Study of Kinematic Planning and Initiation of Hand Movement using Electroencephalography

Thesis submitted in partial fulfilment of the requirements of Five Year BS-MS Dual Degree Program at

Indian Institute of Science Education and Research, Pune

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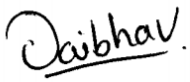
CERTIFICATE

This is to certify that this dissertation entitled "*Study of Kinematic Planning and Initiation of Hand Movement using Electroencephalography* " towards the partial fulfilment of the BS-MS dual degree programme at the Indian Institute of Science Education and Research, Pune represents study/work carried out by Vaibhav Thakur at Indian Institute of Science, Bangalore under the supervision of Prof. Aditya Murthy, Professor, Centre for Neuroscience, Indian Institute of Science, Bangalore during the academic year 2016-2017.



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DECLARATION

I hereby declare that the matter embodied in the report entitled "*Study of Kinematic Planning and Initiation of Hand Movement using Electroencephalography*" are the results of the work carried out by me at the Centre for Neuroscience, Indian Institute of Science, Bangalore, under the supervision of Prof. Aditya Murthy and the same has not been submitted elsewhere for any other degree.

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Contents

Abstract:

The current study has made an attempt to understand two important aspects of movement preparation – velocity (kinematics) planning and the temporal planning. To do so, I had designed a novel reaching movement task where subjects make a reaching movement to the target with an instructed velocity. Also, unlike the previous studies on temporal planning using EEG, the current task provided the hold time for the preparation of movement after the instructing the movement parameters. The results from the first part of the study suggest that the gamma power (30-70 Hz) is correlated to the velocity and is likely to represent in the parietal cortex. Also, a chronology of these fluctuations in gamma power indicates that the kinematic parameters are likely to encode in parietal region and then move towards the premotor and motor cortex. The second part of the study demonstrated that for the immediate movements (no hold time) the lateralized readiness potential (LRP) activity follows a LATER type accumulation model while for delayed movements this accumulation model fails to explain the variability in the reaction time. Also, the results of the present study indicate that the extra preparation time after instructing the movement parameters facilitates the response preparation stages instead of response selection processes.

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Chapter 1: Introduction

"Planning without action is futile, action without planning is fatal."

– Cornelius Fichtner

Making movements is a fundamental output of the brain that enables survival of organisms. Even though making movements might appear simple, drawing from research in robotics a number of essential computation are likely to be involved. Thus to make a simple reaching movement to a target a number of hypothesized stages are thought to occur in our brains. Even the simplest movement such as making an eye or hand movement involves many hypothesized stages of planning and execution which are shown as follows:

1) Visual Encoding of Stimuli: In this stage, the visual stimuli of the environment is processed by the retina and other vision related brain areas.
2) Target Selection: The goal of the movement is selected, instructing the brain 'where' to make the movement.
3) Kinematics Planning: Once the target is selected, the decision of the kinematic parameters such as trajectory, displacement, and speed are made. This stage determines 'how' the movement will be executed.
4) Dynamic Planning: During this stage, the movement related dynamic parameters such as force, torque at joint angles is decided.
5) Execution: Once the movement parameters are decided, the signal is sent to the muscles, and after activation of muscle to a particular threshold, a movement is generated.
6) Correction: After the initiation of the execution, the movement is continuously supervised. So that if any correction is required or the action plan is changed the brain can start to plan the corrected movement.

Thus at least three decision processes involve in carrying out a movement:

i) WHERE - This process decides the goal of the movement.

ii) HOW - How this target is going to be reached i.e. the decision about trajectory, velocity, and force.

iii) WHEN – Once the decisions about where and how are committed. The next process will be to decide when the movement is going to be initiated.

The current study makes an attempt to understand the mechanism of two out of three essential decision-making processes i.e. how movements are planned and when they are executed. The emphases will be to understand the representations underlying velocity and the temporal flow of this information across different brain areas.

1.1 Planning of Kinematics:

A fundamental question in motor systems research is to understand whether different area of the brain code for distinct aspects of movement planning such as kinematics and dynamics. The studies on neuronal recordings in awake behaving monkeys found that the firing rate of neurons in M1 area (primary motor cortex) was correlated with the force of the upcoming movement (Evarts, 1968).

