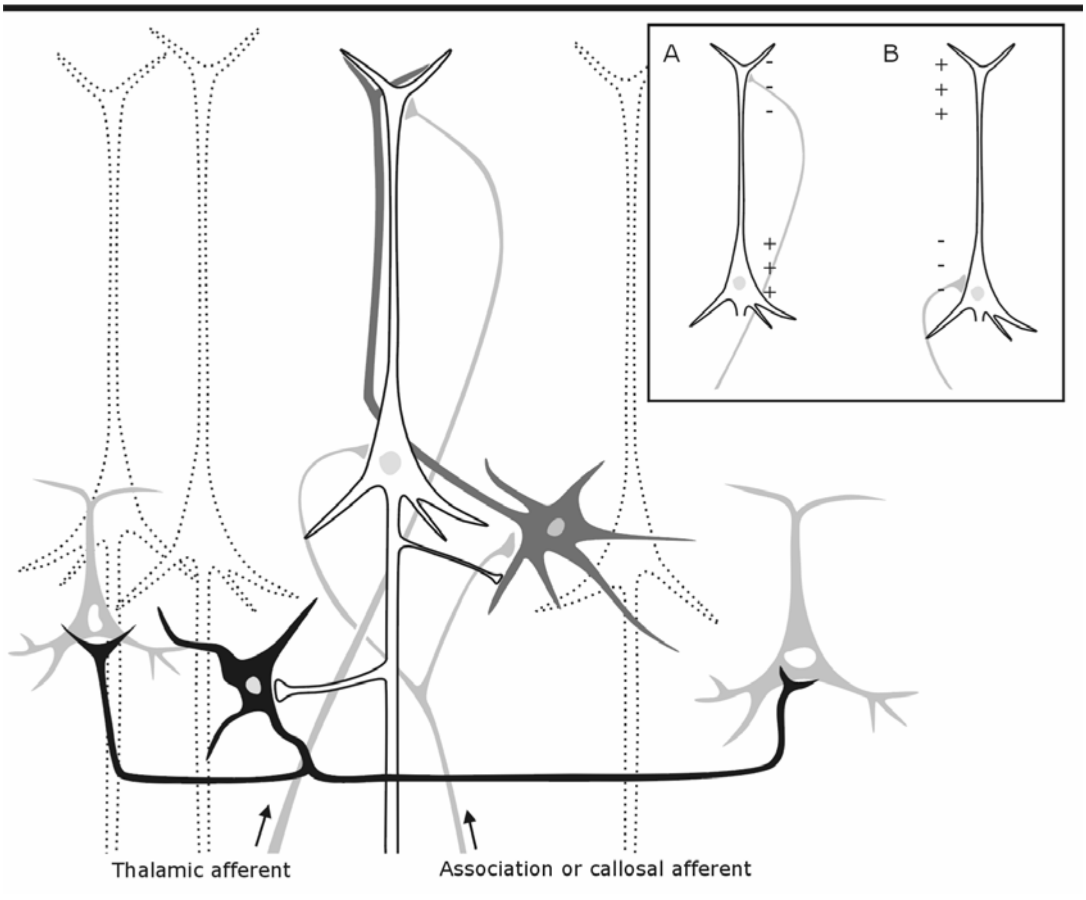


Figure 1.1. Pyramidal neurons in the cortex.
The outside of the cortex would be at the top of the picture. Extracellular currents as a result of stimulation of pyramidal cells (white) can be measured outside the scalp if a substantial amount of pyramidal cells is stimulated simultaneously. Activation of for example basket cells (black) and stellate neurons (dark grey) can not be measured outside the scalp. The polarity of equivalent dipoles depends on the location of the stimulating synapse. An EPSP in A would register as a negative signal, while an EPSP at B would register as a positive signal. For IPSP's these polarities are reversed.

To interpret EEG, it is important to know what areas send EPSP's and IPSP's to what locations on the apical dendrites of pyramidal cells in the cortex. Most of the input received by neurons in cortical motor areas is generated by the thalamus and by other cortical motor areas (see Figure 1.2.) (Ghez in Kandel et al (eds.), 1991b). Thalamus axons most often end on the apical dendrites near the soma of pyramidal cells. Cortical axons most often end at the other side of the apical dendrite. Two kinds of connections between cortical motor areas can be distinguished: associative connections, projecting to nearby neurons in the same hemisphere and callosal connections, projecting to similar neurons in the other hemisphere.

Now, suppose a group of pyramidal neurons is simultaneously excited by thalamic and cortical neurons, its firing rate will most likely be high but the net measured EEG might be low. Or suppose a group of pyramidal neurons is simultaneously excited by thalamic neurons and inhibited by cortical neurons, or

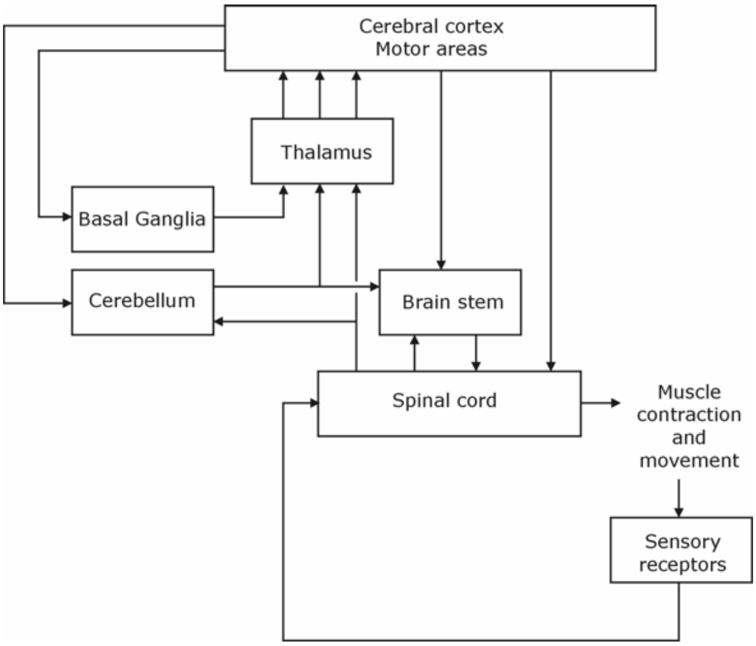


Figure 1.2. Motor areas in the brain.
The motor areas in the cortex dictate movement directly through the spinal cord and indirectly through the brain stem. The cerebellum coordinates movement by comparing the motor commands provided to the brain stem and the spinal cord with sensory feedback. The basal ganglia and the thalamus are involved in planning and coordination of complex movements (Ghez in Kandel et al (eds.), 1991 a).

vice versa, its firing rate will most likely be low but the net measured EEG might be high. This would mean that if the measured EEG is low, it does not necessarily mean nothing happened in the brain, and if the measured EEG is high it may still be an underestimation of actual activity level.

Therefore, in every experiment using EEG, assumptions should be made on what kind of input an area of cortex receives from which areas. The cortical areas involved in motor control are: the primary motor cortex, the lateral premotor area (or premotor cortex) and the supplementary motor area. For the location of these areas see Figure 1.3. The input to cortical motor areas from the periphery, the cerebellum and the basal ganglia are mediated by other areas of the cortex.

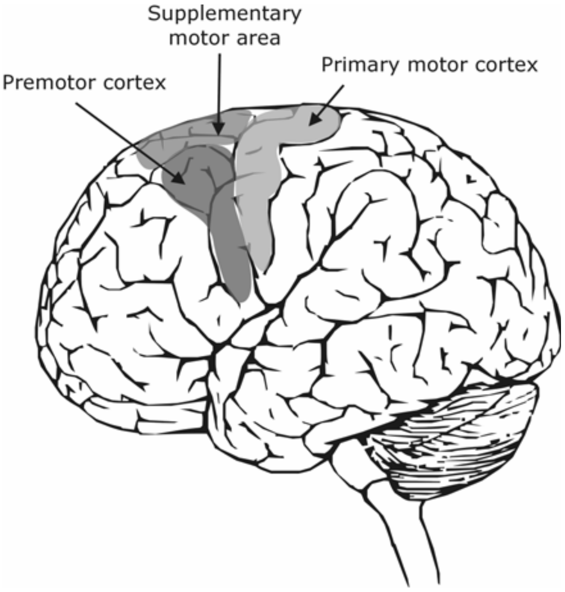


Figure 1.3. Cortical Motor Areas.

Peripheral sensory input comes from the thalamus and the primary somatosensory cortex. Input from the cerebellum and the basal ganglia is relayed through the thalamus. Information from the cerebellum acts to control and improve the accuracy of movements by comparing descending motor commands with information about the resulting motor action (Ghez in Kandel et al (eds.), 1991a). The basal ganglia receive input from all cortical areas and project through the thalamus principally to the premotor, motor and prefrontal association cortex. Combined with the fact that the basal ganglia have very little connections with the brain stem and no direct connections with the spinal chord, this suggests that the basal ganglia are involved in higher- order, cognitive aspects of motor control (such as planning and execution of complex motor strategies) (Côté and Crutcher in Kandel et al (eds.), 1991). Besides motor control, the basal ganglia are involved in other processes related to goal-directed behaviors including elements that drive actions, such as emotions, motivation, and cognition (Haber, 2003; Schultz et al, 1998).

In experimental tasks where subjects sit very still, have few sensory experiences, except for the experimental stimuli and make very short movements requiring no feedback, the role of the somatosensory cortex and the cerebellum in planning and execution of movement will be minimal. As a result, most relevant input from outside will come from the basal ganglia through the thalamus. The thalamus and the cortex are highly interconnected. Almost all connections between the thalamus and the cortex are filtered by the thalamic reticular nucleus. The thalamic reticular nucleus can operate in a 'tonic' or 'burst' mode which relay activation in an unmodified, linear way and in a non-linear way respectively. In the latter mode the signal to noise ratio appears to be higher than in the tonic mode (Guillery et al, 1998). These two modes of the thalamic reticular nucleus may be related to two different components in the Contingent Negative Variation (CNV) which will be explained below. The tonic mode could be interpreted as spreading general readiness across the cortex while the burst mode could function to selectively activate or deactivate certain parts of the cortex. On the other hand, on the basis of their perceptron-like modelling work Schmitt et al (2003) conclude that the thalamus plays no role of significance in the spread of cortical activation in rats.

1.2.2. The Contingent Negative Variation

The CNV appears in S1-S2-R experiments, where S1 provides information on S2 (Requin et al, 1991), and consists of two functionally independent components (review: Rockstroh et al, 1989); the initial CNV is related to processes of stimulus evaluation and the terminal CNV is related to processes of expectation and response preparation. The initial- and terminal CNV are also called orienting wave and expectancy wave, O wave and E wave respectively (e.g. Loveless & Sanford, 1974). The amplitude of the initial CNV can be manipulated by changing the complexity of S1. The amplitude of the terminal CNV can be manipulated by changing the complexity of the required response. Although these two components are functionally independent they are not temporally independent and affect the amplitude of the CNV simultaneously.

Since the complexity of S1 in most experimental tasks will be related to the amount of information it carries on S2 and R, the correlation between the initial CNV amplitude and the terminal CNV amplitude will usually be high. However, this depends on the subject being able to use the information in S1 for motor preparation and this can not always be assumed a priori. In other words: an increase in CNV amplitude is not necessarily related to an increase in motor preparation, which makes interpretation of CNV data difficult. An advantage in interpreting the CNV is that it appears that the initial and terminal CNV have different scalp topographies (Leynes et al, 1998). Frontal electrodes may pick up more of the initial CNV, or possible preparation and electrodes over the pre-motor or motor areas may pick up more of the terminal CNV, or actual preparation. It is therefore advisable to test the CNV on multiple locations and to compare it with other measures.

Trillenberg et al (2000) found an effect of ageing versus non-ageing S1-S2 intervals on RT and on the Contingent Negative Variation (CNV; an EEG measure explained below). RT's were lowest when the a posteriori chance of having to respond after one of a small set of SOA's was highest. An equivalent effect was found in the CNV. It may be that there is an interaction effect of CNV with preparation interval in the Rogers and Monsell task switching paradigm which does not reflect preparatory processes per se.

1.2.3. The Lateralized Readiness Potential

The LRP can be used in tasks where subjects selectively prepare a response on one side of there body, usually the left or the right hand. To calculate the LRP both left and right responses must be measured at C3’ and C4’ electrode locations (or C3 and C4). C3’ and C4’ are located 1 cm anterior to C3 and C4. The EEG measured at the electrode contralateral to the response side has a higher amplitude than the ipsilateral EEG. Averaging the difference between C3′ and C4′ for both response sides results in a measure of motor preparation asymmetry corrected for other asymmetries (De Jong, 1988; Coles et al, 1988):

$$\frac{\left(C3'_L - C4'_L\right) + \left(C4'_R - C3'_R\right)}{2}$$

Where $C3'_L$ and $C4'_L$ are the amplitudes of the EEG measured at C3′ and C4′ for the left hand responses and $C3'_R$ and $C4'_R$ are the amplitudes of the EEG measured at C3′ and C4′ for right hand responses.

The LRP is a pure measurement of lateralized motor preparation under the assumption that asymmetries unrelated to motor preparation are equal for right and left sided responses. The LRP also hides possibly interesting differences between motor preparation related asymmetries for left and right sides responses.

1.3. EEG Measures of Motor Preparation: Frequency Bands

The frequency bands used in this investigation are the theta, alpha and beta band. The possible functionality of these frequency bands will be discussed here as well as the technique used in this experiment to extract the Instantaneous Amplitude (IA): wavelet analysis.

1.3.1. Theta Activity

Theta band activity (4 – 7 Hz) has been linked to conscious retrieval of information (Klimesch et al, 2001) and the exchange of information between working memory and long-term memory (Sauseng et al, 2002) Theta and alpha activity during memory task are related to each other, perhaps even phase-locked, and reflect individual differences in performance at memory tasks (Klimesch et al, 2004; Klimesch et al, 2000). In rats, hippocampal theta oscillations have been related to the learning and recall of mazes (Kahana et al, 2001). The relationship between theta activity and motor preparation may be that for effective preparation a motor program or task set has to be retrieved from memory, generating theta activity prior to behavior.

1.3.2. Alpha Activity

The traditional view of the functional role of alpha activity (8 – 12 Hz) as cortical idling has recently been updated with the notion that alpha activity may function to suppress irrelevant cortical areas (Cooper et al, 2003) and may be involved in memory processes (Klimesch et al, 1999; Sauseng et al, 2002). Klimesch et al (1998) found that during an oddball task using warning signals preceding a target or non-target, alpha activity desynchronizes only after warning signals and targets. If alpha activity was only an idling rhythm (being inversely correlated to external stimulation) it would have responded to non-targets as well. For motor preparation this means that during preparation alpha activity may desynchronize over the relevant motor cortex and change when task set is retrieved from memory.

Bastiaansen and Brunia (2001) found an event related desynchronization (ERD) in the alpha band during anticipation of information on performance of a previous task. This suggest a link between alpha band activity and the CNV, but a dissociation between alpha band activity and CNV has been reported by Filipović et al (2001). Filipović et al (2001) used a go/no-go task where the CNV proved to be sensitive to the preparatory differences between the go and the no-go trials whereas alpha band event related desynchronization may have been a correlate of the overall engagement of the underlying cortical cells.

1.3.3. Beta Activity

Beta oscillations (14 – 30 Hz) have often been found to decrease during and prior to voluntary movement (e.g. Jasper and Penfield, 1949). More recent research has suggested that reactivity of beta band activity to motor related task demands is selectively distributed over the scalp with the largest decrease contralateral to the side of movement (Pfurtscheller et al, 2003; Neuper and Pfurtscheller, 2001). Combined with the finding that spinal motorneurons show beta oscillations as well (Salenius and Hari, 2003) this suggests that beta band ERD is a strong correlate of motor preparation in the motor cortex. However, Jantzen et al (2001) found that beta band ERD in a syncopation task decreased with practice.

1.3.4. Instantaneous Amplitude

Several frequency bands within the human EEG have been linked to brain activity and brain functions relevant to motor preparation as described above. Assemblies of neurons may maintain their own activation by oscillating at a certain frequency or assemblies of neurons may be temporarily connected, e.g. by oscillating in phase of each other (Riehle et al, 2000). This may even extend to coherency in activity between cortical motor areas and spinal motoneurons or muscle-cells (Brown, 2000; Salenius and Hari, 2003).

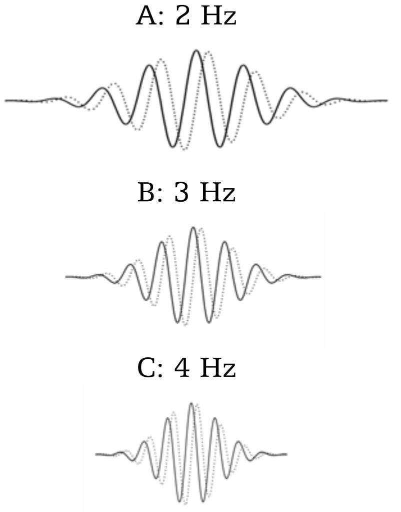


Figure 1.4. Morlet Wavelets.
Black lines are cosines multiplied with a gaussian. The dotted lines are sines multiplied with the same gaussian. The cosines and sines correspond to the real and imaginary parts of the wavelet, respectively.

The EEG is built up from signals with many different frequencies. A way to extract frequency information from EEG recordings is wavelet analysis. Samar et al (1999) give a description of it's use in cognitive neuropsychology. A very short description of wavelet analysis is that it amounts to convolution of a set of waveforms with different frequencies (often Morlet waveforms), split up into a real and imaginary part, with the EEG signal to decompose the EEG into the contributing frequencies with a relatively high time resolution. This description will be elaborated below.

A single data point does not have frequency characteristics. To estimate the contribution of different frequencies to a signal at a given moment in time, a sample of the signal before and after that moment is needed. But the further a data point is away from the moment we are trying to decompose into it's contributing frequencies, the less important it is. This is expressed in the shape of the Morlet waveform as can be seen in Figure 1.4 B. A Morlet waveform can be calculated like:

$$a(t) = \frac{1}{\sigma_t \sqrt{2\pi}} \cdot \exp\left(-\frac{t^2}{2\sigma_t^2}\right) \cdot \cos(2\pi f t)$$

Where *a* is the amplitude of the wavelet as a function of time *t* and the frequency is determined by *f*. In this formula the Morlet wavelet has an infinite width. For the analyses of data in the present experiment the width of the wavelet was taken at $\pm 4\sigma_{t.}$ From the formula describing the wavelet it follows that the relationship between the frequency and width of the high amplitude part of a Morlet wavelet is determined by the formula:

$$\sigma_t \cdot \sigma_f = \frac{1}{2\pi}$$

This implies that if the frequency of the wavelet is increased, the duration is decreased, and vice verse as can be seen in Figure 1.4 A and C. One could think of this as keeping the amount of effective oscillations contributing to the Instantaneous Amplitude constant. This also means that when using wavelet analysis one has to keep in mind that a different set of datapoints has contributed to the estimation of the power of each component frequency at each moment. In other words: the time scale of the output of wavelet analysis is not exact and its' imprecision differs over frequencies.

For those interested, the formula used for convolution of a wavelet with an EEG-signal is:

$$f \otimes g = \int_{-\infty}^{\infty} f(\tau) g(t-\tau) d\tau$$

In which f is the EEG signal and g is the wavelet. The two signals f and g are compared as a function of time (t) and the centre of the wavelet is positioned at moment τ. If this is computed with wavelets of different frequencies over enough trials and then averaged, a dependable estimation of the frequencies contributing to the Instantaneous Amplitude (IA) of a condition is the result. Comparisons of the power of a frequency in different conditions can then be made.

1.4. Task switching, modality and preparation

Previous research (Gladwin, Lindsen and De Jong, in preparation) suggests that preparatory processes are expressed in Instantaneous Amplitude and Phase Locking value as well as in time domain measures such as the LRP and CNV. The study by Gladwin et al used a task switching paradigm where each of two tasks was coupled to either the auditory or visual modality. The task used in that study will be described briefly as well as the experimental results and the implications for motor preparation and the present study.

1.4.1. Task switching and modality

The task used by Gladwin et al was a Rogers and Monsell-like task switching paradigm (Rogers and Monsell, 1995) in which two tasks are performed in an AABBAABB… sequence. To study shifts of attention from one modality to another, one task used visual stimuli (an "H" or an "L") and the other used auditory stimuli (a high or a low beep). The visual and auditory stimuli were presented simultaneously. Subjects could keep track of which task had to be performed in a given trial because the visual stimuli were presented in a clockwise manner in a frame with four squares of which the upper two quadrants were associated with one task and the lower two quadrants with the other task. Each modality was linked to one hand and each stimulus was linked to either the index or middle finger. The assignment of quadrants and response hands to tasks was varied systematically over subjects.

1.4.2. Successful and unsuccessful switching

Gladwin et al used the failure-to-engage (FTE) hypothesis (De Jong, 2000; Nieuwenhuis & Monsell, 2002) to distinguish between successful and unsuccessful preparation. The FTE hypothesis states that in switch trials with a long preparation interval, subjects either succesfully switched task set or they did not. According to the failure-to-engage hypothesis, the subset of prepared trials is fully prepared, while the subset of unprepared trials follows from a failure to engage preparatory capabilities that would have been sufficient to switch tasks. In the trials where switching did not occur during the preparation interval, subjects switch on presentation of the stimulus which costs extra time. This results in two mixed distributions of RT's which have to be separated as well as is possible if the differences between the two types of trials on for example EEG measures are to be investigated. The maths of the FTE hypothesis will not be discussed here, but it is based on a comparison of the RT distributions of long PI switch trials with short PI switch trials (typically 150-200 ms, unprepared) and long PI non-switch trials (fully prepared).