Kalaska and colleagues (Kalaska et al., 1990) shown that the firing activity of neurons in the superior parietal cortex was correlated with the kinematic parameter of the movement (direction) and not the dynamic parameters (force). Other neuronal studies have also found a correlation of kinematic parameter in the parietal area (Averbeck et al., 2005). Thus current evidence suggests that kinematic parameters such as movement direction are encoded in parietal cortex while dynamic parameters are encoded in the primary motor cortex. Nevertheless, other studies have also suggested that some kinematic parameters such as direction can be encoded in the premotor cortex, a region rostral to the motor cortex. This finding is consistent with the anatomical data suggesting strong reciprocal connections between premotor and parietal cortex. The premotor cortex may be a critical junction in the conversion of kinematic to dynamic transformation. To

test this hypothesis we used electroencephalogram (EEG) electrodes placed over the motor, premotor and parietal cortices.

Studies of kinematics in the parietal cortex have thus far largely focused on representations of the target location and displacement with respect to eye/hand position to study the mechanism underlying coordinated transformations. Much less is known regarding the representation of other aspects of kinematics such as velocity and trajectory representation. One such aspect of kinematic planning that remains controversial is the representation of velocity. Interestingly there have not been many studies on this aspect. The only study of velocity representation has been observed in the premotor cortex where neurons that code for faster movements has been shown to have higher firing rates compared to the same movement made with the slower speed (Churchland et al., 2006). Very few studies have looked at the kinematic signatures in EEG data (Amengual et al., 2014; Kirsch and Hennighausen, 2010). Amengual et. al., 2014 have looked at the direct relationship between velocity and event-related potentials (ERPs). However, these studies report the kinematic parameters only during execution stages. Also, in their task, the velocity was not instructed explicitly, and the ERPs were compared at the time of peak velocity.

Also, to study kinematic representations, some studies have shown that different frequency components of the EEG such as alpha, beta, and gamma reflect signatures that have the potential to reveal neural processing mechanisms in the context of movement kinematics.

Alpha (8-12 Hz) and Beta (13-28 Hz) frequency band decrease during movement preparation and execution (Pfurtscheller and Lopes, 1999). Moreover, the Gamma (30-80 Hz) power increases during execution. Many studies have reported the correlation of the frequency band modulation with velocity (Bradberry et al., 2010; Kim et al., 2014; Lv et al., 2010; Yang et al., 2015a, 2015b; Yeom et al., 2013). However, most of them instruct the subjects to perform continuous self-paced movements (where velocity may remain similar) or discrete fast paced movements (where all the movements are fast). Such analysis might not result in the appropriate correlation as the velocity used in those

studies had a narrow range. Also, all these studies on decoding the kinematic parameters have regressed multiple frequencies to show the correlation with velocities.

In the present study, I have designed a task explicitly to explore the velocity. We instruct the subjects to move with either fast or slow velocity. Then analyze the data for these two distinct velocity profiles.

1.2 Initiation of Movements:

Most of the early work movement initiation was based on two important measures of overt responses, i.e., response accuracy and response time (Bizzi et al., 1971; Bonnet et al., 1991; Miller, 1982; Rosenbaum, 1980; Sternberg, 1969). The reaction time (RT) is defined as the time between go stimulus and the movement execution. Typically the RTs are longer than afferent visual delay and efferent motor delay; this suggests certain movement-related decision processes are happening during this time. Although reaction time can be used to determine whether experimental factor affect the behavior or not, it does not provide access to the mechanism of these decision processes. To solve this issue, many studies have tried to model the movement initiation process. One of these models is explained below.

One important property of RT is the variability. Repeatedly performing even a simple movement produces variable reaction time. One of the highly successful models used to predict these RTs is Linear Approach to Threshold with Ergodic Rate (LATER) (Carpenter, 1981; Noorani and Carpenter, 2016). The underlying assumption of the model is that there is a single linear process which accumulates a sensory evidence across time. Once this accumulation reached the threshold, the decision is made, and an overt response occurs. This model predicts the reaction time distribution based on two parameters: accumulation rate and decision threshold. The key concept of LATER model is that the trial by trial variability in the reaction time can only be explained by the accumulation rate. Neither the starting point nor the threshold can account for this variation. This model has been tested in the eye and hand movements through single unit recording (Hanes and Schall, 1996). However, it has not been tested in the EEG studies. There are potential components in the ERP signals that represent the motor planning.