1.4.3. Preparatory effects

Gladwin et al found effects of successful/unsuccessful preparation on the P300 and the CNV, which both had larger amplitudes for trials with successful preparation. They also found more theta activity during the preparation interval of trials with successful preparation and more post stimulus theta activity in trials with unsuccessful preparation. LRP-onset covaried with fast and slow reaction times.

No differences were found between the two tasks in the time- and frequency domain. There were effects of switching on the alpha and beta instantaneous amplitude measured over the motor cortex and there were lateralized phase locking effects between frontal areas and the relevant motor areas during the preparation interval.

In short, the results make it likely that switching was not accomplished by shifting attention to another modality but by pre-activating cortical motor areas representing the correct hand. This motor preparation approach to optimizing performance was possible because the stimuli were uniquely mapped to responses. A possible mechanism that makes use of this property of the task is that the motor areas representing the responses had temporary and reciprocal connections with sensory areas representing the stimuli. By pre-activating the correct motor areas, the corresponding sensory areas would then be pre-activated as well. An additional effect would be that the responsiveness of the motor areas to any input would be increased.

The research by Gladwin et al raises several questions about motor preparation:

- First; if task switching in their setup was accomplished by some kind of motor preparation, will a similar setup without the unique S-R mapping and modality switching produce similar results? Task switching would then purely reflect preparation of the correct hand.
- Second; Instantaneous Amplitude and Phase Locking proved to be good predictors of switching or motor preparation. Do they predict motor preparation in other tasks as well?

- Third; the LRP and CNV also proved to be predicting switching or motor preparation. What is the relationship between these time domain measures and the frequency domain measures IA and PLV?

If we test measures of motor preparation in a simplified Rogers and Monsell paradigm another question may be asked: the difference between results found here and results found by Gladwin et al may be due to a difference in task complexity. If subjects did not put any effort in shifting attention from one modality to another, what effect does a manipulation of effort put into a task or complexity of a task have on frequency- and time domain measures?

1.5. Hypotheses

To formulate hypotheses a simple differentiation is proposed in which time domain measures of motor preparation are more an expression of pre-activation of motor programs and frequency domain measures are more an expression of organisation, processing or representation of information. This is consistent with an investigation into single-neuron activity during movement preparation in monkeys by Riehle et al (2001) who found that synchronization between cell activity increases untill a movement is initiated. At that moment, synchronization drops while firing rate increases.

The first set of hypotheses pertains to a task switching paradigm similar to the one used by Gladwin et al with the unique stimulus-response mapping removed and without switching modality. The second and third set of hypotheses involve motor preparation in different settings: preparation in a task where effort is manipulated and preparation in a task where multiple movements have to be made in sequence, respectively. The fourth set of hypotheses deals with how all measurements vary over tasks.

Hypothesis 1.1. RT's will be higher in switch-trials than in non-switch trials. Short preparation intervals will be used to ensure that subjects use the whole of the long preparation intervals for task-set reconfiguration (Sohn & Carlson, 2000).

Hypothesis 1.2. The amplitude effects of task switching on the LRP found by Gladwin et al will be found in this experiment as well.

Hypothesis 1.3. The absence of an amplitude effect of task switching on the CNV found by Gladwin et al will be found in this experiment as well.

Hypothesis 1.4. There will be effects of task switching on lateralized alpha and beta IA in this experiment as these were found in the experiment by Gladwin et al.

Instantaneous Amplitude measures did not predict task switching in the experiment by Gladwin et al while ERP measures did. If the subjects in their task used a form of motor preparation to switch tasks, this dichotomy between rate- and pulse coded motor preparation could show in other tasks used to investigate motor preparation. One such task is the choice/go-nogo task. This task uses an S1-S2-R setup, with S1 providing some information on S2 and R. S2 also contains information that tells the subject wether a response has to be made or not. The chance of having to make a response is manipulated over blocks. According to the proposed simple distinction between rate- and pulse coded motor preparation, time domain measures should be sensitive to manipulation of go-probability, whereas frequency domain measures should not. To test this, a choice/go-nogo task with 100% go-probability and 50% go-probability will be used. Another task manipulation is the cue type. Cues providing hand information (left- or right hand) will be contrasted with cues providing only time information.

Hypothesis 2.1. Both cue type and go probability will have an effect on RT: providing hand cues will result in lower RT's than providing non informative cues, and in the high go-probability condition RT's will be lower than in the low go-probability condition. These effects will interact.

Hypothesis 2.2. The terminal CNV will be higher when hand cues are provided than when time cues are provided. The terminal CNV will be higher in high go-probability conditions than in low go-probability conditions.

Hypothesis 2.3. Within hand cue LRP's there will be an effect of go-probability. The LRP on time cues will not be analysed.

Hypothesis 2.4. Go-probability does not affect preparatory IA in any of the three frequency bands analysed. Hand cues evoke stronger alpha and beta ERD than time cues.

Hypothesis 2.5. Go-probability does not affect lateralized IA on hand cues. Lateralized IA on time cues will not be tested.

A further differentiation between rate- and pulse coded motor preparation might be made by using a task that asks subjects to produce a sequence of movements specified by a stimulus and giving cues that provide some information on the stimulus. The effect of providing information about the first movement may be wholly different from the effect of providing information about the second movement. According to the proposed, simple differentiation between time- and frequency domain measures, if subjects are able to process information about a response that is to be made after another response, this should be expressed in frequency domain measures and not in time domain measures. To test this, a task will be used where subjects are required to make a sequence of two responses. The stimuli are preceded by four cue types: non-informative cues, cues about the second movement, cues about the first movement and cues about both movements.

There is little knowledge about preparation of sequences of movements, but a few experimental results should be mentioned here. Ulrich et al (1990) found that it is not possible to prepare a second component of a movement if the first component is not cued. In their setup however, the starting position of the second movement component is dependent on the completion of the first movement. In the setup of the current experiment this dependency will be eliminated. Ulrich et al (1990) hypothesize that the small RT advantage found when cueing the second component is not due to motor preparation but in reduced information processing on stimulus presentation.

Alegre et al (2004) studied alpha and beta ERD of subjects making a sequence of movements; a wrist flexion followed by a two-finger pinch. These different movements were chosen to make execution of the task more easy if subjects used two different motor programs. Alegre et al concluded that beta ERD was linked to completion of the whole motor process and not to the end of each motor program.

Hypothesis 3.1. RT's will be highest in the non-informative cue trials, followed by second element only cue trials, then first element only cue trials and then all information cue trials. Within these RT's there will be another effect of having to respond with the same key twice or not (sequence type). If two different keys have to be pressed, responses will be slower than when one key has to be pressed twice.

Hypothesis 3.2. If only the second movement is cued, preactivation of relevant motor areas is not possible, so there is no CNV development and hence no LRP development following this type of cue.

Hypothesis 3.3. In contrast to hypothesis 3.2., providing information on the first sequence element enables preactivation of relevant motor areas and hence a CNV and LRP should develop.

Hypothesis 3.4. No preparatory theta IA differences will be found between cue types, since the task set remains equal. Beta and alpha ERD will be a function of the amount of information provided by the cue.

Hypothesis 3.5. After all informative cues there is a lateralized effect of IA in the beta band as all informative cue types enable some kind of preparation regardless of the possibility to preactive relevant motor areas. The cues providing information on one sequence element (the first or the second) will evoked a higher lateralized beta IA than non-informative cues. Cues providing both sequence elements will evoke higher laterized beta IA still. Alpha IA will lateralize differently for different kinds of sequences (equal or different responses) since in sequences with equal responses one side of the motor cortex may still be suppressed as irrelevant while for sequences with different responses both sides of the motor cortex need to participate.

2. Methods

2.1. Subjects

Sixteen paid subjects were used for this study. Seven were male and nine were female. All subjects had normal or corrected to normal vision. All subjects were right-handed and had no neurological trauma's. The average age of the subjects was 25 years.

2.2. Setup

The experimental tasks were programmed in MEL 2.01 (Schneider, 1997) and were run on an IBM-compatible PC that also gathered the behavioral data. The EEG and EMG data was collected on an IBM-compatible PC using ADA software (instrumentation service). Subjects performed the tasks in a sound proof chamber, which was also a Faraday-cage, preventing auditory and electrical interference from outside.

During the first 45 minutes to 1 hour the subjects were trained in all three tasks. Then the EEG-cap and all single electrodes were applied. The tasks were more or less self-paced (see task-descriptions in 2.3) and in between blocks subjects could take breaks as needed. For three tasks there are 6 possible orders of tasks. Subjects were assigned a task order based on subject number. In between the second and the third tasks subjects were given a long break. All breaks were meant to reduce effects of fatigue.

Ag-AgCl electrodes were used for all EEG and EMG measurements, with a Na-Cl solution as paste. All impedances were kept below 5kΩ, except those of the EMG, which were kept below 10 kΩ. Of all 64 channels measured, the following EEG electrodes of the international 10-20 system were selected for analysis: AFz, Fz, AF8, F3, F4, FC3, FC4, FC1, FC2, FCz, C3, C4, Cz, CP3, CP4, P3, P4 and Pz.

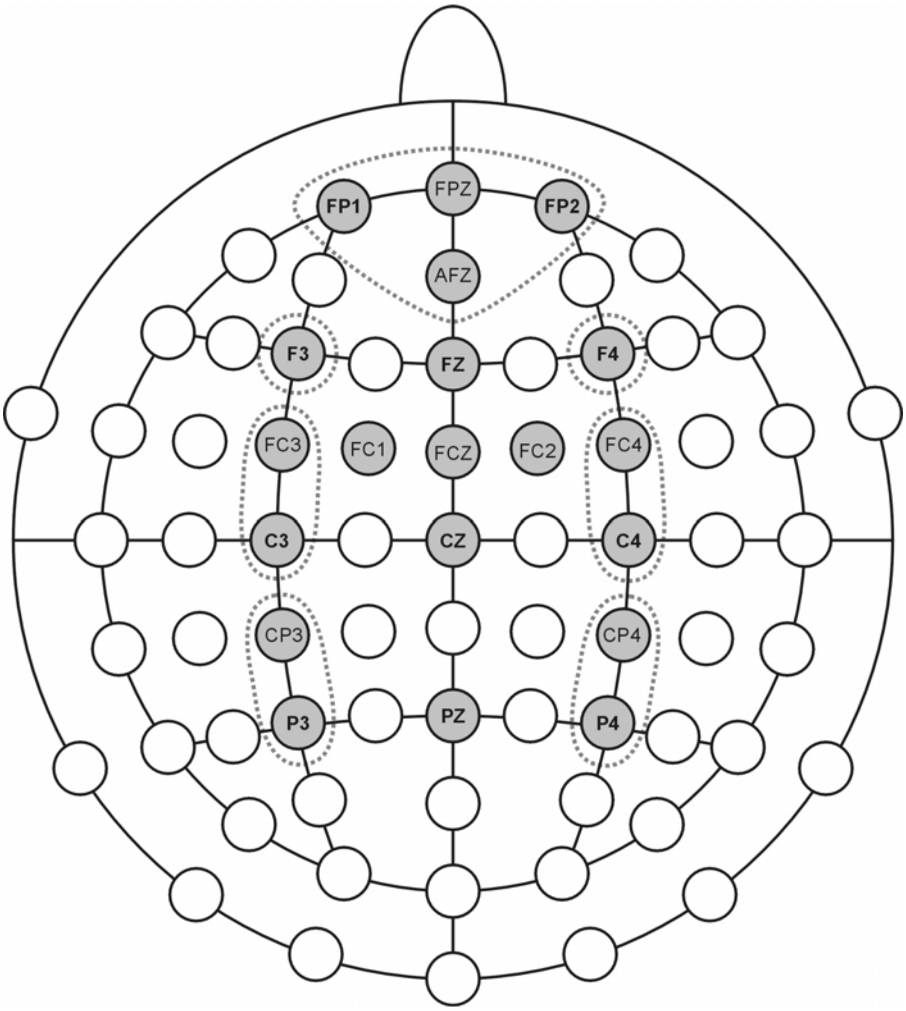


Figure 2.1. Electrode positions and Regions of Interest.
The international 10-20 system electrode positions are used. The names of the Regions of Interest are given in Table 2.1.

Horizontal eye movement, measured using two electrodes at the outer canthi, and vertical eye movement, measured above and below the left eye, were used for ocular correction. The electrical average of both ear lobes was used as reference and a common electrode was placed at the top of the sternum. EMG was measured using an electrode at ⅓ and ⅔ of the left and right flexor digitalis superficialis, but EMG was not analysed.

For all EEG analyses (CNV, LRP and IA) the same trials were used as for the RT analyses, minus trials with EEG artefacts. The EEG of all trials was inspected visually for artefacts. Gratton & Coles ocular correction was performed, as well as baseline correction, exporting data for IA analysis and calculation of CNV's and LRP's, using Brain Vision Analyser 1.0.3.

Region of Interest:	Electrodes:
Frontal	FP1, FPz, FP2, Afz
F3	F3
F4	F4
Motor Left	FC3, C3
Motor Right	FC4, C4
Parietal Left	CP3, P3
Parietal Right	CP4, P4

Table 2.1. Regions of Interest and electrodes.

2.3. Experimental tasks

2.3.1. Rogers and Monsell task

The paradigm used by Rogers and Monsell (1995) for predictable task switching was adapted to measure motor preparation. During this task a framework of four squares was continuously shown on the screen. Stimuli were presented in a clockwise fashion in these four squares.

Two of the squares were assigned to each hand. Either the two topmost squares were assigned to the right hand and the two lower squares to the left hand or vice versa. The assignment of squares to hands was kept constant with each subject and the assignment was based on subject number so that half the subjects had one stimulus-response (S-R) assignment and the other half had the other S-R assignment. The subjects had to use their hands in an LLRRLLRR… order.

The stimuli presented was either an 'X' or an 'O' and it was shown for 250 ms. An 'X' required subjects to press a key with their index finger (press the 'x' or the '.' on the keyboard). An 'O' required subjects to press a key with their middle finger (press the 'z' or the '/' on the keyboard). The subjects' eyes were approximately 40 cm. from the screen and the stimuli occupied about 2° horizontally as well as vertically.

As soon as the subject responded, or when 30 seconds had passed, an interval of either 500 ms or 1000 ms was started after which a new stimulus was

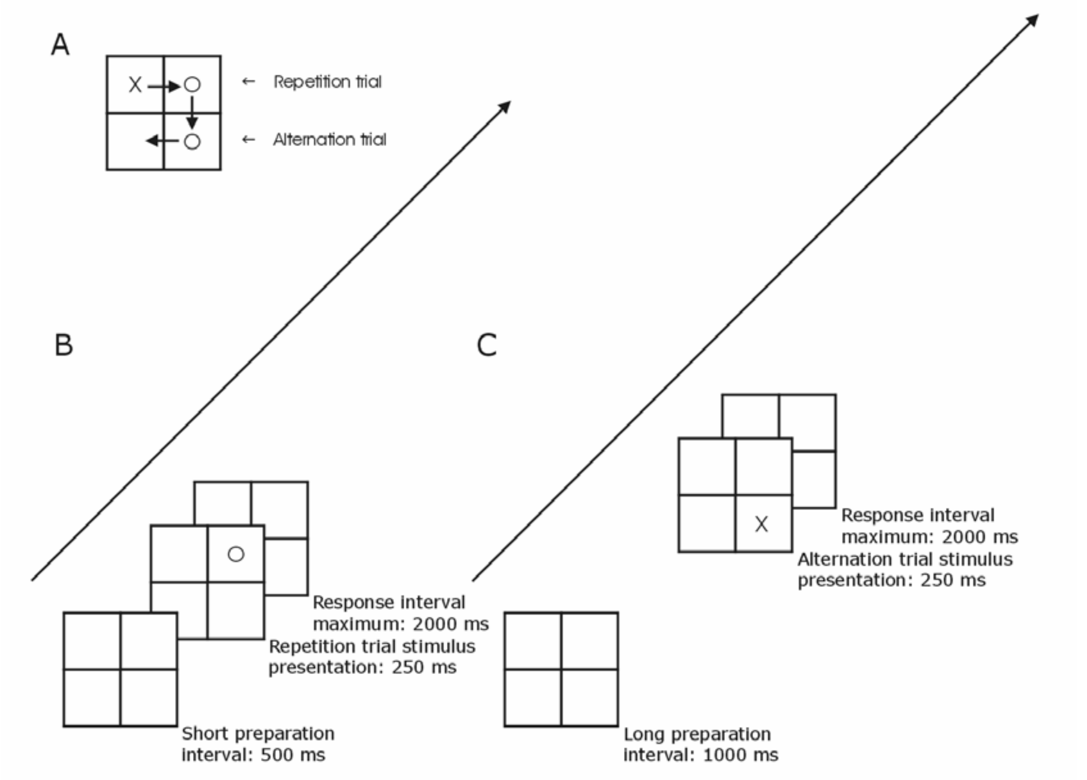


Figure 2.2. Trial timing for Rogers and Monsell task switching.
A. Trials were presented clockwise. B. A repetition trial with a short preparation interval. The previous stimulus was presented in the upper left quadrant. C. An alternation trial with a long preparation interval. Trial B might have preceded trial C. All responses slower than 2000 ms were omitted from the data prior to analysis.

presented. Subjects were instructed to use this interval to prepare for the next trial. The trials with the 500 ms preparation interval occurred randomly and had a one out of three chance of occurring. These short intervals were inserted to keep subjects alert and optimally prepared at trials with a long preparation interval. For all psychophysiological and behavioral analyses only the trials with long preparation intervals were selected.

Prior to the experiment subjects were given a short training. The training task consisted of two 'pure' blocks of 15 trials each, which trained each hand (and did not require task switching) and a 'mixed' block of 15 trials (which did require task switching). During training incorrect repsonses generated a beep and after the 'mixed' block an overview of reaction times on non switch trials and switch trials as well as an error-rate was given. If subjects had a higher difference between average response times on switch and non switch trials than 50 ms and made more than one mistake, they engaged in another ‘mixed’ block until performance was acceptable. Right before the experimental task was performed all subjects got three 20 trial ‘reminder’ blocks: a ‘pure’ block for both hands and a ‘mixed’ block with task switching. The actual experiment consisted of 8 blocks of 75 trials. Because approximately one third of the trials had a short preparation interval, and was to be discarded, this setup resulted in 400 usable trials; approximately 200 alternation trials and 200 repetition trials, which were distributed equally among both hands.

Task switching in this setup was completely predictable: subjects have to either repeat a task (use the same hand) or alternate between tasks (switch to the other hand). Previous, unpublished research using the same task, showed that a long preparation interval reduces switch costs to a minimum. No analysis of switch costs will therefore be made. Subjects were instructed to make optimum use of the time and information they had for their preparation.

2.3.2. Choice/go-nogo task

A choice/go-nogo task was used in which subjects were presented with a cue followed by a preparation interval of 1 second. The cue remained on the screen during the preparation interval and was replaced by the stimulus at the end of the preparation interval. Subjects had 2 seconds to respond, except in no-go trials where the stimulus was removed from the screen after 750 milliseconds. After a response was given or at the end of the stimulus presentation the screen was blank for 750 milliseconds before a new trial started.

A response was a button-press with one of four fingers: left middle-finger, left index-finger, right index-finger or right middle-finger. Each block of stimuli had either cues with hand-information or cues with no information (except timing) and either 50% chance of go-stimuli or 100% chance of go-stimuli. Each subject performed the task for six blocks of 100 trials: one time-cue block of each go-probability and two hand-cue blocks of each go-probability. Hand-cue blocks were doubled because lateralized preparation was possible in these blocks so enough information for each hand was gathered to enable calculating valid LRP's.

Stimuli consisted of two characters, one above the other, in the centre of the screen. The top letter indicated the hand to respond with: an 'L' or 'R' for the left and right hand respectively. The lower letter indicated the finger to respond with: an 'M' or 'I' for the middle- and index-finger respectively. A cue consisted of two characters information not given was replaced with an asterix ‘*’. So time-cues consisted of two asterixes and hand-cues consisted of an 'L' or 'R' above an asterix. Subjects sat approximately 40 cm from the screen so that cues and stimuli were 2° vertically and 1° horizontally. On go-trials the light-grey cue was replaced by the white stimulus and on no-go trials the light-grey cue was replaced by a red stimulus.

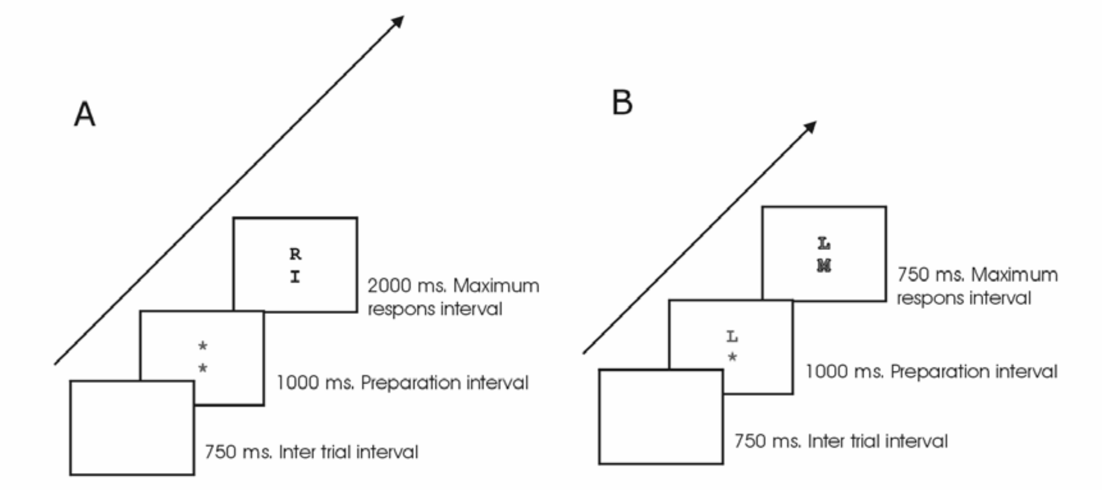


Figure 2.3. Choice/go-nogo trial timing.
A time cued go-trial (A) and a hand cued nogo-trial (B).

During the training subjects conducted one block of 15 trials of each of the four block types. Any mistake was immediately followed by a beep. After the four blocks behavioral data was shown on the screen. If subjects were slower than 600 ms or made more than 4 mistakes they repeated all four blocks again until performance was at an acceptable level.

2.3.3. Sequence Element Cueing task

The Sequence Element Cueing task used was specifically designed for this experiment. Subjects were required to give a response consisting of two button presses in a specified order. These button presses could be produced with the left and right index fingers, using the 'z' and '/' keys of a standard computer keyboard. This results in four possible sequences: left-left, right-right, left-right and right-left.

Stimuli consisted of two letters, with one letter presented above the other. The top letter indicated the first response to be made and the lower letter indicated the second response to be made. The letters could be an 'R' for the right index finger or an 'L' for the left index finger. Subjects were approximately 40 cm from the screen with their hands resting on the table and their left- and right index fingertips resting on the relevant key tops. Both letters were about 1° high and wide and were separated by 0.5°. A cue was provided at the same location as the stimulus of which the first and second element both had a 50% chance of being cued. Uncued sequence elements were replaced with an asterisk (*). This resulted in four cue types: non-informative cues (e.g. $\genfrac{}{}{0pt}{}{*}{*}$), cues with information on the second response only (e.g. $\genfrac{}{}{0pt}{}{*}{L}$), cues with information on the first response only (e.g. $\genfrac{}{}{0pt}{}{R}{*}$) and cues with full information (e.g. $\genfrac{}{}{0pt}{}{L}{L}$). Non-informative cues will be called time cues subsequently, as they

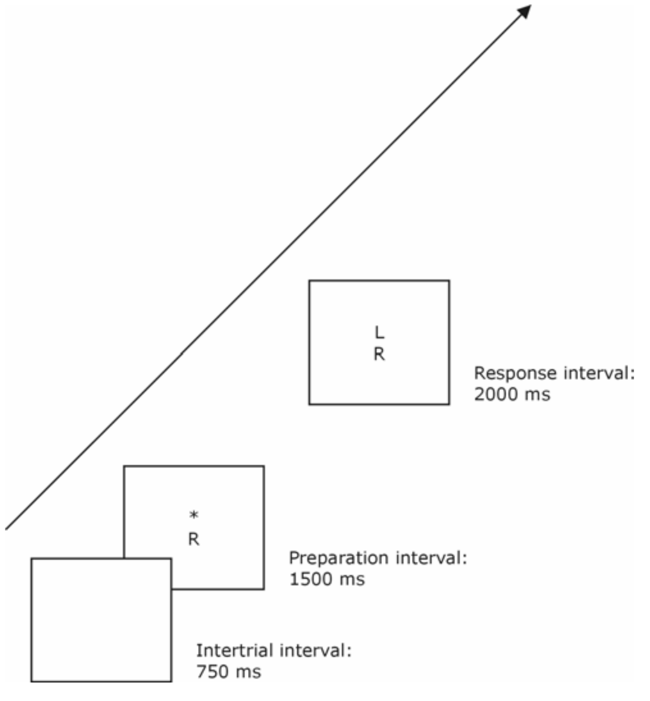


Figure 2.4. Sequence Element Cueing timing of trials.

do provide information on the time of appearance of the stimulus: stimulus onset asynchrony (SOA) was kept at a constant 1500 ms.

Each trial started with an empty black screen presented for 750 ms. Then the cue was presented in grey and a preparation interval of 1500 ms started. After the preparation interval the cue was replaced by the stimulus, which was white. The color contrast between cue and stimulus served to enable subjects to distinguish full information cues from stimuli. As soon as two valid keys were pressed (only 'z' and '/' key presses were registered) or 2 seconds had elapsed the next trial began.

Each subject performed the Sequence Element Cueing Task for 8 blocks of 100 trials each. Training consisted of a block of 30 trials, with beeps indicating errors and average RT and error rate displayed at the end of the block. This block was repeated as long as subjects had an average RT over 500 ms and an error rate over 7% (2 errors were allowed).

2.4. Data analyses

For all tasks, average RT's will be analysed using MANOVA. RT distributions will be shown using Vincentizing as described by Ratcliff (1979) to illustrate average within-subject variability and standard error boxplots to illustrate between-subjects variability. Only RT's of correct responses and RT's above 100 ms and below 2000 ms are analysed. An exception is made for the RT's of second key press in the Sequence Element Cueing task as this is expressed as the time between the first and the second key press. For these RT's a minimum value of 25 ms is used and a maximum of 1000 ms.

The RT's of practice blocks are discarded as well as the RT's on the first four trials of each block in the Rogers and Monsell task switching paradigm, to allow a pattern of alternation and repetition to be established. No other behavioral data will be analysed.

After analyses of RT's, the amplitude of the CNV and LRP will be analysed using MANOVA. For all three tasks the amplitude of the CNV and the LRP is expressed as the average amplitude of these measures during the last 200 ms of the preparation interval.

The analyses of the Instanteneous Amplitude (IA) were performed using the Gamma VX Complex Demodulation software (De Jong, 2003). Comparisons of conditions will be made over the theta, alpha and beta frequency bands.

The IA in the theta-band is expressed as the average of 5, 6 and 7 Hz. frequency IA's. The alpha-band IA is expressed as the average of 10, 11, 12 and 13 Hz. frequency IA's. The beta-band IA is expressed as the average of 17, 19, 21 and 23 Hz. frequency IA's. One second was taken as phase-in and phase-out lag. These 1 second periods will not be displayed.

For each frequency-band analysis, t-values are calculated for every data point, after running average smoothing over three data points. Significant t-values were selected from the data using False Discovery Rate (FDR) (Benjamini & Hochberg, 1995; Genovese et al, 2002) which was controlled at a level of 5%.

3. Results

All subjects participated in all three tasks and the order of the tasks was randomized over subjects. Still it is possible that the order in which the subjects executed the tasks affected their performance. First, for each subject the average RT over all valid trials was calculated and for each task these RT's were transformed to z-scores. The RT's were then reordered into RT's on tasks that were performed first, second and third. Repeated measures analysis showed there was no difference between these variables (F(2,14) = .437, p = .654).

3.1. Rogers and Monsell task

3.1.1. RT's

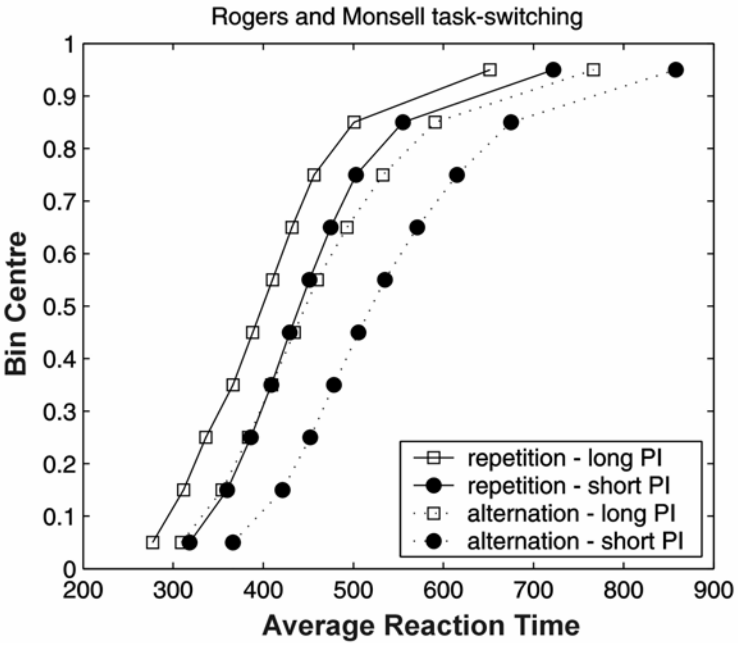


Figure 3.1.1. Rogers and Monsell task-switching RT distributions.
It appears as if the skewness of alternation is the same for long and short PI'sas well as the skewness of repetition for both PI's.

Trials with response times under 100 miliseconds and above 2 seconds were excluded from the analysis of reaction times, as were trials with inaccurate responses and short preparation intervals. The first four trials of each block were discarded to allow subjects to warm up to the task.

First, to test if the addition of the the short PI had the desired effect (optimal switching in trials

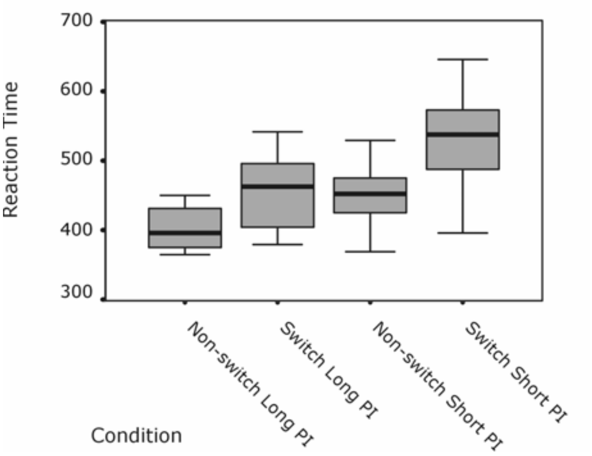


Figure 3.1.2. Spread of RT's over subjects. The horizontal fat lines in the middle indicate the median RT.

with a long PI), a MANOVA on the average RT's for both switch and non-switch trials and long (1000 ms) and short PI (500 ms) has been performed. There were main effects of switching (F(1, 15) = 29.092, p = .000) and PI length (F(1, 15) = 88.344, p = .000). An interaction effect between switching and PI length (F(1, 15) = 18.921, p = .001) was found as well. In other task switching experiments (Monsell, 2003) it is seen that most switch costs reach asymptote after PI's of about 600 ms. In this experiment there is still a significant decrease in switch costs between 500 ms PI's and 1000 ms PI's. It can be concluded that the experimental manipulation of adding the 500 ms PI trials worked, so that subjects switched acceptably in long PI trials. Or perhaps effects of task set inertia (Monsell & Yeung, 2003) were overcome in the long PI by trying to prepare for the short PI.

The average long PI RT was 413 ms for repetition trials and 473 ms for alternation trials, leaving a switch cost of 60 ms. For short PI's the average RT for repetition trials was 461 ms and the average RT for alternation trials was 548 ms, leaving a switch cost of 87 ms. For the rest of the analyses only the long PI trials are used. ANOVA shows there is a main effect of switching on RT (F(1,14) = 21.78, $p < .001$) within long PI trials.

In Figure 3.1.1. the skewness of both repetition curves looks roughly the same as well as both alternation curves. Within subjects there appears to be more spread of RT's in alternation trials than in repetition trials. Figure 3.1.2. shows the standard error of the distribution of average RT's of subjects within each condition. Between subjects the largest spread of RT's occurs in the short PI with some increase of spread for alternation trials over repetition trials.

As shown in Figure 3.1.3. subjects that had their right hand assigned to the two topmost squares of the screen responded about 32 ms faster than subjects who had their left hand assigned to the two topmost squares. There appears to be no effect of the actual response hand. Repeated measures analysis shows there is no main effect of response hand (F(1,14) = .129, p = .752) and no effect of hand assignment (F = .642, p = .436). As it appears in Figure 3.1.3. no interactions were significant (all p's > .278).

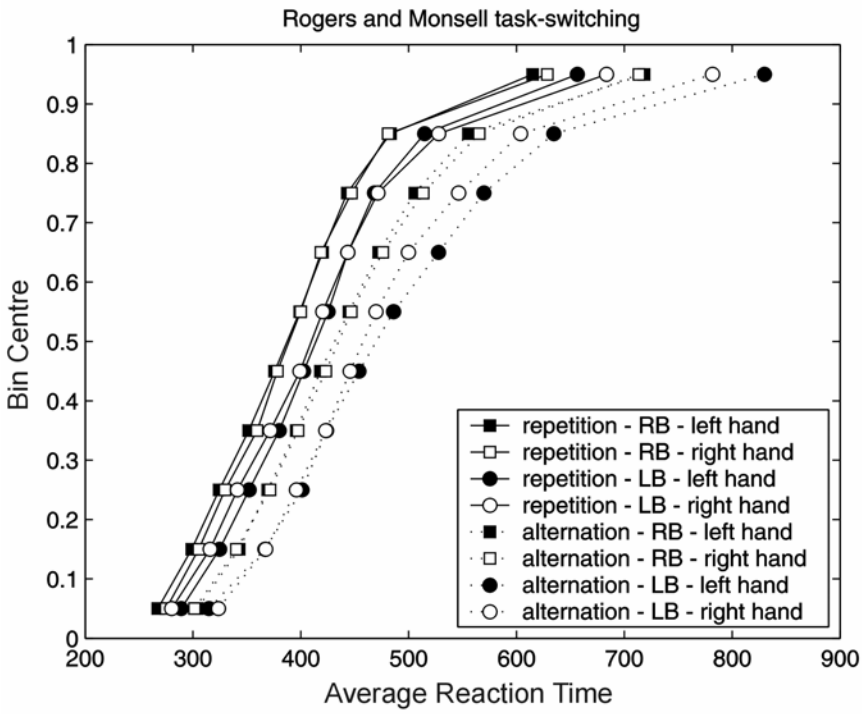


Figure 3.1.3. RT distributions for Rogers and Monsell task switching. Alternation and repetition are the same switching and no switching conditions as shown in figure 3.1.1. Shown here additionally are the effects of hand assignment and hand used to respond: RB means the right hand is associated with the two squares on the top of the screen and the left hand with the lower squares. LB means the left hand is associated with the two squares in the upper half of the screen and the right hand with the lower two.

3.1.2. CNV and LRP

MANOVA over the average amplitude of CNV's using electrode position (Fz, Cz and Pz) and task switching (switch and non-switch) as factors indicated there was a main effect of electrode position (F(2, 14) = 18.307, p = .000) and no main effect of task switching (F(1,15) = .178, p = .679). The two way interaction between electrode position and task switching was borderline significant however (F(2,14) = 3.576, p = .056), so the effect of task switching was tested seperately for each electrode.

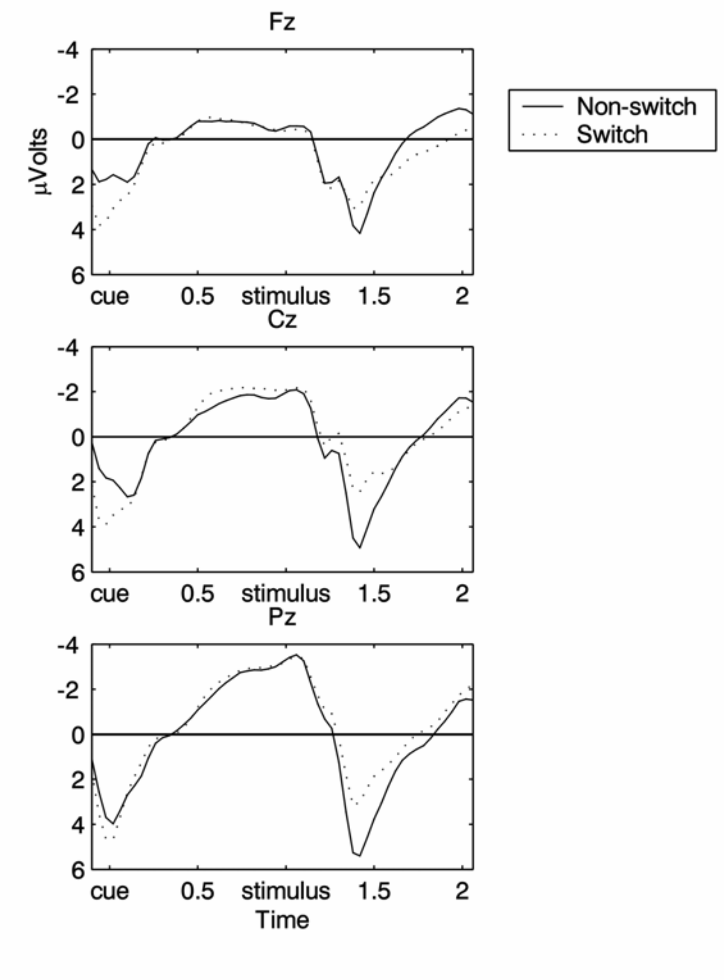


Figure 3.1.4. Rogers and Monsell CNV's.

However, the effect of task switching was not significant on each of three electrodes (all p's > .366).

For the Rogers and Monsell task switching paradigm the LRP was calculated according to the lateralization in the previous trial. ANOVA signifies that the difference between the amplitudes of the LRP's of the alternation and repetition conditions is significant (F(1, 15) = 13.295, p = .002).

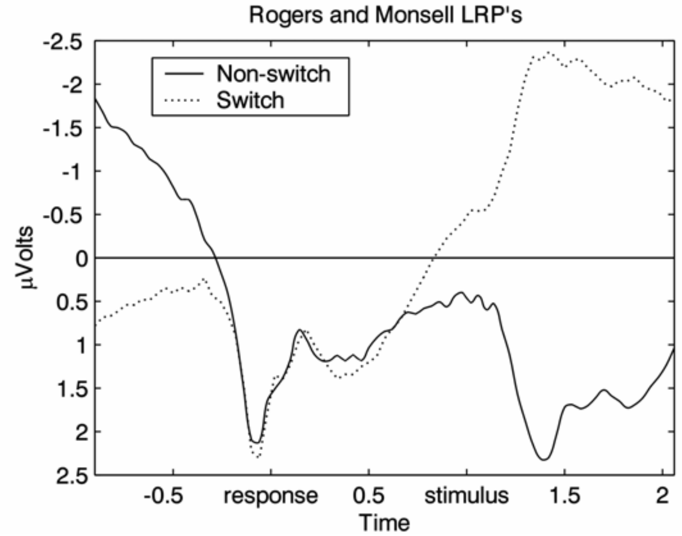


Figure 3.1.6. Rogers and Monsell LRP's.
For this figure, the baseline level is put exactly between the maximum amplitudes of the stimulus-locked action LRP's of repetition and alternation. The amplitude of the curves has been made equal in the period from 50 ms before the previous response to 50 ms after the previous response.

This was calculated over the last 200 miliseconds of the preparation interval as shown in Figure 3.1.6. Because the baseline was chosen, rather than calculated, the meaning of this effect is relative. A possible interpretation is that non-switch LRP did not return to baseline value (some lateralization remained) and that switch LRP did return to baseline or even exceeded it in favour of the correct hand.

3.1.4. Instantaneous Amplitude

As can be seen in Figure 3.1.7. theta band effects were large but completely response related. Figure 3.1.8. shows there are some preparatory and response related alpha band effects but none were significant. In Figure 3.1.9. it can be seen that there were preparatory and response related beta band effects of which a small portion was significant in the Frontal ROI. Lateralized IA was significant only for the beta band. A bold line in the significance plots indicates that that t-value exceeded the FDR threshold for significance.