Hence one of the aims of this study was to test if LATER type activity is evident in EEG components.

The typical reaction times are of the order of 500 ms, so they are very fast. Therefore to dissect the architecture of these stages we use EEG which has a high temporal resolution and then try to understand different aspects of kinematics and how the movements are initiated.

1.3 Electroencephalogram:

Electroencephalogram (EEG) is a non-invasive technique which can detect the brain activity from the scalp. Richard Caton, an English physician, discovered the electrical activity in the exposed brain of rabbits and monkeys. In 1924, Hans Berger confirmed that the electrical activity of the brain could be recorded non-invasively using a simple amplifier. He showed that the EEG produce sinusoidal oscillations in awake and relaxed subjects (Berger, 1935). Since then the EEG technique is widely used in the electrophysiological experiments. The electrical activity detected by EEG is mainly due to the bipolarity in the vertically oriented pyramidal neurons in cerebral cortex. The dendrites of a pyramidal neuron are extended upwards to more superficial layers and axons reaching the deeper levels (Lopes da Silva, 1991). The polarity of the surface electrodes depends on the polarity at dendrites of pyramidal neurons. However, the exact source of the EEG signal is not clear. Hence EEG technique has a low spatial resolution but high temporal resolution. The two widely studied EEG component are:

Event-related potential: The event-related potential (ERP) are identified as the fluctuation in voltage activity due to the external (sensory) or internal (cognitive or motor) event. The amplitude of ERP is comparatively very lower than the EEG signal. Hence ERPs may not be identified in the raw data. The ERPs were extracted by showing the stimulus multiple times and taking the average activity of time-locked signal (Gevins, 1998).

Lateralized Readiness Potentials (LRP): Before any voluntary movement a negative potential is observed over the contralateral hemisphere of motion, i.e. if the

subject is making a right-hand movement, the negativity is seen in the left hemisphere. This signal is extracted by taking the differential activity at contralateral electrode with respect to the ipsilateral electrode. The magnitude of LRP is maximum at the central and frontocentral electrode as these electrodes lie on the motor cortex (M1) and somatosensory cortex. Hence the LRP can be considered as the online measure of response-related activity or motor preparation (Coles, 1989).

The LRP analysis is done using two measures 1) Stimulus-locked LRP (S-LRP) and 2) Response-locked LRP (LRP-R). It has been reported that the LRP onset occurs after the completion of hand selection and beginning of motor planning (Masaki et al., 2004). Hence the duration between go cue and the S-LRP onset represents the perceptual processing and the response selection. While the duration between LRP onset and the start of response is considered to represent the motor programming stages like the specification of movement direction, velocity, and force (Schröter and Leuthold, 2009). Thus, if the experimental conditions affect the S-LRP, we can conclude that these factors influence the pre-motoric processes. On the contrary, if the experimental conditions affect the LRP-R then the factors may affect the motoric processes.

Reaction time and LRP:

Both LRP and reaction time represents the motor preparation where former is a covert activity and later is the overt response. Hence many studies have examined the effect of reaction time on the lateralized readiness potential (Gratton et al., 1988; Hackley and Miller, 1995; Masaki et al., 2004; Miller and Hackley, 1992; Müller-Gethmann et al., 2003). The study by Gratton (1988) suggests that the LRP peak at the time of EMG onset remained constant for different reaction time supporting the “variable-baseline/fixed-criteria” hypothesis. Other studies (Hackley and Miller, 1995; Mordkoff and Grosjean, 2001; Smulders et al., 1995) have reported that the onset of stimulus-locked LRP (S-LRP) differs for distinct reaction times. These studies then suggest that the variability in reaction time is due to the response selection stage rather than motor programming/ response preparation stage. On the contrary, one study (Müller-Gethmann et al., 2000) have reported that the advance information influences the LRP dependent on the information. When the movement direction was informed in advance the effect was seen on S-LRP

and LRP-R, but when information about movement force is provided, they saw differences only on S-LRP.