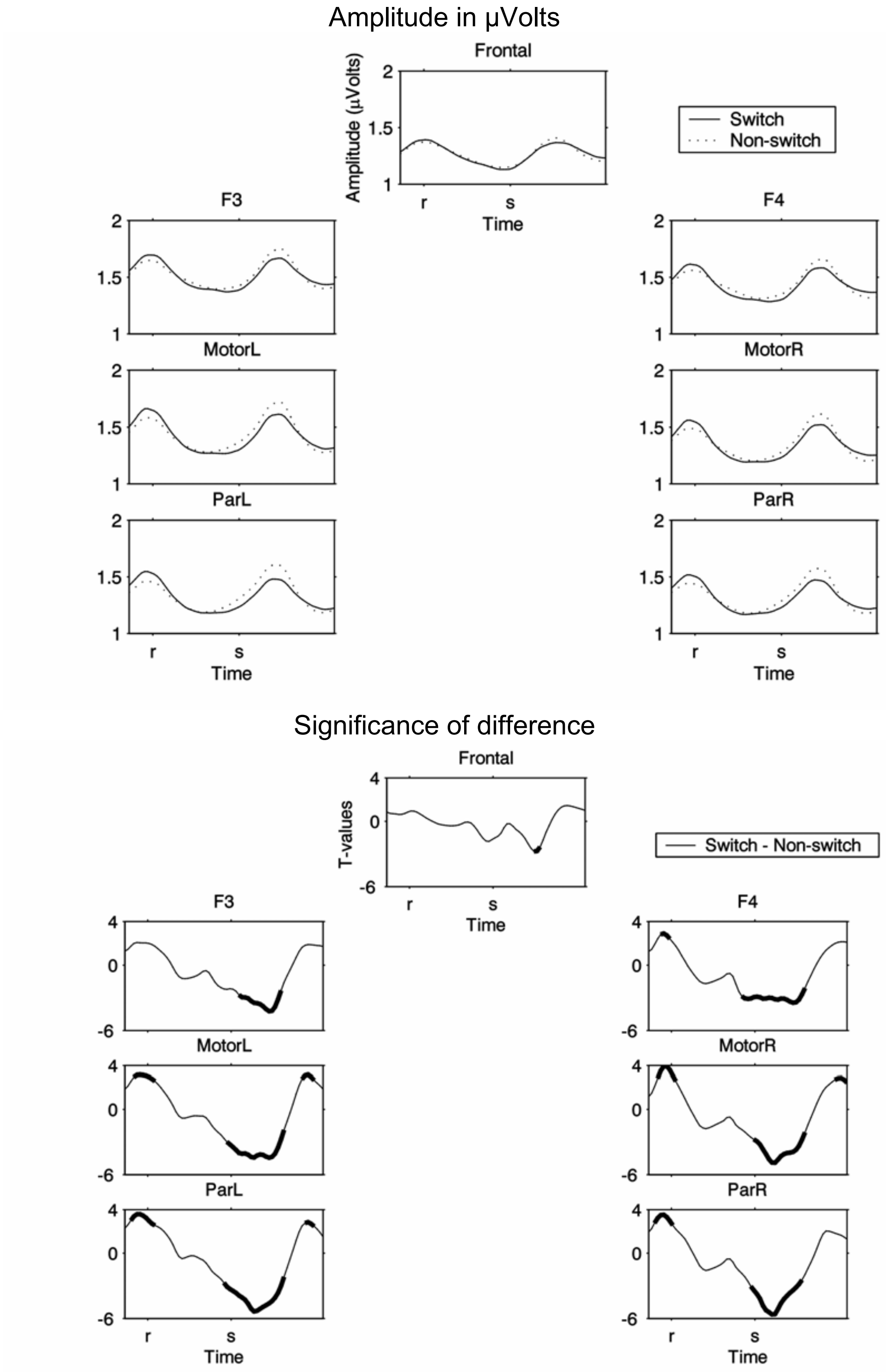


Figure 3.1.7. Rogers and Monsell instantaneous theta band amplitude and difference.

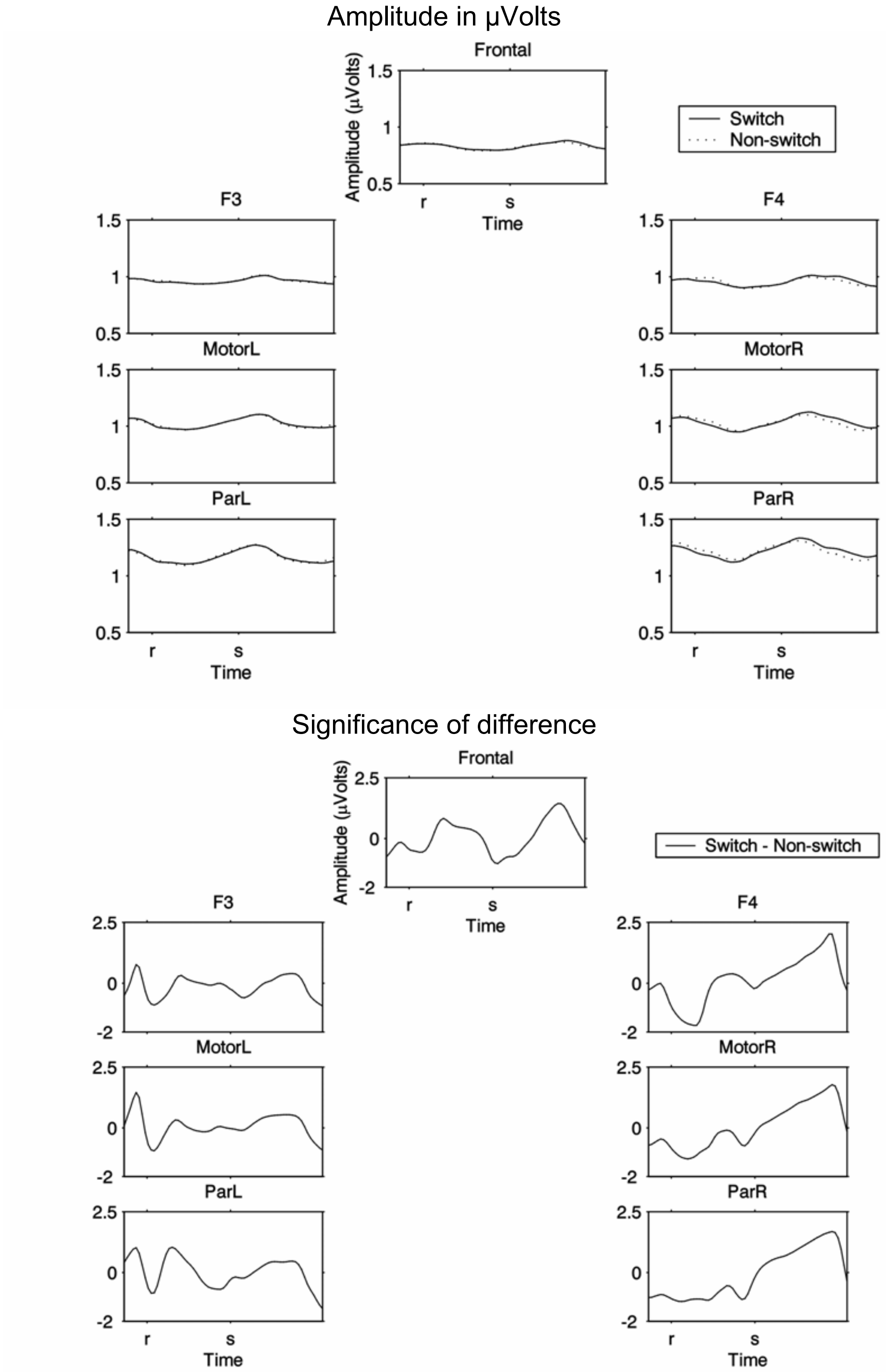
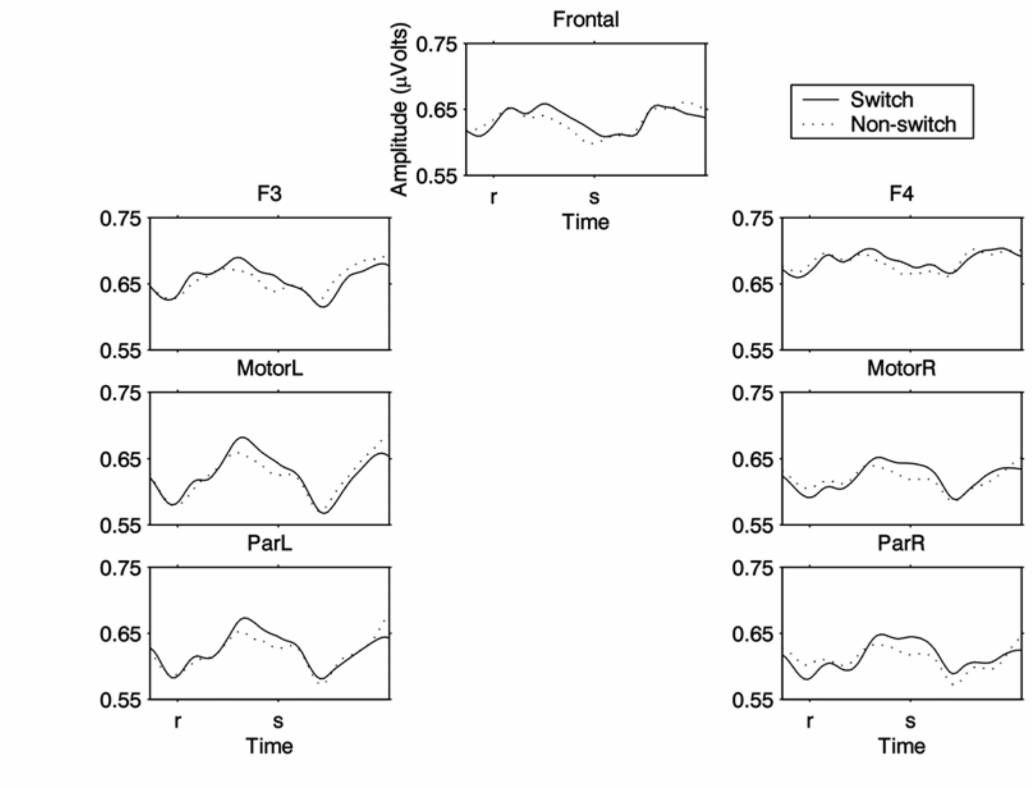


Figure 3.1.8. Rogers and Monsell instantaneous alpha band amplitude and difference.

Amplitude in μVolts



Significance of difference

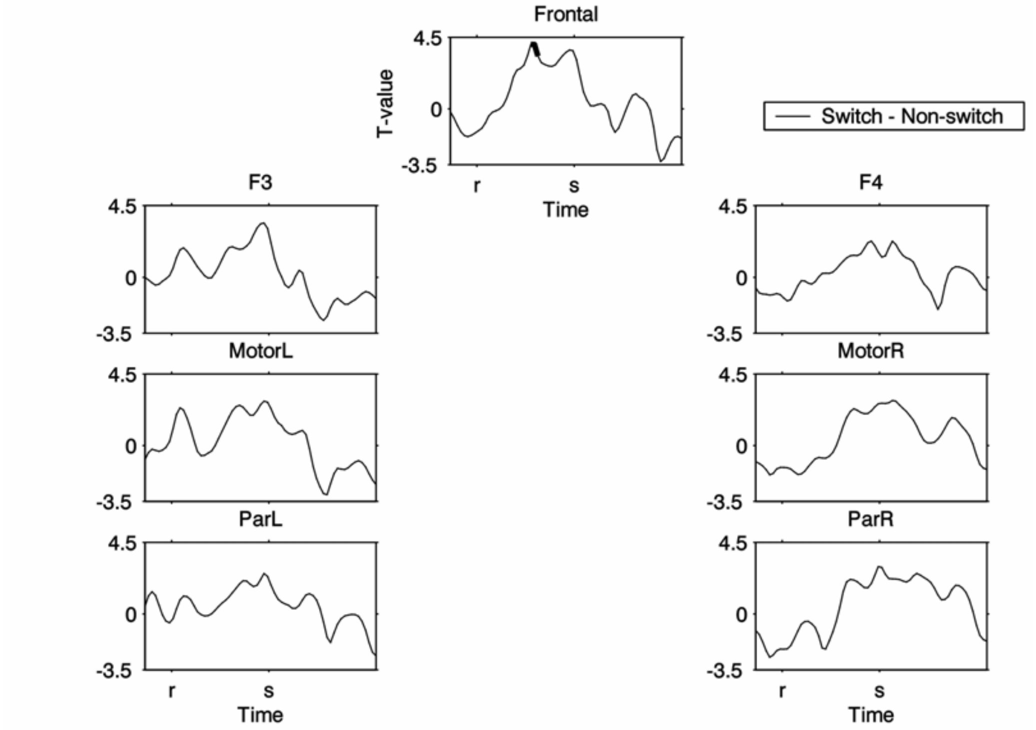


Figure 3.1.9. Rogers and Monsell instantaneous beta band amplitude and differences.

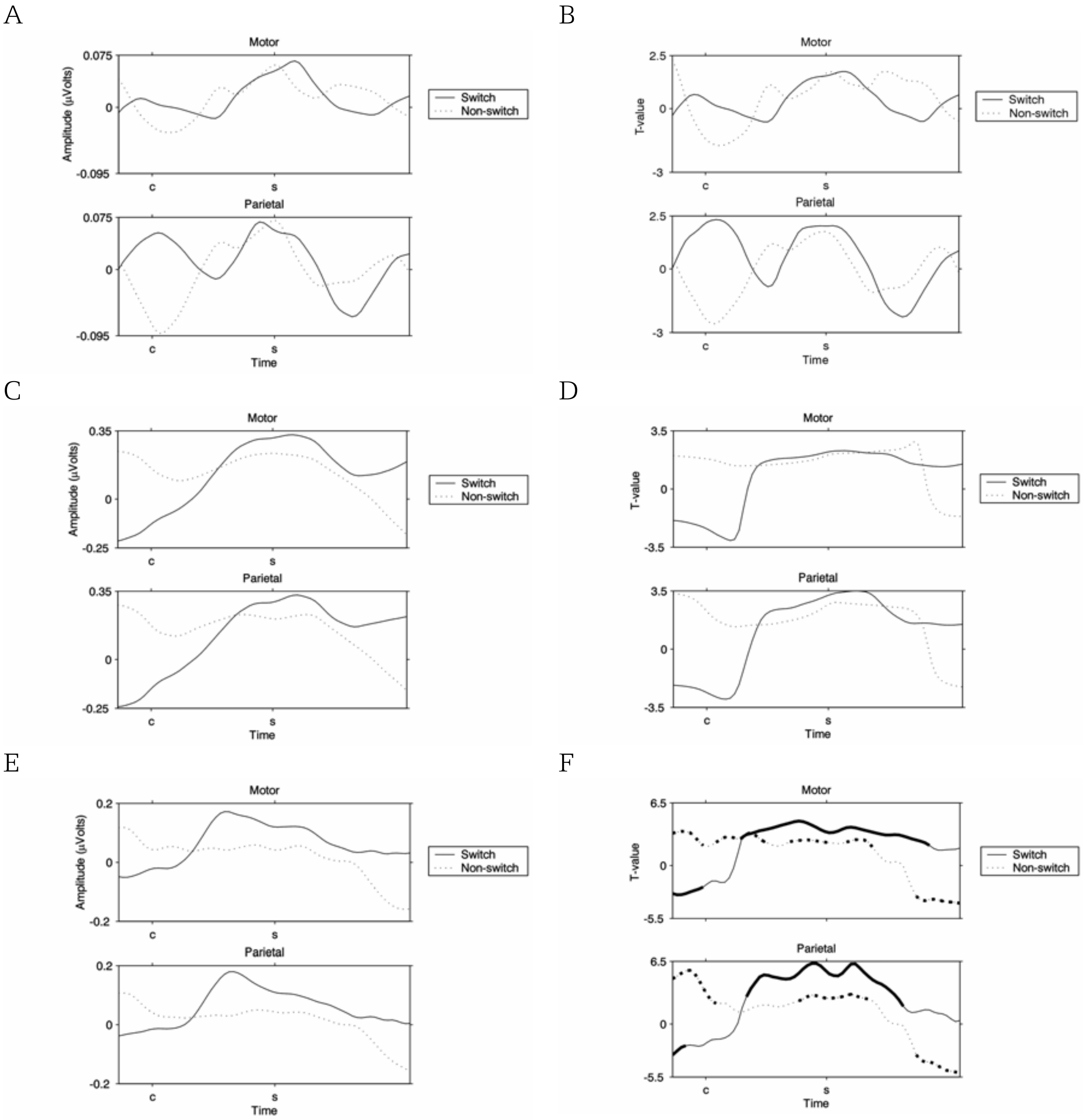


Figure 3.1.10. Rogers and Monsell Lateralized Instantaneous Amplitude.
A. Theta band LIA amplitudes. B. T-values of theta band LIA. C. Alpha band LIA amplitudes. D. T-values of alpha band LIA. E. Beta band LIA amplitudes. F. T-values of beta band LIA.

The largest effects in lateralized areas were seen in the Motor and Parietal ROI's. The difference between these areas was tested for each frequency band, and some significant differences were found in the beta band. The results are shown in Figure 3.1.10. For both alternation and repetition trials lateralized activity was calculated according to formula 2:

$$LIA = (LeftMotor_L - LeftMotor_R) - (RightMotor_L - RightMotor_R)$$

This is equivalent to the formula for the LRP, except that it isn't parted by two The same calculation was performed for the Parietal ROI's.

3.2. Choice/go-nogo

3.2.1. RT's

For analysis of RT, trials with incorrect responses and RT's under 100 ms were rejected. There were twice as many blocks with hand cues as there were with time cues, and approximately half the trials within the 50 % go condition could

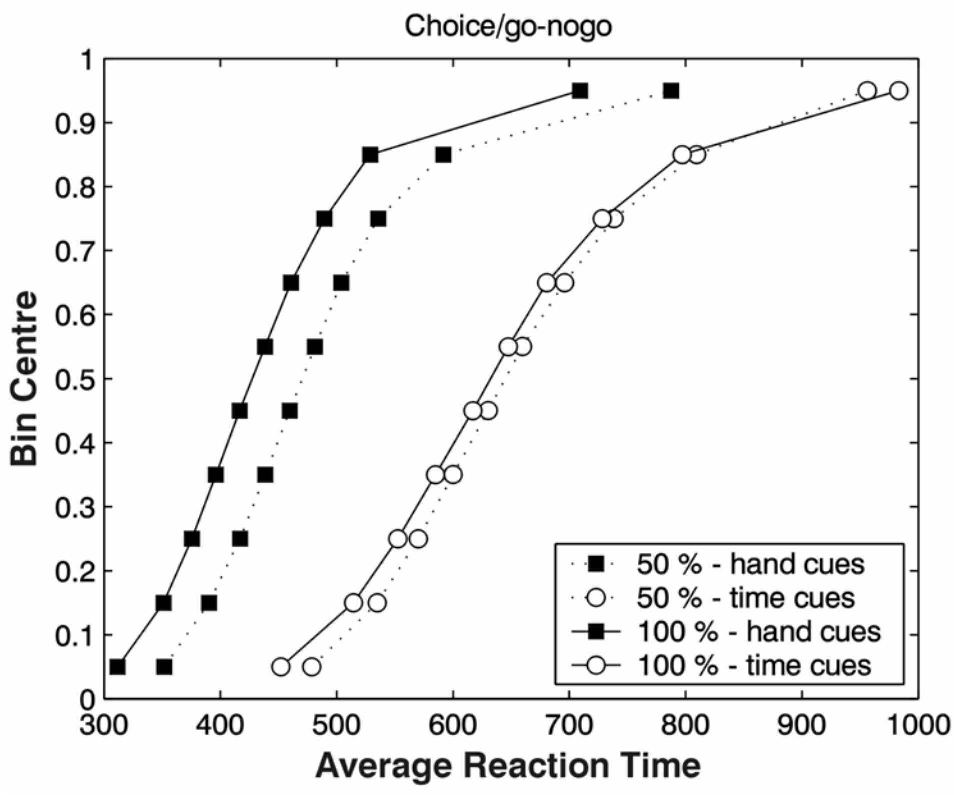


Figure 3.2.1. Choice/go-nogo RT distributions.

not be used as there was no RT. This means that there is a different number of trials in different conditions.

As can be seen in Figure 3.2.1. RT was lower for hand cues (472.2 ms) than it was for time cues (661.9 ms), and there is a small difference in RT between 100% go (552.6 ms) and 50 % go (581.4 ms). It can also be seen in the RT distributions that the go-probability had a different effect on RT given a different cue.

Repeated measures MANOVA was used to analyse the distribution of RT's within each condition. There were main effects of both cue type and go probability on RT (F(1,15) = 108.27, p < .001 and F(1,15) = 15.43, p = .001 respectively). The interaction between these two factors was significant as well (F(1,15) = 15.75, p = .001). The skewness of the distributions suggests and extra source of variability for conditions with time cues in contrast to hand cues, but this was not tested. Individual RT distributions can be seen in Appendix A. Figure 3.2.2. shows between-subject variability in RT. Most variability can be found in the time cue conditions.

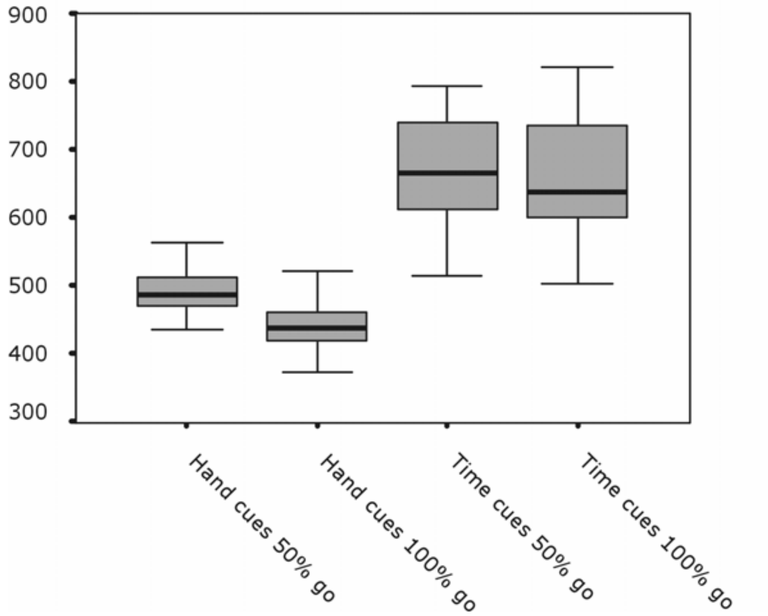


Figure 3.2.2. Choice/go-nogo between subject variation in average RT.
The horizontal fat lines in the middle indicate the median RT.

3.2.2. CNV

The CNV amplitude was higher over posterior regions than it was over anterior regions. This high amplitude was reason to use Fz, Cz and Pz in the analyses, to test the CNV's sensitivity for preparatory processes in the different tasks at different scalp locations.

In Figure 3.2.3. it can be seen that all cue types and go probabilities elicit a CNV on all electrode positions. The amplitude of the CNV on the seperate electrode positions does interact in different ways with cue type and go probability. It is interesting to see that on Pz, the cues elicit a larger P300-like effect than on the other electrodes, for hand cues only.

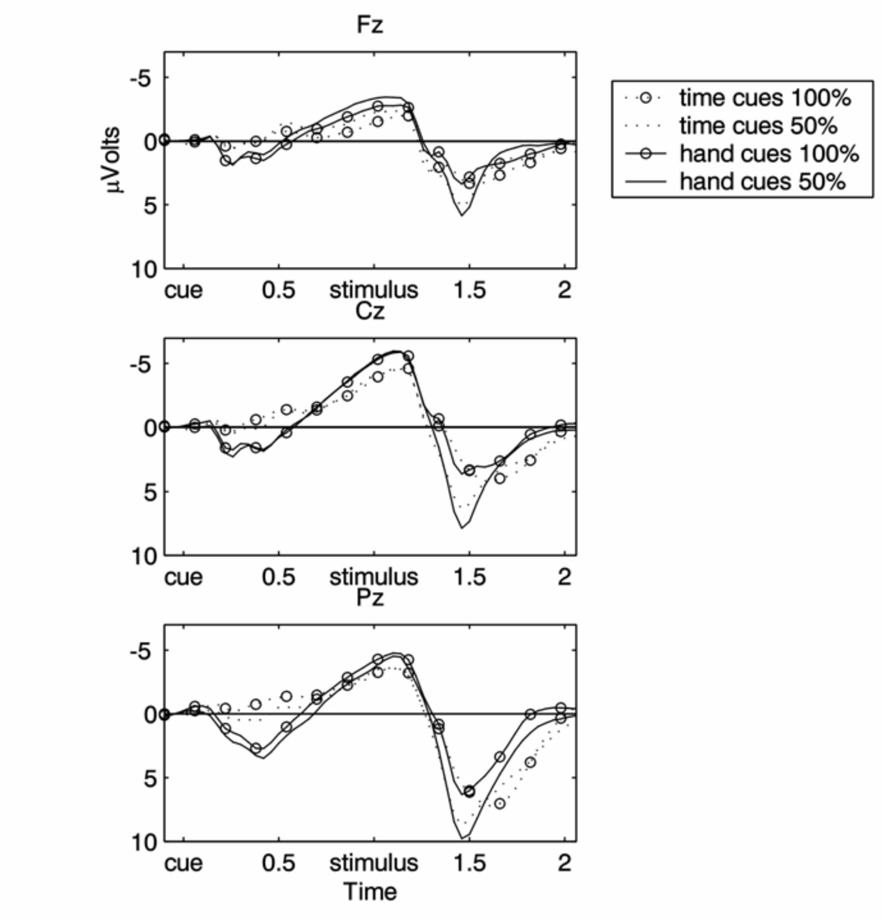


Figure 3.2.3. Choice/go-nogo CNV's.

MANOVA was conducted using electrode position (Fz, Cz and Pz), cue type (hand cue and time cue) and go-probability (100% go chance and 50% go chance) as factors over the average amplitude of the CNV during the last 200 ms of the preparation interval. There were significant main effects of electrode position (F(2,14) = 11.421, p = .001) and cue type (F(1,15) = 5.678, p = .031). There was no main effect of go probability (F(1,15) = .373, p = .550). There were two-way interaction effects of electrode position and cue type (F(2,14) = 5.292, p = .019) and electrode position and go probability (F(2,14) = 5.085, p = .022). The two-way interaction of cue type and go probability was not significant (F(1,15) = .327, p = .576). The three way interaction between electrode position, cue type and go probability was significant (F(2,14) = 4.018, p = .042).

The effects of cue type and go probablity were tested for each electrode seperately. On Fz the main effect of cue type was significant (F(1,15) = 10.491, p = .006) and the main effect of go probability was borderline significant (F(1,15) = 4.338, p = .055). The two way interaction between cue type and go probability was not significant (F(1,15) = .006, p = .940).

On Cz the main effect of cue type was significant (F(1,15) = 5.627, p = .031) but the main effect of go probability (F(1,15) = .131, p = .722) and the two way interaction between cue type and go probability (F(1,15) = .089, p = .769) were not significant.

On Pz neither the main effects of cue type (F(1,15) = 1.552, p = .232) and go probability (F(1,15) = .324, p = .578) nor the two way interaction between cue type and go probability (F(1,15) = 1.897, p = .189) were significant.

It appears as though only Cz and Fz can distinguish between hand cues and time cues, whereas only Fz can distiguish between go probabilities as well.

3.2.3. LRP

ANOVA shows there is an effect of go probability (100% chance and 50% chance go chance) on the LRP (F(1,15) = 6.753, p =.020). LRP’s are shown in Figure 3.2.2. The action LRP’s in the 50% go condition have half the amplitude of the

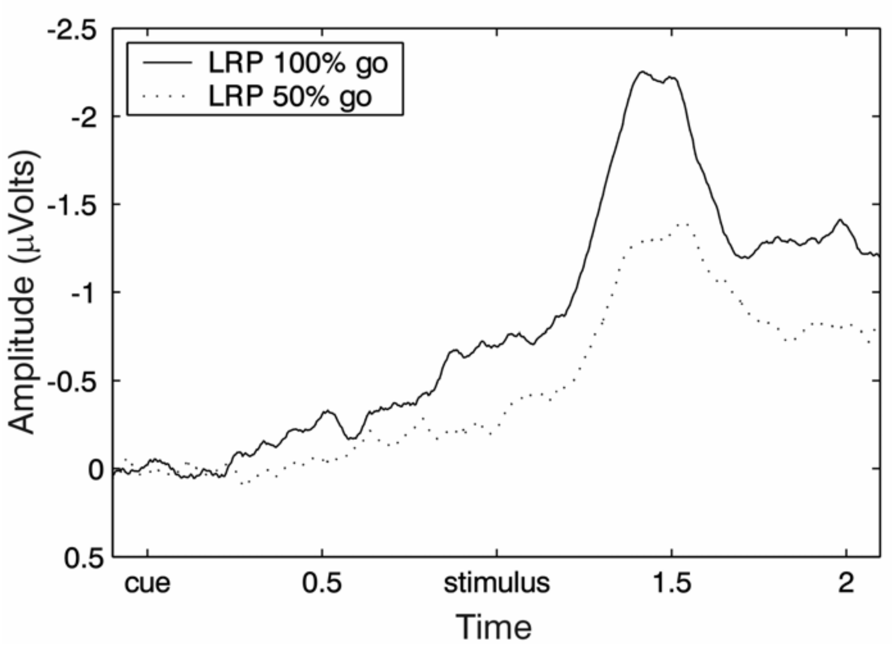


Figure 3.2.4. Choice/go-nogo LRP's for 100% go condition and 50% go condition.

action LRP's in the 100% go condition because no-go trials from the 50% go condition were included as well.

To interpret the LRP, a MANOVA analysis was performed on the ERP's of electrodes C3 and C4 using the factors cue type (left and right), go probability (100% go chance and 50% go chance) and electrode position (C3 and C4), which can be seen in Figure 3.2.5. There were no main effects (all p's > .127) and there was no two-way interaction of cue type and go probability (F(1,15) = .003, p = .958). There was a two way interaction of cue type and electrode (F(1,15) = 10.175, p = .006) and a borderline significant two way interaction of go probability and electrode (F(1,15) = 3.088, p = .099) The three way interaction of cue type, go probability and electrode was significant as well (F(1,15) = 6.753, p = .020). This is exactly equal to the effect of go-probability on the LRP, as it should be.

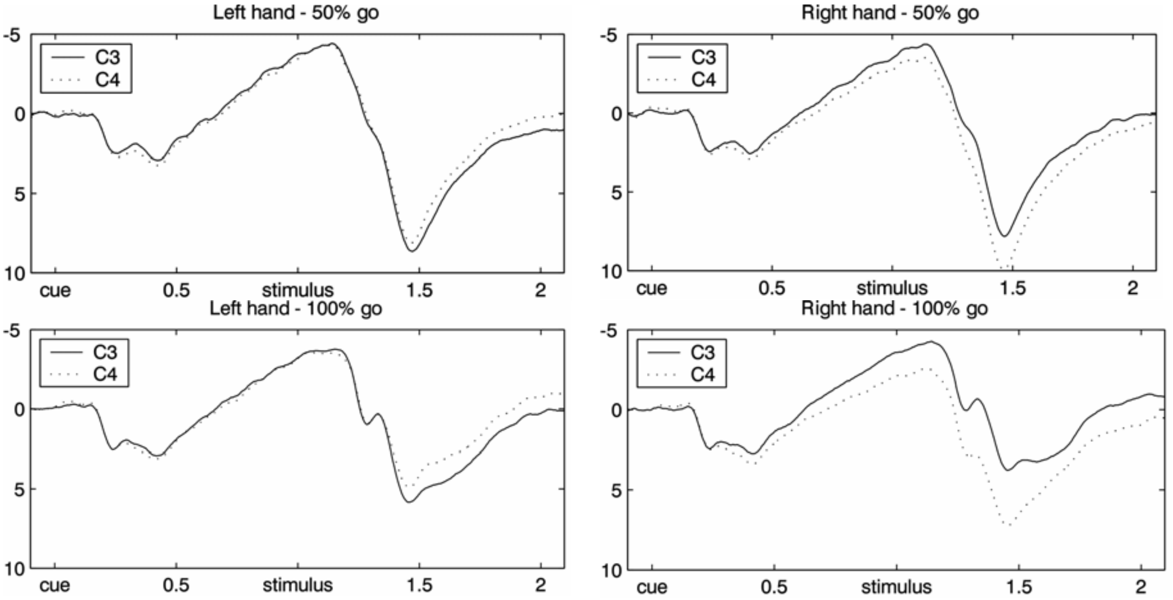


Figure 3.2.4. Choice/go-nogo CNV's for electrodes C3 and C4.
The 50% go condition is shown in the upper two graphs and the 100% go condition in the lower two graphs. The left hand cues are shown on the left and right hand cues on the right.

3.2.4. Instantaneous Amplitude

As can be seen in Figure 3.2.6. there was a small preparatory theta band effect on F4 only for the contrast between 100% go hand and time cues. Bold lines in the significance plot indicate t-values that exceeded the FDR threshold for significance again. Equally small alpha band effects can be seen in Figure 3.2.7. on the Frontal and Right Parietal ROI's for cue type by go-probability interaction and the 100% go hand cues and time cues contrast respectively. The Frontal effect of cue type by go-probability interaction was preparatory, and the Right Parietal 100% go hand cues minus time cues effect was repsonse related. The beta band as depicted in Figure 3.2.8. shows some more effects, both preparatory and repsonse related. The largest beta band effects can be found parietally.

Lateralized IA (see Figure 3.2.9.) is significant only in the beta band for 100% go probability. It is interesting to note that the theta band appears to be somewhat lateralized prior to cues and that both the alpha band and beta band first lateralize the wrong way, before the correct lateralization is started.

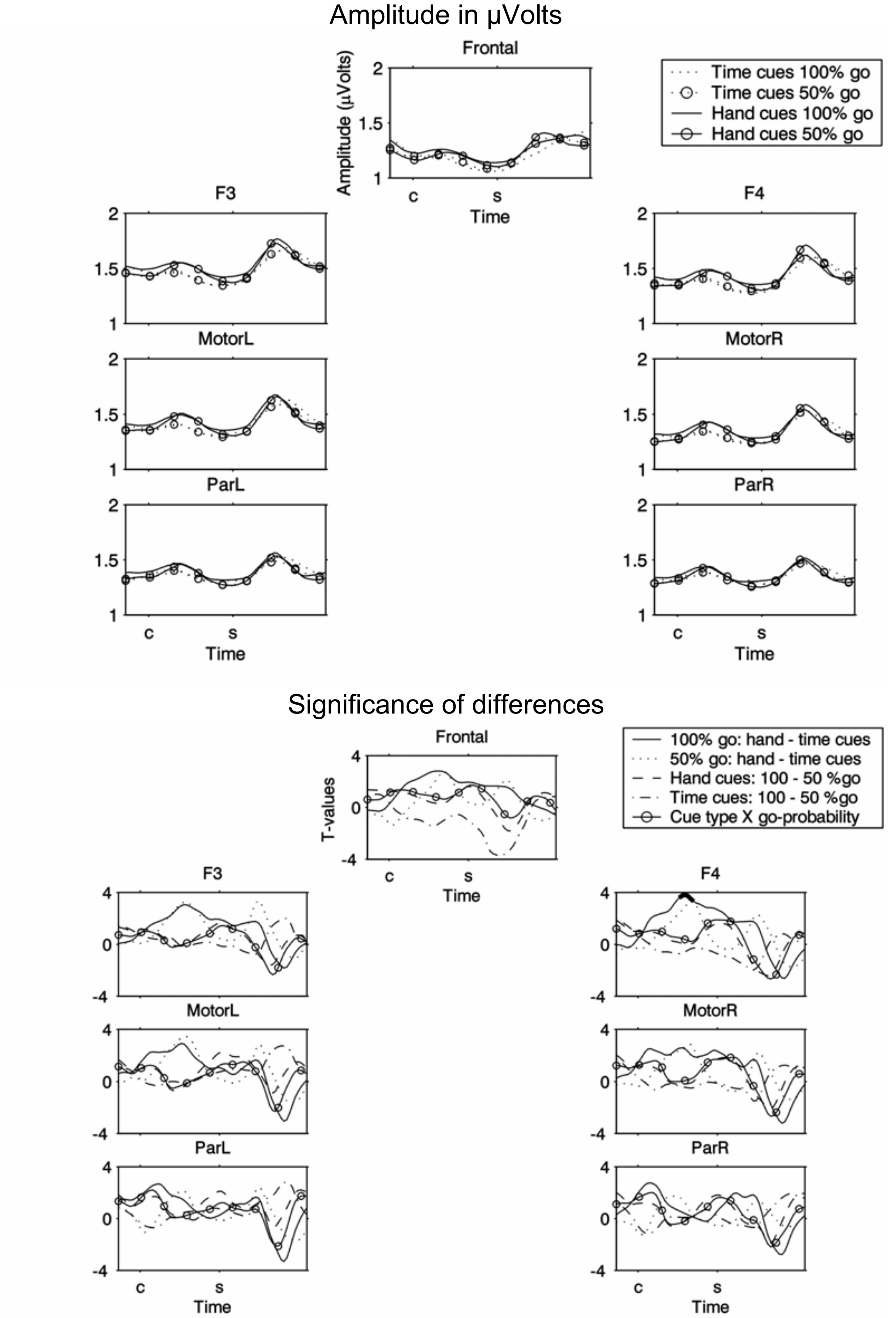


Figure 3.2.6. Choice/go-nogo theta band instantaneous amplitude.
The lower plot shows the significance of the difference between 100% go and 50% go trials for time cues and hand cues as well as the interaction between go-probability and cue type.

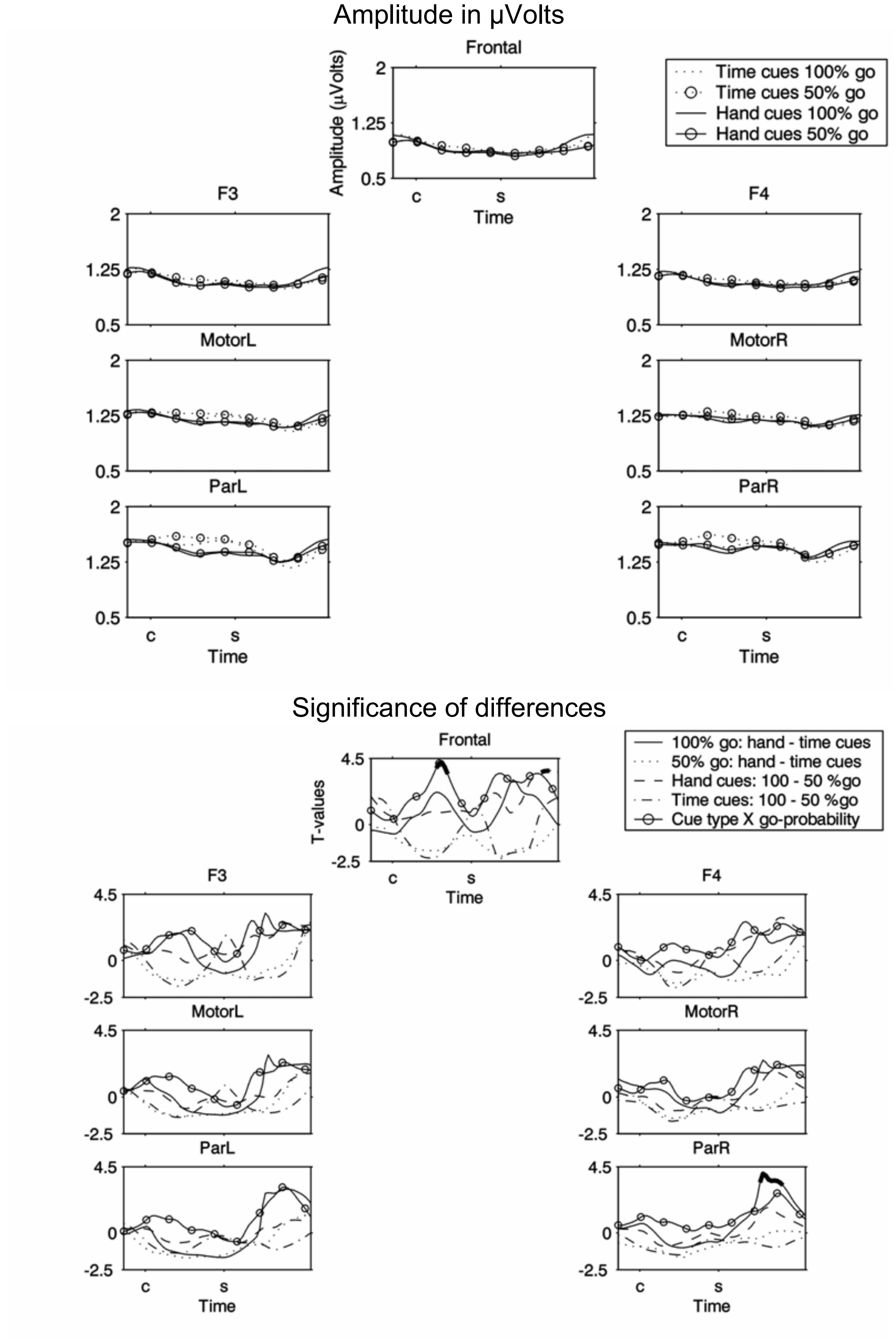


Figure 3.2.7. Choice/go-nogo alpha band instantaneous amplitude.
The lower plot shows the significance of the difference between 100% go and 50% go trials for time cues and hand cues as well as the interaction between go-probability and cue type.

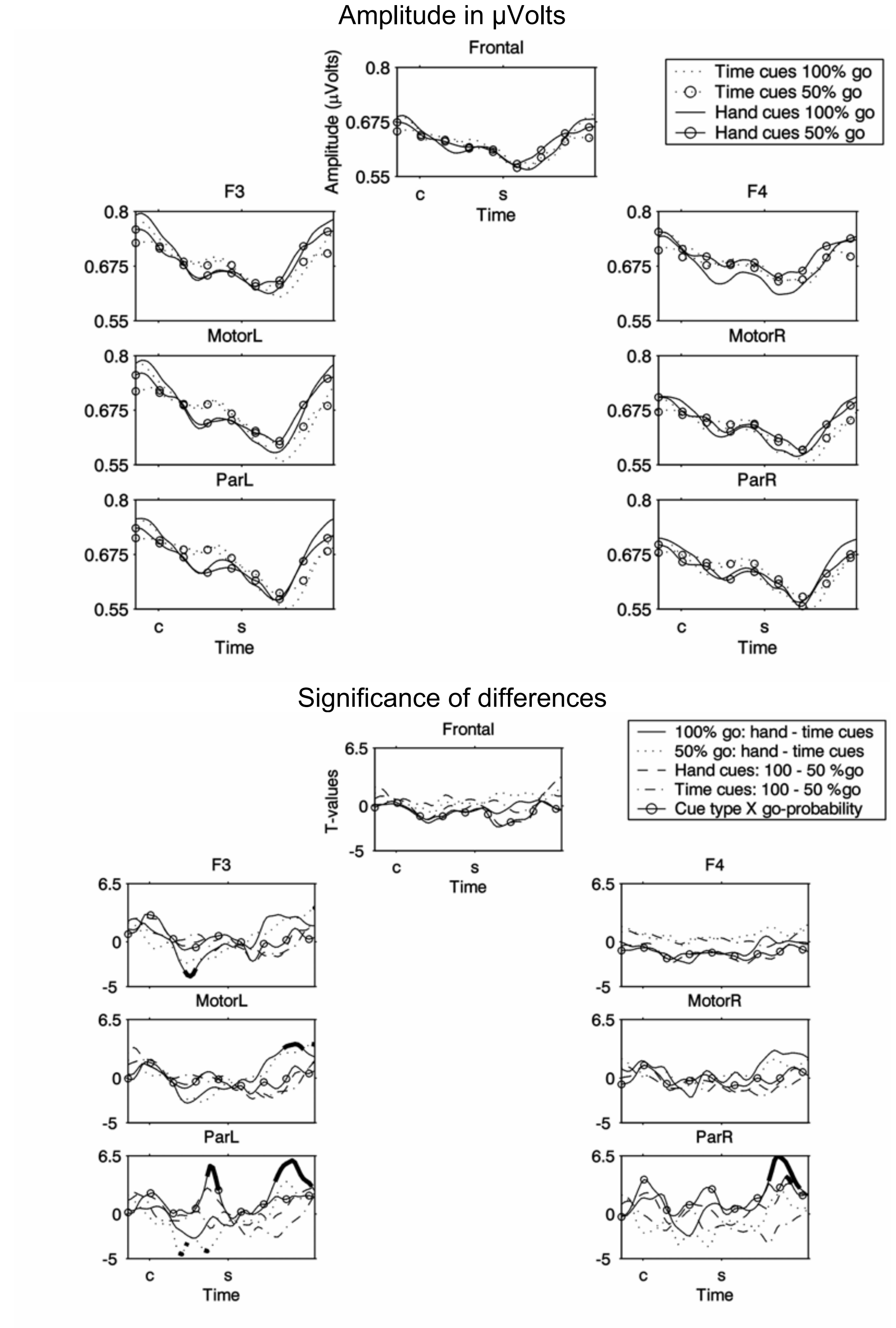


Figure 3.2.8. Choice/go-nogo beta band instantaneous amplitude.
The lower plot shows the significance of the difference between 100% go and 50% go trials for time cues and hand cues as well as the interaction between go-probability and cue type.