In conclusion, most of these studies suggest that the reaction time effect is seen only in the response selection process, but the study by Gethmann indicate that different the advance information about movement may have a different effect on LRP. Hence I wanted to see in the case of advance velocity information how the LRPs are changing and can these reaction times be predicted from the LRPs.

Hold time effect

The reaction time tasks are designed in such a way that it reveals the mechanism of the preparation. One of such manipulation is the foreperiod/hold time. In these tasks, the subjects are warned about the upcoming movement beforehand thus giving the subjects extra time to prepare for the movement. Such task also shows that the reaction time is strongly affected by the variation in hold time. The reaction time decreases for constant hold time but with unpredictable hold time, the reaction time increases (Drazin, 1961; Hohle, 1965; Karlin, 1959) because of temporal uncertainty.

The theoretical studies on reaction time (Hohle, 1965; Sanders, 1998; Teichner, 1954) proposed that the preparation happening during hold time affect the motor-related processes. A study by Sanders (Sanders, 1998) where he manipulates instruction about muscle tension and hold time. He reported that foreperiod/hold time manipulated RT stronger with muscle tension. He suggested that the manipulation of muscle tension is a late motor programming stage which was showing interaction with the hold time. The Additive-Factor Method, AFM, (Sternberg, 1969) claims that if the experimental factors affect at least a single common stage, the factors should show the interaction. According to this theory, the hold time is influencing the same processing stage as the muscle tension, i.e., motor preparation stage. Hence Sanders concludes that the hold time effect is part of motor programming. The corollary, many studies have shown that the factors related to response selection stages do not alter the effect of hold time (Frowein and Sanders, 1978; Posner et al., 1973). Also, factors affecting motor stages alters the effect of hold time (Spijkers, 1990).

The contrary view in the literature suggests that the hold time duration influences the response selection stages. These studies reported that there is a larger effect of hold time on RT in incompatible and weak visual stimulus than compatible and strong visual stimulus condition (Broadbent and Gregory, 1965; Müller-Gethmann et al., 2003; Niemi and Lehtonen, 1982). However, the hold time did not affect the duration of EMG onset and overt response (Botwinick and Thompson, 1966).

It is known that the hold time modulates the reaction time, but there is a conflict in the literature about the mechanism behind this effects. In this study, I tried to address this question on how the hold time plays a role in modulating reaction time.

Chapter 2: Methods

2.1 Participants:

Fourteen healthy human volunteers were recruited in this study. All the participants were a right-handed male with age ranging from 20 to 29 years. The right-handedness was measured using Edinburgh Handedness Inventory (Oldfield, 1971). None of the participants had any psychiatric or neurological problems, and had normal or corrected to normal vision. Subjects gave written informed consent as per guidelines of the Humans Ethics Committee of Indian Institute of Science, Bangalore that approved the protocol. The proper instructions and the purpose of the study were explained to the subjects beforehand. Subjects were monetarily rewarded for every correct trial to keep them motivated and also compensated for their time.

2.2 Experimental Setup:

For this experiment, visual stimuli were shown using TEMPO/VIDEOSYNC software (Reflective Computing, St, Louis, MO). Simultaneously, a BLACKROCK microsystem was used to collect all EEG/EMG data at a temporal resolution of 1 ms. Eye-movements were monitored with a sampling rate of 240 Hz using a pupil tracker (ISCAN, Boston, MA). The hand movement was tracked using an electromagnetic tracker (LIBERTY; Polhemus, Colchester, VT), which measured the movement of the index finger at a sampling rate of 240 Hz. All the systems were interfaced with TEMPO (reflective Computing, USA which collected data in real time with a sampling frequency of 961 Hz. Experiments were performed in a custom-made wooden frame which housed monitor (SONY SGI, 21-in., 60 Hz refresh rate) overhead, which displayed visual stimuli. A partial reflecting mirror was placed below the screen so that subjects could see the visual cues and make a reaching movement on a transparent acrylic surface placed below the mirror. A battery-powered LED bulb was strapped to the subject's index finger to provide visual feedback. The subject's head movement was restrained using a chin rest, and two temple bars; head movements were captured using a head-mounted camera. This whole setup

was grounded using a copper mesh wrapped around a wooden frame. Such a virtual reality setup was used to minimize any electrical disturbance from the monitor. All the recordings were performed in a darkened room.