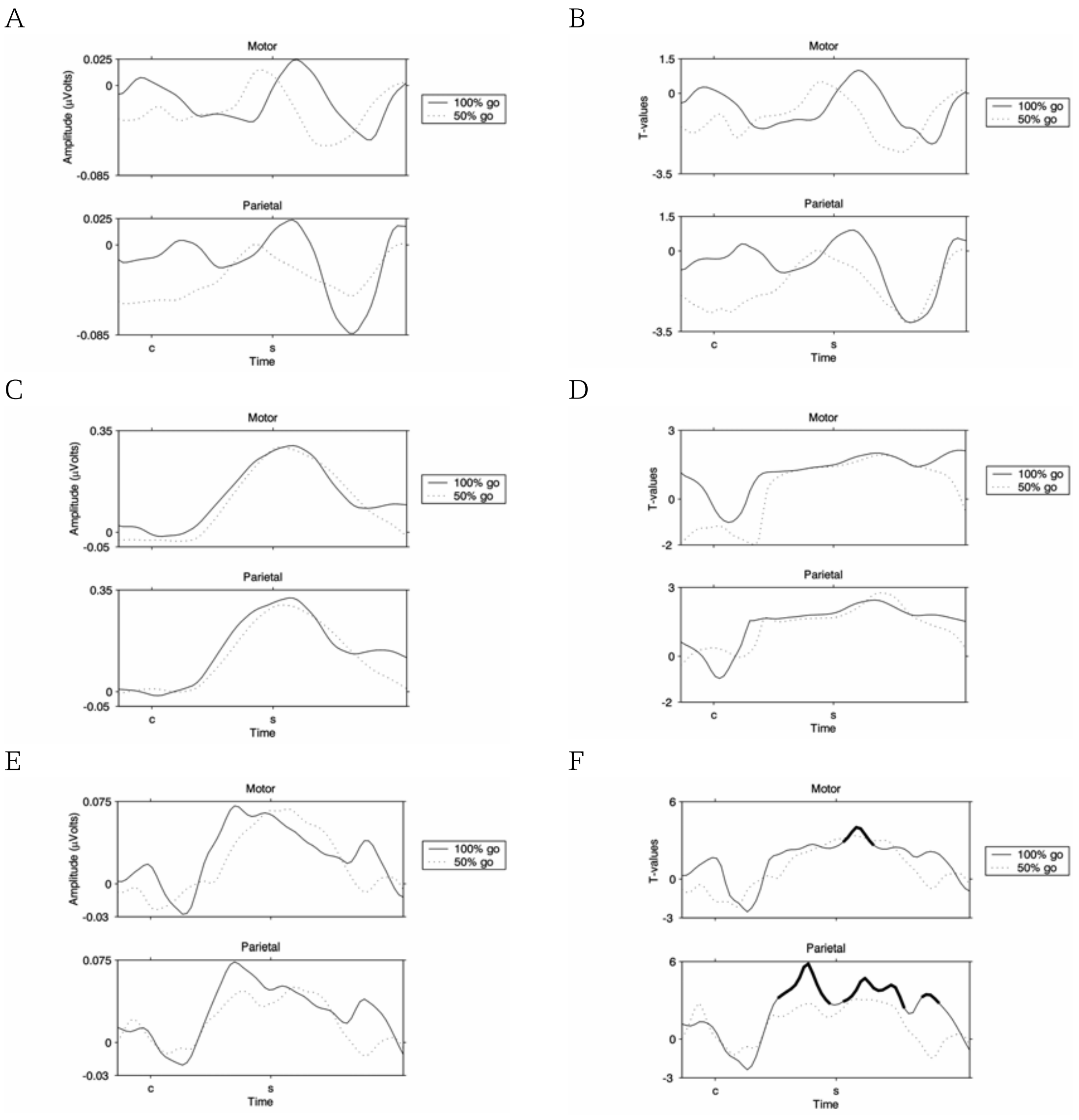


Figure 3.2.9. Choice/go-nogo Lateralized Instantaneous Amplitudes.
A: theta band LIA. B: theta band LIA significance. C: alpha band LIA. D: alpha band LIA significance. E: beta band LIA. F: beta band LIA significance.

3.3. Sequence Element Cueing

3.3.1. RT's and errors

Two Reaction Times are involved in the SEC task. The time between stimulus-presentation and the first registered key stroke and the time between the first and second key stroke. For the first response (RT1), only RT's between 100 and 2000 ms were accepted from trials with correct responses. For the time between the first and second key stroke (RT2) only RT's between 25 and 1000 ms were accepted from trials with correct responses.

Figure 3.3.1 illustrates the distributions of RT1 per condition. The fastest responses are given when the full sequence is cued (mean: 276 ms), followed by cueing the first response (mean: 385) and the second response (mean: 444 ms). No information generated the slowest responses (mean: 504 ms). If RT's are further split up according to whether the first and second response are the same or not, the general order of speeds is maintained but modulated slightly and differently for each type of cue. When all information is cued RT1 is not affected by the kind of response sequence required (double or different). If the first sequence element is cued a double response sequence is 17 ms slower. When the second sequence element is cued a double response sequence is 32 ms slower. If no sequence elements are cued a double response is 25 ms faster.

There is no main within–subjects effect of double response (different or same keys) (F(1,15) = 2.308, p = .149). There are effects of cueing the first response (F(1,15) = 536.788, p < .001) and of cueing the second response (F(1,15) = 113.591, p < .001) which both result in lower RT's if the information is given. There is no two-way interaction of double response and cueing the first response (F(1,15) = .776, p = .392), but there are two-way interactions of double response and cueing the second response (F(1,15) = 42.621, p < .001) and of cueing the first and cueing the second response (F(1,15) = 7.174, p = .017).

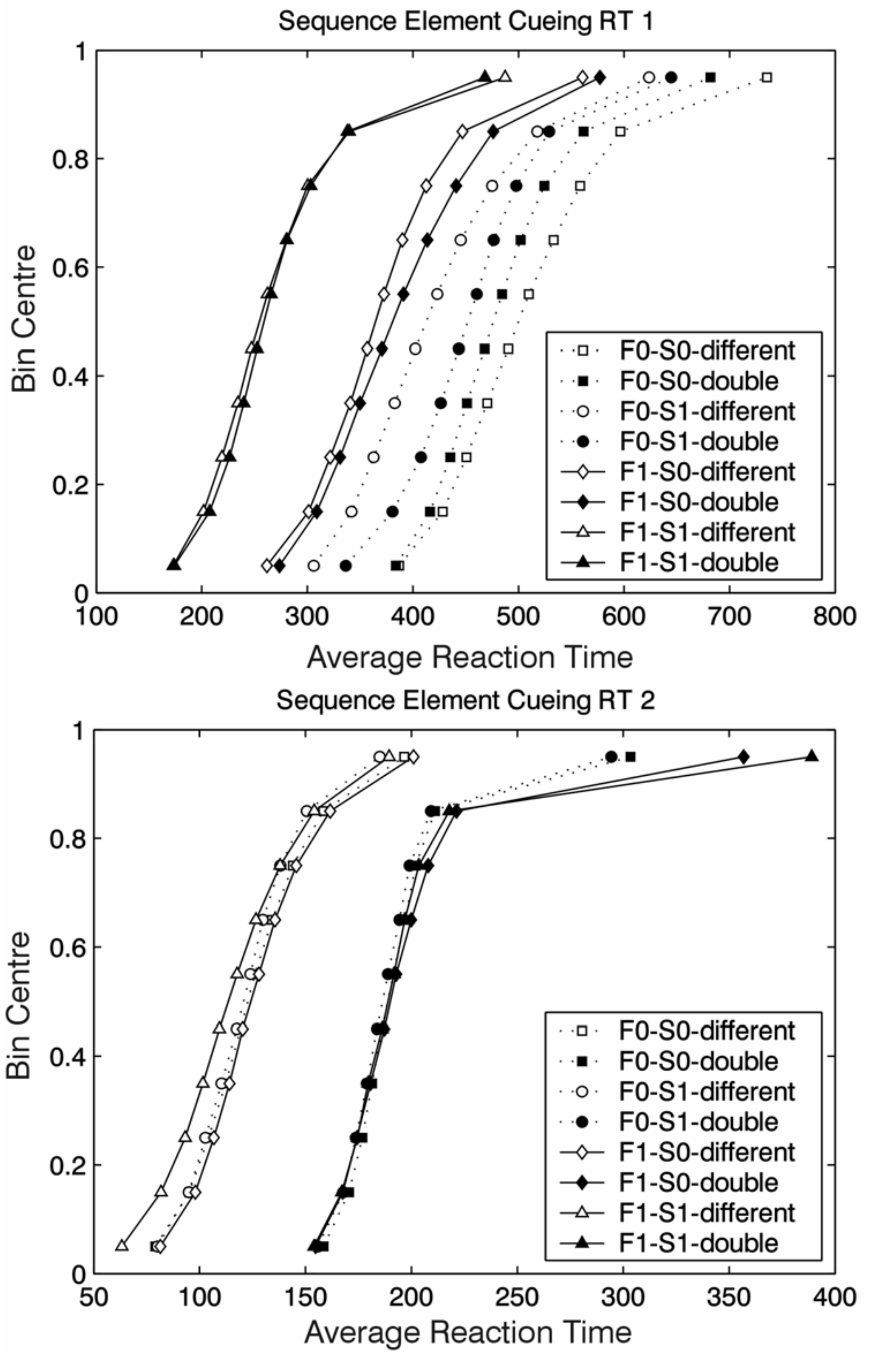


Figure 3.3.1. Sequence Element Cueing RT1 and RT2 distributions. Distribution of the time between stimulus presentation and the first response made. 'F1' indicates the first sequence element is cued whereas 'F0' means it is not cued. 'S1' indicates the second sequence element is cued and 'S0' means it isn't cued. 'Double' means the two responses were the same and 'different' means the repsonses were different.

There is a three-way interaction of double response, cueing the first response and cueing the second response as well (F(1,15) = 17.141, p = .001).

Inspection of the distributions of RT2, the time between the first and second response, suggests there is only an effect of double response on this aspect of the behavioral data. The difference between the average of trials with the same responses and trials with different responses is 76 ms.

Multivariate testing however, reveals that in addition to a main effect of double response on RT2 (F(1,15) = 69.586, p < .001) there is a main effect of cueing the second response (F(1,15) = 8.709, p = .010) as well as a borderline significant effect of cueing the first response (F(1,15) = 3.804, p = .070). There are second order effects of double response and cueing the first response (F(1,15) = 9.023, p = .009) and of double response and cueing the second response (F(1,15) = 5.712, p = .030) but there is no effect of cueing the first response and cueing the second response (F(1,15) = .647, p = .434). There also appears to be a third order effect of double response and cueing the first and second response (F(1,15) = 7.755, p = .014).

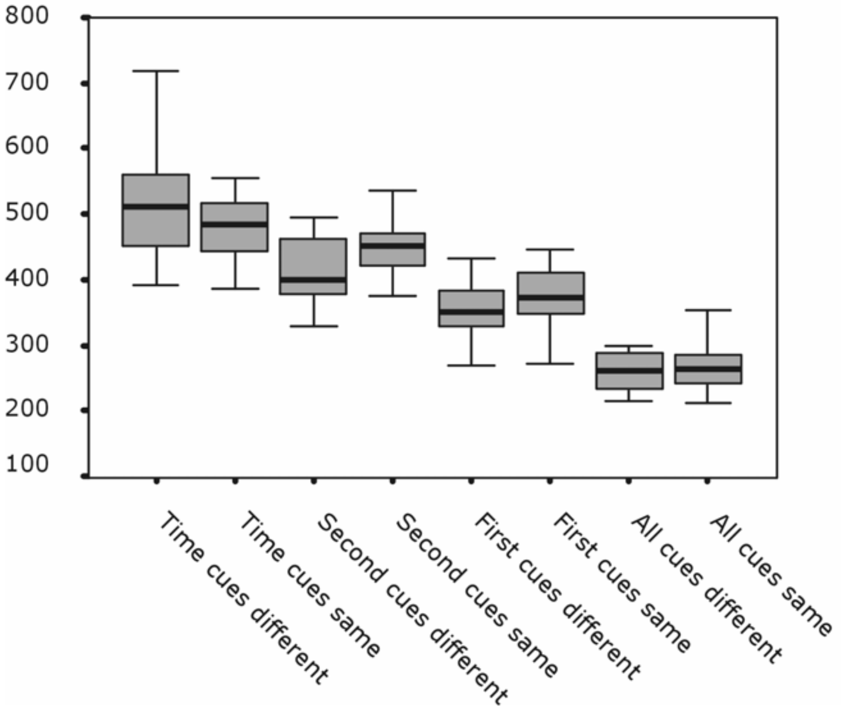
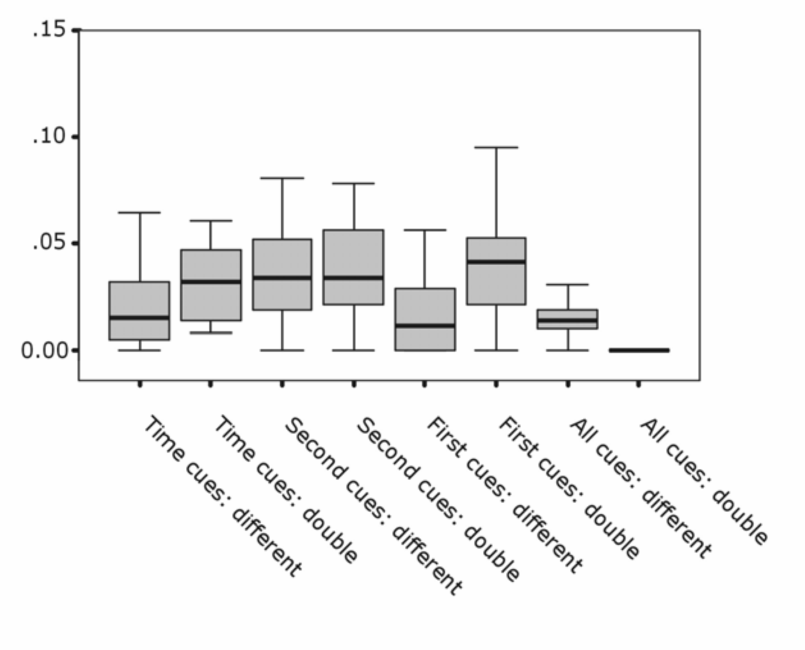


Figure 3.3.2. Sequence Element Cueing between-subject variability on RT1. The horizontal fat lines in the middle indicate the median RT.



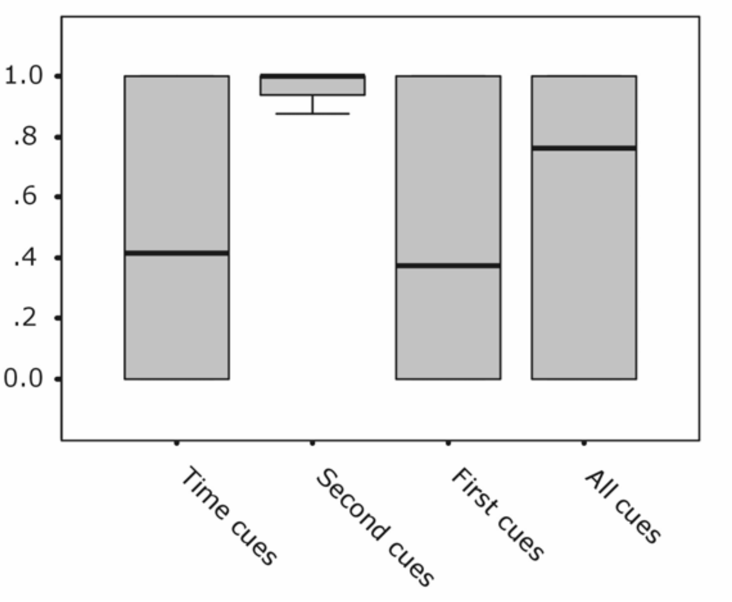


Figure 3.3.4. Error proportions.
On the top are the proportion of trials that were errors for each cue type and for double and different responses required. The lower graph shows the proportion of double errors for stimuli with two different responses.

In Figure 3.3.4. the proportion of trials that were errors are shown and the proportion of trials that required different responses to be made and where both responses were wrong. These errors could be seen as 'reversal of response order' errors. It looks like subjects were more likely to make these reversal errors when the second sequence element was cued.

Generally it appears subjects waited with their response untill the full sequence had been determined, since the main determinant of RT2 is the type of sequence: double keys or different keys. The time between the stimulus and full determinantion of the response sequence was based on the amount and kind of information provided by the cue.

3.3.2. CNV

The first explorative analysis was performed using the factors electrode position (Fz, Cz and Pz) and cue type (time cues, second element cues, first element cues,

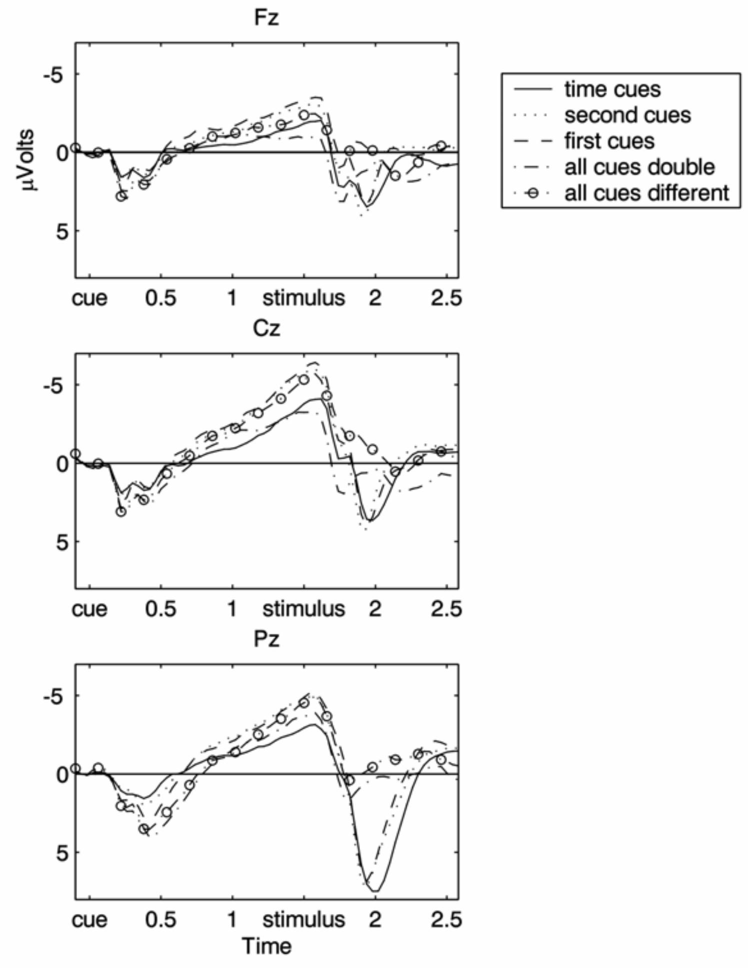


Figure 3.3.5. Sequence Element Cueing CNV’s.

all element cues double and all element cues different). To reduce data different and double responses were grouped for cues that did not give information on both sequence elements as preparation should not differ between different and double respsonse trials given an incomplete or non-informative cue. The comparison of Fz, Cz and Pz was included because the amplitude of the CNV was larger on posterior positions, as can be seen in Figure 3.3.5. An interesting difference in post-stimulus ERP can be seen as well; on Pz cues with incomplete information evoke a P300 which is much smaller on Fz and Cz.

There were main effects of both factors electrode position (F(2,14) = 11.553, p = .001) and cue type (F(4,12) = 4.602, p = .017). The two way interaction between electrode and cue type was not significant (F(8,8) = 2.015, p = .171). An ANOVA was performed to test the effect of cue type on the CNV for all electrode positions seperately. The effect was significant for Fz (F(4,12) = 4.129, p = .023), Cz (F(4,12) = 4.967, p = .014) and Pz (F(4,12) = 3.683, p = .035).

A second MANOVA was performed using the factors electrode position (Fz, Cz and Pz) and cue type (all elements cued with double responses and all elements cued with different responses). The main effect of electrode was significant (F(2,14) = 9.403, p = .003). The main effect of cue type (F(1,15) = 3.787, p = .071) was borderline significant but the two way interaction effect between electrode position and cue type (F(2,14) = 2.468, p = .121) did not reach significance. On Fz the ANOVA to test the effect of double or different responses with complete cues revealed a borderline significant effect (F(1,15) = 4.165, p = .059). On Cz this effect was just significant (F(1,15) = 4.695, p = .047).On Pz the same test revealed that the effect was not significant (F(1,15) = 1.275, p = .277).

3.3.3. LRP

As can be seen in figure 3.3.6., there seems to be a preparatory LRP only when both elements are cued and the two responses required are different. Note that

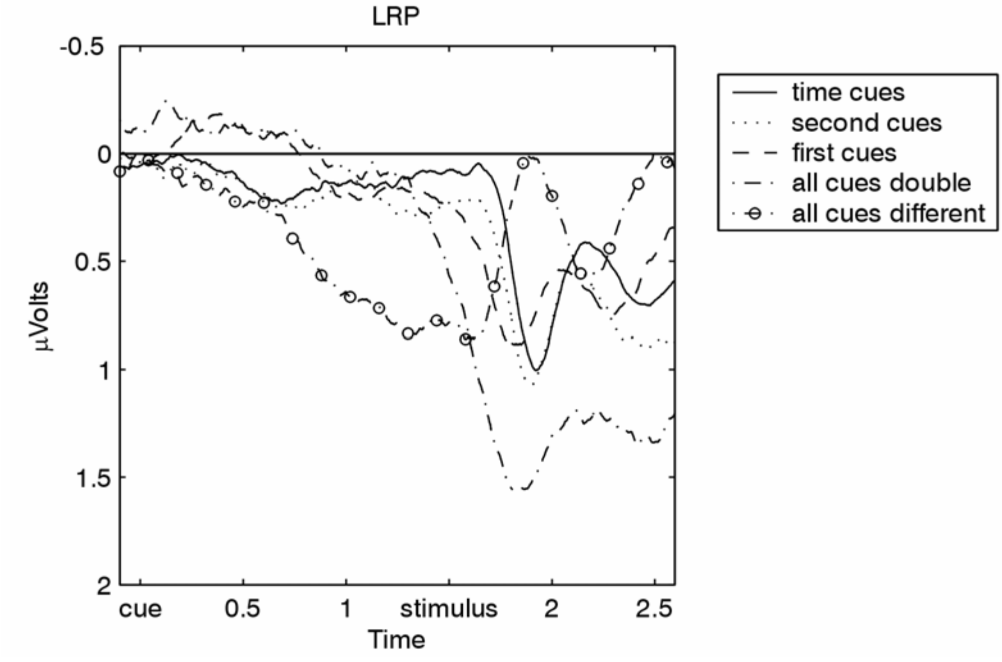


Figure 3.3.6. Sequence Element Cueing LRP's.

post-stimulus LRP's show an alternating pattern that goes on well after the second response has been given.

An ANOVA over the average LRP amplitude during the last 200 miliseconds of the preparation interval using cue type as factor (with the same five cue types used for the analyses of the CNV) revealed that there was no significant main effect of cue type (F(4,12) = 2.344, p = .114).

In an ANOVA using only complete cues as cue types there was a significant main effect of double or different responses (F(1,15) = 7.103, p = .018).

3.3.4. Instantaneous Amplitude

Figure 3.3.6. shows that there are only significant effects in the theta band in the response interval. There seem to be some stimulus or response locked apha band effects, but none of them reaches significanca as can be seen in Figure 3.3.7. In Figure 3.3.8. it can be seen that there are preparatory beta band effects of informative cues versus time cues and some stimulus or response related effects

in almost all contrasts. In Figure 3.3.9. it can be seen that in the alpha band and the beta band there are lateralization effects when both sequence elements are cued and equal. This preparatory lateralization reaches significance in the beta band only.

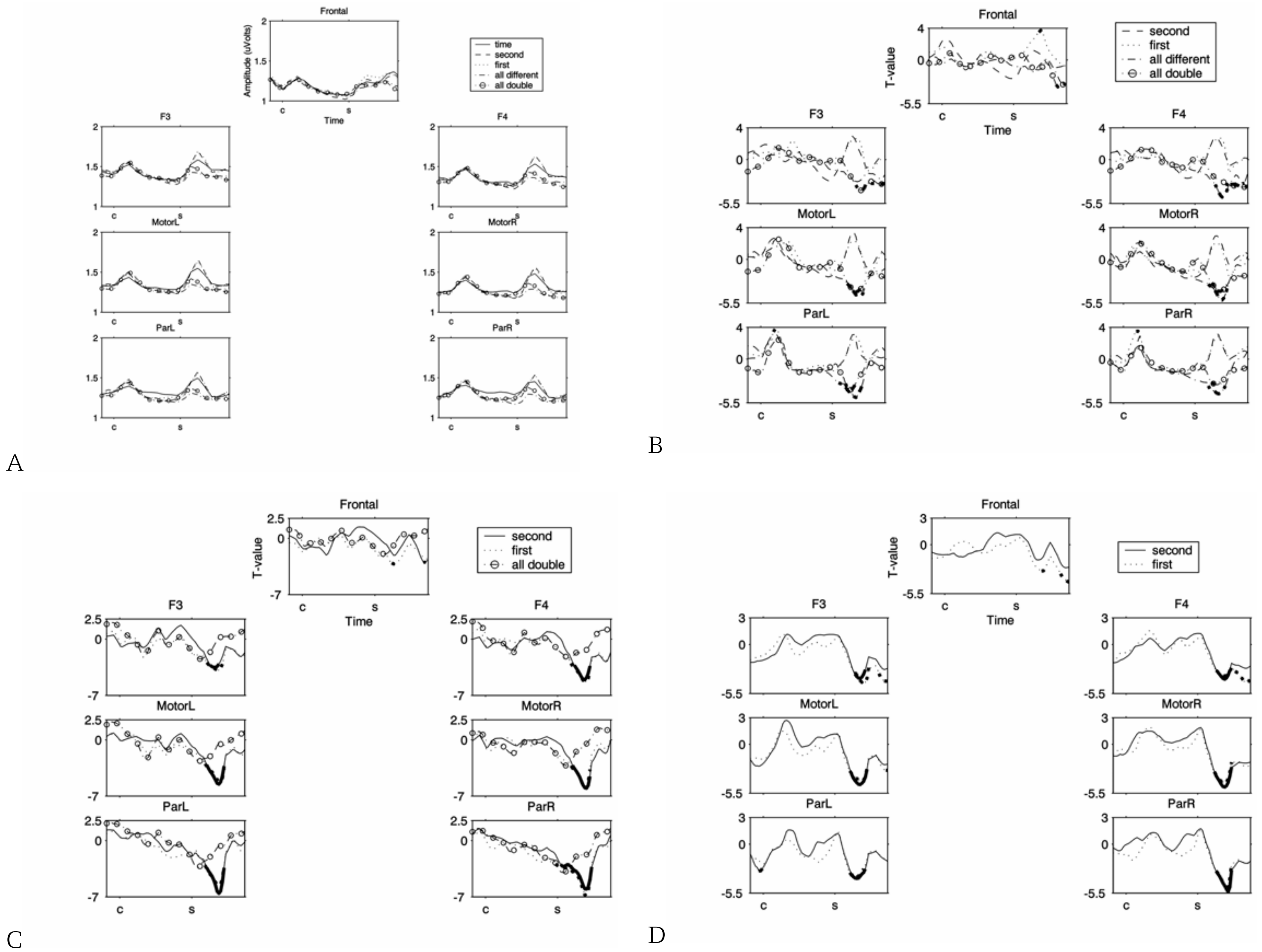


Figure 3.3.7. Sequence Element Cueing instantaneous theta band amplitude and differences.
A. Instantaneous Amplitude per condition. B. T-values of the contrasts between the time-cue condition and all other conditions. C. T-values of the contrasts between All-info cues with different responses and all other conditions. D. T-values of the contrasts between All-info cues with the same response twice and all other conditions.

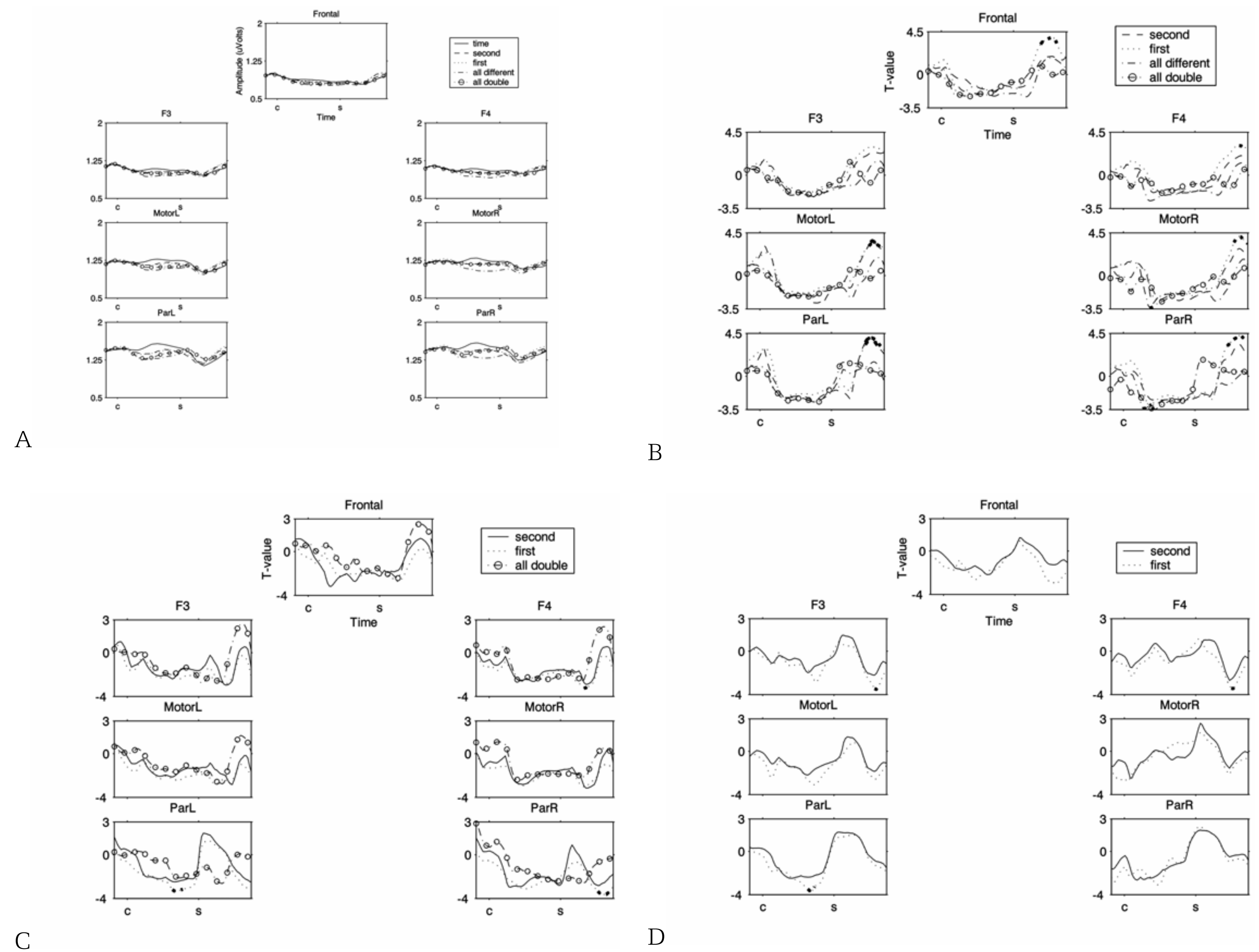


Figure 3.3.8. Sequence Element Cueing instantaneous alpha band amplitude and differences.
A. Instantaneous Amplitude per condition. B. T-values of the contrasts between the time-cue condition and all other conditions. C. T-values of the contrasts between All-info cues with different responses and all other conditions. D. T-values of the contrasts between All-info cues with the same response twice and all other conditions.

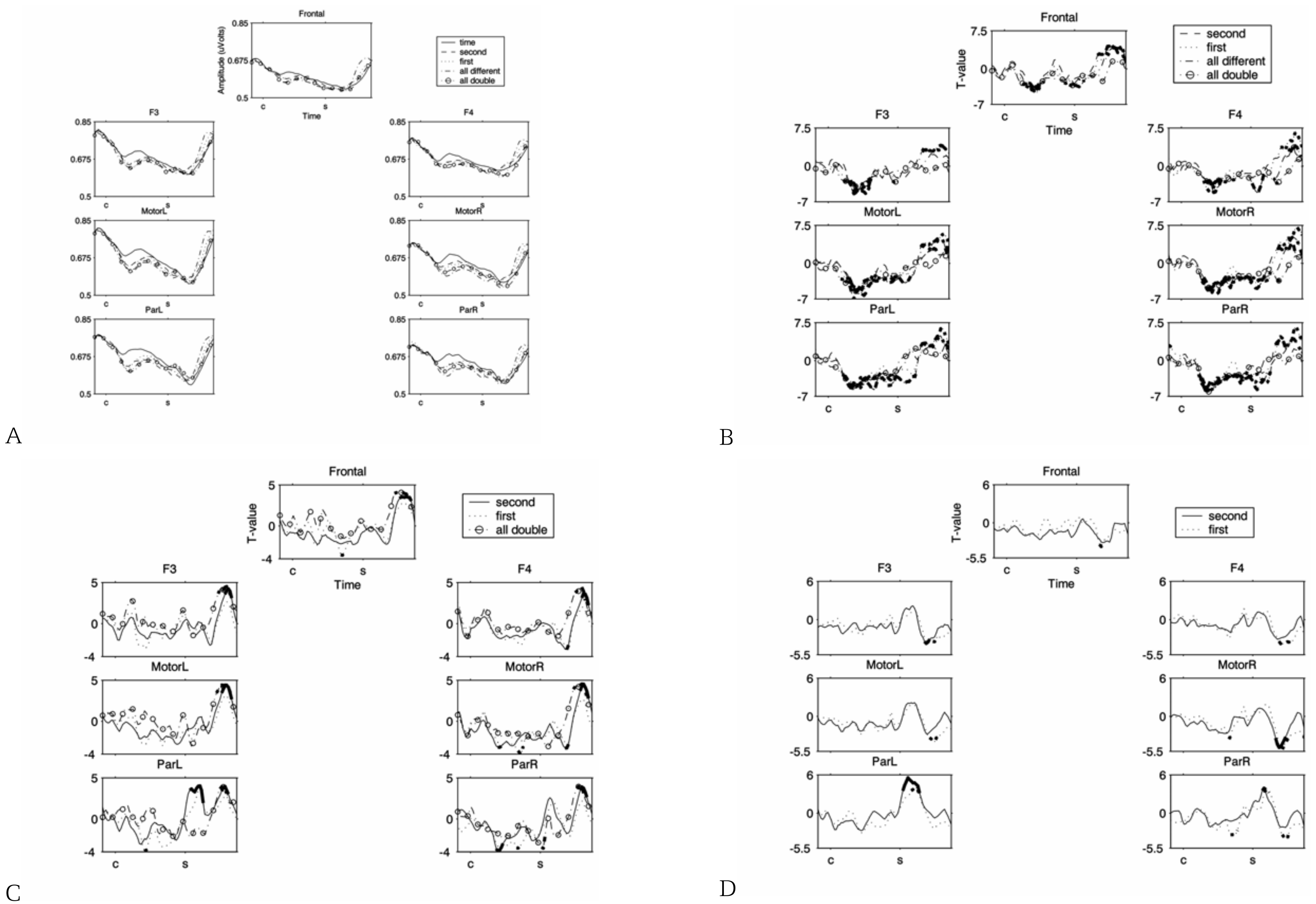


Figure 3.3.9. Sequence Element Cueing instantaneous beta band amplitude and differences.
A. Instantaneous Amplitude per condition. B. T-values of the contrasts between the time-cue condition and all other conditions. C. T-values of the contrasts between All-info cues with different responses and all other conditions. D. T-values of the contrasts between All-info cues with the same response twice and all other conditions.

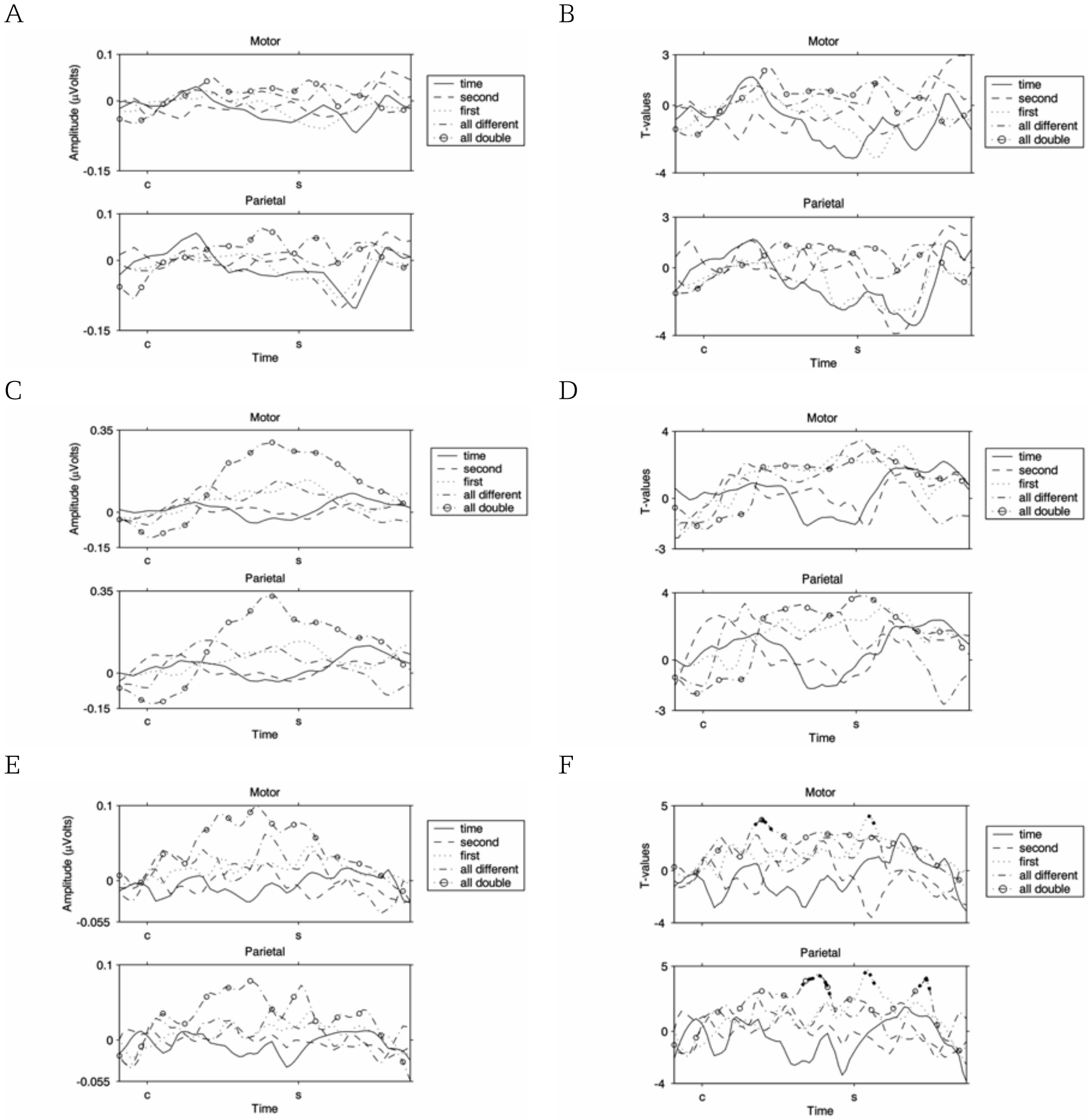


Figure 3.3.9. Sequence Element Cueing Lateralized Instantaneous Amplitude.
A: Theta band amplitude. B: Theta band t-values. C: Alpha band amplitude. D: Alpha band t-values. E: Beta band amplitude. F: Beta band t-values.

4. Discussion

First the hypotheses will be discussed in the light of the experimental results presented above. Then a short conclusion with an overview over all tasks and measures will be given.

4.1. Rogers and Monsell hypotheses

Hypothesis 1.1. RT's will be higher in switch-trials than in non-switch trials. Short preparation intervals will be used to ensure that subjects use the whole of the long preparation intervals for task-set reconfiguration (Sohn & Carlson, 2000).

This hypothesis is confirmed. The interaction between preparation interval and task switching was significant. In specific, the RT decrease between long and short PI's was larger in switch trials than in non-switch trials. Apparently, switch costs decreased over time, suggesting that subjects engaged in preparatory activity in the extra time they had in long PI's. This activity may be reflected in physiological measures.

Hypothesis 1.2. The amplitude effects of task switching on the LRP found by Gladwin et al will be found in this experiment as well.

The shapes of the LRP's found in this study strongly resemble those found by Gladwin et al. Within alternation trials the lateralization of the LRP seems to switch to the correct side, unlike the LRP found by Gladwin et al. But, as explained before, the choice of baseline in this experiment may be the cause of the difference. The effect may also be explained by the removal of modality from the task. In a simpler task subjects may be able to focus more on motor preparation.

Hypothesis 1.3. The absence of an amplitude effect of task switching on the CNV found by Gladwin et al will be found in this experiment as well.

There was no effect of task switching on the amplitude of the CNV, but there is an effect of electrode location on the CNV with stronger amplitudes located more posteriorly. This would suggest that the CNV in this task is not an effect of control or information processing, which would generate an increased effect on Fz. Although at the end of the preparation interval the amplitude of the CNV's of switch and non-switch trials was equal on all electrodes, there may have been a small effect of task switching halfway the preparation interval. This is untested, but may signify that subjects prepared some more on switch trials but were equally prepared at the end of PI's in switch and non-switch trials. It may also be an effect related to the short PI trials. Subjects may somewhat prepare for a stimulus halfway the long PI.

Hypothesis 1.4. There will be effects of task switching on lateralized alpha and beta IA in this experiment as these were found in the experiment by Gladwin et al.

No effect of task switching on theta IA was found. The peaks around stimulus and response may be the result of a response related P300 as the duration of the P300 falls within the range of frequencies in the theta band.

There appears to be an effect of task switching in the beta band during preparation, but it does not reach a significant level. It may be that testing a subset of fast trials obtained with FTE results in stronger task switching effects on beta IA. Gladwin et al did not find a preparatory beta IA effect of task switching after applying FTE though.

Lateralized alpha and beta IA seem to be changed by task switching, but the effects do not reach significance. As with beta IA, FTE may prove usefull, but the results found by Gladwin et al suggest otherwise.

In short, RT and ERP effects were reproduced, but IA effects were not, which may possibly be remedied by using FTE.

There is a possible explanation for the differences in the results found here and those found by Gladwin et al. Although Gladwin et al found no differences between the two tasks/modalities, motor preparation may have been facilitated by the complete seperation of stimulus-response sets by modality in their setup.

On the other hand, Rogers and Monsell-like task switching may not be an adequate paradigm to study motor preparation in the first place. Especially in the LRP results the lack of a baseline period is a serious problem. This hampers not only the analysis of data, but interpretation of the results as well. For example, the LRP effects can be viewed as a combination of two processes (Leuthold and Jentzsch, 2002; Jentzsch and Leuthold 2002). The action LRP is decaying while a preparatory LRP is building up. Is the lateralization in non-switch trials a small preparatory effect or is it residual action LRP? Is the lateralization in switch trials due to sped up delateralization of the action LRP or is it a genuine preparatory LRP? What is worse is that it is hard to say if these problems are not inherent to the IA and lateralized IA as well. For example, it appears that in the alpha band there is a response locked decrease of IA after a response (possibly related to eye-movement in between trials). This effect may have masked any preparatory alpha IA increases or decreases.

The first derivative of a function expresses the function's change over time, without a relation to the starting level of the function. At first glance, the first derivative may be used to overcome baseline problems in the Rogers and Monsell task switching paradigm for the ERP-measures discussed here. The first derivative of the CNV and LRP do not express the amplitude of the ERP measures, but the strength of their development in a given period of time. This means that an average of the first derivative should be calculated over the period of time in which the measure is developing. However, the changes in CNV and LRP most probably take place relative to a neutral level, which can not be determined in the Rogers and Monsell task switching paradigm. This means that the first derivative will not only express development of preparatory CNV and LRP, but the behavior of these measures relative to their unknown neutral level as well. Thus, the first derivative is unfit for analysis of CNV and LRP data in this paradigm as well.

4.2. Choice/go-nogo hypotheses

Hypothesis 2.1. Both cue type and go-probability will have an effect on RT: providing hand cues will result in lower RT's than providing non informative cues, and in the high go-probability condition RT's will be lower than in the low go-probability condition. These effects will interact.

The effect of cue type and go-probability on RT are both significant. The effects interacted: hand cues had more advantage over time cues when the go-probability was high instead of low. The effect of cue type is larger than the effect of go-probability. This is not surprising since cue type determines if a hand can be prepared while go-probability only modulates the intensity or the kind of preparation.

Hypothesis 2.2. The terminal CNV will be higher when hand cues are provided than when time cues are provided. The terminal CNV will be higher in high go-probability conditions than in low go-probability conditions.

A high go-probability actually results in a lower CNV than low go-probability, though this effect is only found on Fz. Hand cues do seem to elicit higher CNV's than time cues, at least on Fz and Cz.

Aside from significant effects it is striking to see that a low go-probability elicits a larger CNV than a high go-probability on Fz and that this seems to reversed, only for hand cues, on Pz. Also, the differences between high and low go-probablity are not significant on Cz and Pz, where CNV amplitude is higher than on Cz. On Fz this difference is significant. This suggests that some processes involved in motor preparation that are affected by go-probability are performed in more frontal regions. For example, the premotor area and supplementary motor area may do more of preparation in low go-probability conditions than in high go-probability conditions. It may be that these areas prepare by building up a motor program which is not passed on to the motor areas in low go-probability but has to be kept at the ready. It may also be that in low go-probability conditions these areas play a role in making the go/no-go decision that does not have to be made in the 100% go-probability condition. Alternatively, these areas are kept ready to actively inhibit a response if a no-go stimulus is presented.

Another fact to reckon with is that on Pz there is a larger cue-locked P300-like effect on hand cues than on time cues. This may have masked any CNV effects of cue type on the Pz CNV. If this is so, the effects on Pz would strongly resemble those found on Cz.

If the different effects found on Fz are indeed an expression of a process that keeps the premotor area and supplementary motor areas ready to pass some information to the primary motor cortex, it should not very be sensitive to further variations in level of go-probability. A setup using for example, 75%, 50% and 25% go probabilities might supply contrasts of high and low go-probability conditions all including a go/no-go decision. The 100% go condition should be treated as qualitatively different from other go-probabilities since it lacks the go/no-go decision. However, precisely because the 100% go condition lacks the go/no-go decision it provides context to interpret differences found between other go-probabilities and it enable a comparison to other tasks investigating motor preparation which also lack a go/no-go decision.

Hypothesis 2.3. Within hand cue LRP's there will be an effect of go-probability. The LRP on time cues will not be analysed.

The Choice/go-nogo LRP's behave exactly as expected: the 100% go-probability results in a higher LRP than the 50% go-probability.

For this task the CNV's composing the LRP have been displayed (see Figure 3.2.4.) and tested. There are two interesting facts to be found in this data. First, the preparatory LRP found in this task is attributable to differences in C3 and C4 CNV during preparation for right hand responses only. Preparation for left hand responses does not contribute to the LRP. All subjects were right handed, so this may be an effect of the subjects' disposition for their right hand. There does appear to be a response related difference between C3 and C4 on both left- and right hand responses though. Second, the fact that on left hand responses the preparatory CNV's on both C3 and C4 reach the amplitude of the CNV found on C3 for right hand responses is interesting.

These two pieces of information may point out that preparation is achieved by a general pre-activation of the motor cortex, combined with inhibition of the incorrect side. This inhibition may be more difficult for the hand contralateral to the preferred hand of subjects.

Hypothesis 2.4. Go-probability does not affect preparatory IA in any of the three frequency bands analysed. Hand cues evoke stronger alpha and beta ERD than time cues.

In the theta band there appears to be an insignificant preparatory difference between hand cues and time cues. Go-probability has no effect on theta IA. Hand cue trials show somewhat more theta activity than time cue trials which is significant only on F4 right after cue presentation. Recall of task set is not a probable explanation, but commitment of which hand has to be used to working memory may be. Unfortunately a larger P300 following hand cues (Figure 3.2.3.) is a sufficient explanation for the significance of the cue related differences in theta IA as well. There are some effects of theta IA lasting well into the preparation interval, which do not reach significance and suggest that subjects engaged in more memory related processes when hand cues were provided.

In the alpha band a desynchronization on hand cues can be seen that appears post stimulus as well for time cues. The effect is located primarily parietally and the difference between hand cues and time cues is not significant. This seems to be an effect of keeping information in the system, either visual information provided by the cue or a (partially constructed) motor program.

In the beta band there is more desynchronization on hand cues than on time cues as well. However, the desynchronization on time cues catches up with hand cue ERD well before the stimulus. This rules out that the beta ERD is related to preactivation of relevant motor areas. Perhaps the task itself provided enough information for some preparation to occur. Subjects might have prepared for all four possible reactions in the time cue blocks just before stimulus presentation. This would mean that if subjects were provided with full information, beta ERD would have been stronger. Or that if subjects were to choose from more alternatives, beta ERD on time cues might not catch up with beta ERD on hand cues before the stimulus. It would be interesting to see what would happen if subjects were given cues that provided information on which finger to respond with (index- or middle finger) but not which hand. If beta ERD is indeed inversely correlated to the number of response alternatives left, such finger cues should evoke the same amount of beta ERD as hand cues in this experiment (or beta ERD with the same latency). On the other hand, beta ERD was significant only in a few datapoints.

Hypothesis 2.5. Go-probability does not affect lateralized IA on hand cues. Lateralized IA on time cues will not be tested.

There appears to be some preparatory alpha and beta lateralization of IA, but it is significant only for 100% go-probability beta activity. Go-probability does have an effect.

4.3. Sequence Element Cueing hypotheses

Hypothesis 3.1. RT's will be highest in the non-informative cue trials, followed by second element only cue trials, then first element only cue trials and then all information cue trials. Within these RT's there will be another effect of having to respond with the same key twice or not (sequence type). If two different keys have to be pressed, responses will be slower than when one key has to be pressed twice.

The first part of this hypothesis is partially confirmed: more information generates faster responses. The second part is not confirmed: sequence type (equal or different responses) has no effect on RT1 for full information cues and a reversed effect for partial information cues. The main effect of RT2 is that of sequence type. Cue type has some statistically significant but very small effects. The effect of sequence type seems to be related to the physical differences between the response sequences. If keys are different the second key can be pressed down while the first is being released. This is not possible for double responses. Any other effects found on RT2 might therefore not reflect any preparatory effects.

The main effect of sequence type found on RT2 may interpreted as evidence that subjects complete a full motor program that specifies both responses before any action is taken. This may have been facilitated by the short and simple response sequences which can possibly be treated as if they are one response or action. Perhaps this can be compared to piano key-strokes, which are not remembered individually but as grouped sequences by experienced musicians.

Motor program completion may provide an explanation for the effects of sequence type on RT1. With cues providing full information, the motor program is completed before the stimulus is shown, so sequence type has no effect. With non-informative time cues, the motor program is generated completely after the stimulus. Apparently it is easier to enter two equal responses into a motor program simultaneously than it is to enter two different responses simultaneously. Which can be viewed from a binding-perspective: less information has to encoded in the motor program, or the same action is bound twice to the program.

The two cue types providing partial information result in a motor program being built in stages: first one response is entered and after the stimulus a second response is entered. Entering the second response in the motor program is more difficult if it has already been entered before. The new binding is interfered with by the already existing binding, which can not be undone but has to be maintained.

The double errors on sequences with different cues provide another interesting bit of information on how this motor program completion may work. Double errors are errors where both responses are wrong. On sequences with two different responses this may be interpreted as a reversal of response order by the subject. Only on second element cues this type of error is made by all subjects almost to the exclusion of other kinds of errors. This suggests that it is difficult to integrate an action in the sequence in front of an already included action. In other words: it is easier to execute actions in the order one fits them into the action plan, or in the order the environment seems to demand actions of an individual.

Hypothesis 3.2. If only the second movement is cued, preactivation of relevant motor areas is not possible, so there is no CNV development and hence no LRP development following this type of cue.

This hypothesis is not confirmed. Although cueing the second response sequence element does not result in an LRP, all cue types evoke a CNV in the preparation interval and the amplitude of the CNV on second element cues is more alike to the CNV found on first element cues than the CNV found on time cues. Interestingly, the amplitude of CNV's is larger frontally than posteriorly, which is the opposite of the CNV amplitude distribution found in the other tasks. According to the discussion of the CNV results found in the Choice/go-nogo task this would suggest that the CNV in the Sequence Element Cueing task is primarily an effect of preparation on the basis of increased or improved processing of information provided by the cue and not of actual preactivation of motor areas.

Hypothesis 3.3. In contrast to hypothesis 3.2, providing information on the first sequence element enables preactivation of relevant motor areas and hence a CNV and LRP should develop.

This hypothesis is not confirmed. The CNV found after the first sequence element is cued is not very different from the CNV found after the second sequence element is cued and no LRP develops following first sequence element cues. The only LRP found is developed after all sequence elements are cued and the responses are different. If the responses are equal the LRP does not differ from other LRP's. Apparently the LRP can only develop if it is known that the sequence elements are different, so cueing all information is a necessary but not sufficient prerequisite for development of an LRP in the Sequence Element Cueing task. Or, it is not possible to preactive motor areas if the two responses to be made are equal. This may be explained by the fact that the finger making the responses has to be moved down and then quickly lifted up before it can be moved down again, making it impossible to prepare for both actions. It may even be that subjects prepare for both the lifting up and moving down of the finger and that the preparatory effects cancel each other out. On different responses the fingers both have to be lifted up eventually, but this may be done after both responses have been delivered or may be done passively by relaxing the flexor muscle instead of activating the extensor muscle.

A way to remedy this in future research is by having subjects make the first response with a middle finger and the second response with an index finger or vice versa (randomized). This may produce competely different LRP's and will at least diminish or perhaps even eliminate the sequence type effect on RT2. According to Hackley and Miller (1995) complex responses elicit larger LRP's, so it may be that this measure will have increased sensitivity in the proposed setup.

Hypothesis 3.4. No preparatory theta IA differences will be found between cue types, since the task set remains equal. Beta and alpha ERD will be a function of the amount of information provided by the cue.

It looks like there are some preparatory theta IA differences with higher theta IA following time cues and lower theta IA following all cues with different responses. None of these effects reaches significance however.

There is an alpha and beta IA desynchronization difference between time cues and other cue types so this is a partial effect of amount of information provided by the cue on alpha ERD. The differences in the alpha ERD between cue types are located primarily posteriorly and do not reach significance.

Hypothesis 3.5. After all informative cues there is a lateralized effect of IA in the beta band as all informative cue types enable some kind of preparation *regardless of the possibility to preactive relevant motor areas. The cues providing information on one sequence element (the first or the second) will evoked a higher lateralized beta IA than non-informative cues. Cues providing both sequence elements will evoke higher laterized beta IA still. Alpha IA will lateralize differently for different kinds of sequences (equal or different responses) since in sequences with equal responses one side of the motor cortex may still be suppressed as irrelevant while for sequences with different responses both sides of the motor cortex need to participate.*

This hypothesis is not confirmed. The only effect on beta IA lateralization is generated by cueing all responses with both responses equal. This may be explained by the preparation of active extension of the response finger in between responses that is only possible with this type of cue. Interestingly the cue type evoking beta ERD is the all element cue type that did not evoke an LRP.

Alpha IA lateralization is not significant but does seem to group in three levels. Time cues and second element cues evoke no lateralization of alpha IA. First element cues and all element cues with different responses evoke a little lateralization of alpha IA. All element cues with equal responses evoke the highest lateralization of alpha IA. Alpha as a suppression-rhythm of irrelevant areas may explain this. On time cues and second element cues no area can be rejected as irrelevant. First element cues should also invite subjects to keep options open for the second element, but they also have a 50% chance of being correct in suppressing the side of the motor cortex opposite to the side that will generate the first response. Why do subjects not take this gamble on second element cues? Possibly it is more difficult to complete their motor programs if they do, as is suggested by the large rate of double errors for second element cues with different responses. The benefits do not outweigh the costs. All element cues for different responses may start a preparatory process that favors the side of the motor cortex that has to generate the first response over the side that will generate the second response. Finally, when the same response has to be given twice and both sequence element are cued, one side of the cortex can be ignored and alpha IA lateralization can fully develop.

If these speculations are correct, the alteration of the task with first responses given with a middle finger and second responses given with an index finger, such as proposed earlier, might change alpha- and beta IA and lateralized IA dynamics as well. Preparation of one response should then be less interfered with by keeping motor program completion possible for the remaining sequences. In other words, the effects of sequence type on IA and lateralized IA within all element cues should be much smaller.

4.4. Conclusion

A simple dissociation between rate- and pulse coded motor preparation was suggested in the introduction: time domain measures of motor preparation (rate coded) are more an expression of preactivation of motor programs and frequency domain measures are more an expression of organisation, processing or representation of information. This dissociation does not hold. For example, the choice/go-nogo CNV seems to be sensitive to information processing and/or information representation and beta band IA lateralizes in the Rogers and Monsell task switching paradigm.

The picture that remains is fragmented and may have been interfered with by task design issues, especially in the Rogers and Monsell task switching paradigm and the Sequence Element Cueing task. The Rogers and Monsell paradigm seems inherently unfit for investigating motor preparation, or at least the difficulties it raises can not be solved easily by adaptation of the task setup. In the discussion of the results found in the Choice/go-nogo and Sequence Element Cueing task improvements to the designs have been proposed as well. In the Choice/go-nogo design the 100% go-probability condition does not compare well with the conditions that include a go/nogo decision. Addition of different go-probabilities can solve this. In the Sequence Element Cueing task sequence type had a large effect on all preparatory effects. This may be solved by making sure all responses are given with different fingers.

It appears that the only way to study ERP-measures during task switching is to use another task switching paradigm than the one used by Rogers and Monsell (1995). A possible way is to use a paradigm similar to the Choice/go-nogo task used in this experiment. Since the task that has to be performed would then be provided in S1, task switching would not be predictable anymore and it would not be triggered endogenously. However, aside from the ability to study ERP-measures in this design, the random order of tasks would also make it possible to look at task set inertia effects. This can be done by grouping 'switch' trials according to the number of previous 'non-switch' trials. The processes involved in switching may also be provided with more context by looking at the differences between first and second 'non-switch' trials.

The results still provide insight in the processes involved in motor preparation and what each different measure may explain. Reaction times (and errors) were strongly related to motor preparation. The CNV proved to be a good predictor of preparation in the Choice/go-nogo paradigm. The LRP was a good predictor of preparation in the Choice/go-nogo paradigm and might also be informative in the Rogers and Monsell task switching paradigm. The CNV and LRP seemed to show little responsiveness to differences in preparation in the Sequence Element Cueing task but where they do show effects these are unexpected and informative. The frequency domain measures showed little significance overall. This may have been due to a lack of power caused by a small group of subjects or by an insufficient amount of trials per condition. It may also have been that performing three tasks was very taxing for subjects, even though no effects of fatigue were found. The alternative is that the tasks were not sensitive to frequency domain measures or that these measures are inadequate for investigations into motor preparation. The latter seems unlikely given results in previous research (e.g. MacKay, 1997; Klimesch et al, 2004; Sauseng et al, 2002; Salenius & Hari 2003). Consequently, ways to improve the power of analyses and the sensitivity of tasks for frequency domain effects should be investigated. Although Gladwin et al did not find any fast/slow effects in their Rogers and Monsell setup, the use of FTE may have it’s benefits for purely motor based task switching as used in this experiment. A better selection of trials may increase the significance of the effects found in the Choice/go-nogo theta, alpha and beta band

IA and a limitation of analysis to the preparation interval may increase the sensitivity of FDR. The same procedure may prove usefull for the Sequence Element Cueing task although here it seems more likely that the dynamics of motor preparation in this task may have been too complex for these relatively simple measures to pick up. An alternative may be to calculate Phase Locking Values (PLV; Lachaux et al, 1999) between the EEG measured above areas involved in this task. PLV's express to what extent a composing frequency of an EEG-signal measured at one location of the scalp has a consistent phase difference with the same composing frequency of an EEG-signal measuerd at a different location. A currently held view is that if two regions of the brain show more than average phase locking they are somewhat connected, for example because the regions exchange information or are involved in the same process (e.g. MacKay, 1997; Klimesch et al, 2004).

The question remains what each measure contributes to our understanding of the different processes involved in motor preparation. In the Sequence Element Cueing task the RT's were related to the amount and kind of information provided to subjects in cues and they showed that some kind of preparation took place. The variety in the amount of preparation expressed in RT's could not be found in most other measures. There was little to no effect of cue type and sequence type on the amplitude of the CNV and only one combination of cue type and sequence type showed an effect on the LRP. In the beta band IA there was only a difference between time cues and other cues, but no other distinction. In the lateralized alpha and beta IA some more distinction could be made if effects were significant. This could mean that the brain has other strategies to prepare for action to use in situations more complex than a standard one-button response experiment. Further investigation of Sequence Element Cueing tasks may shed light on these processes and strategies.

On the other hand, the CNV proved to be sensitive to information processing and the LRP was sensitive to lateralized motor cortex preactivation in the Choice/go-nogo task. It might be interesting to see if there is lateralized activity in the supplementary motor areas sensitive to information processing. In conclusion, the different measures each have their specific sensitivities and benefits, but using rate- and pulse coded measures in combination provides a much richer basis for theories on preparatory motor processes than using only one kind.

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