2.3 Behavioral Task:

Subjects performed a simple reaching task where they had to move their hand from the central fixation spot to the target spot as per the instruction provided. The task paradigm is shown in figure 1. Each trial was 7000 ms long. The initiation of each trial was indicated by a brief flicker in the fixation box. First, the subject was presented with a gray colored fixation spot where they had to fixate their eyes and index finger of the dominant hand. After 530 ms, fixation box changed its color from gray to green or red with equal probability. After an instruction time of 780 ms, the target appears on the screen, 12 cm apart from the fixation point. The target was randomized between top left and bottom right positions with equal probability. The go cue was given to the subject by changing the fixation box from filled to unfilled. The subjects had to make a reaching movement to the target as soon as the go cue was presented. A maximum delay of 1000 ms was allowed to initiate the movement. If subject exceeded this delay, the trial was aborted. The duration between target appearance and go cue was defined as the hold time and kept at either 0 ms or 1000 ms. If the color of the fixation box during the instruction time was red, subjects had to make a slow hand movement; if the color was green, subjects had to make a faster hand movement. Hand and eye movements were tracked throughout the trial. If the movement duration was below 200 ms for fast trials and in between 500 ms to 1000 ms for slow trials, the trial was considered to be correct; else the trial was aborted. Throughout the task, the subjects had to keep the eyes on the fixation box and were instructed to blink, if necessary, after the hand reached the target and before the new trial started. If these conditions were not fulfilled, the trial was aborted. At the end of each correct trial, a sound beep was given to indicate a correct trial. Minimum of 450 trials were recorded from each subject with a break of 2 minutes after 250 correct trials. All the subjects were given a training set of 200 trials to get familiar with the velocity criteria, and the main recording was performed within next three days.

Control Task: The experiment for the control study was the same; however, the instruction to the subjects was different. Here, subjects were told to make self-paced movements irrespective of the color of fixation box during instruction time, and the limitation on movement duration was removed because movement duration was used as the proxy for velocity. The control experiment was carried out to compare the results from velocity task to the normal movement task.

2.4 Electrophysiological Data Acquisition:

Electroencephalographic (EEG) activity was recorded passively continuously from 22 Ag/AgCl electrodes mounted on the head of the subjects with the help of an elastic cap (32 electrode cap) provided by *EasyCap* company (Germany). The electrode's positions were determined by international 10/20 system and already marked on the cap. EEG signals were sampled at 1000 Hz and low-pass filtered by 250 Hz. Impedance was kept below 5kΩ for all electrodes at the start of the recording for all subjects and was also measured at the end of the experiment for few subjects. The fluctuation in impedance before and after the experiment was within limits of 1 - 1.5 kΩ.

Electrode placement:

For this study, we recorded the EEG data from 21 passive electrodes. The electrode positions were selected based on the area of interest to the study. These positions include FP1/FP2, F3/F4, FC1/FC2, C3/C4, CP1/CP2, P3/P4, O1/O2, FC5/FC6, Fz, FCz, Cz, Pz, and Iz. The electrode position AFz was used as the ground for all these recordings and reference average activity of linked left mastoid (LM), and right mastoid (RM) was used. No offline re-referencing was performed.

Data Analysis:

All the offline analysis and statistical tests were performed using MATLAB (MathWorks, Natick, MA). The additional library Chronux 2.12 toolbox, provided by http://chronux.org as an open source, was used for time-frequency analysis.

Data Pre-processing:

All the collected data was parsed into multiple trials. The EEG data was then low-pass filtered till 70 Hz using a Butterworth fourth-order filter. Further, the line noise of 50 Hz was removed from each trial by using a second-order notch filter. Trials with reaction time less than 80 ms or more than 700 ms were removed from the analysis as anticipated trials and delayed trials, respectively. All the trials with an eye blink were also removed from the final analysis. Trials containing eye blinks or eye movements in any part of the trial were removed from the final analysis. Trials with EEG activity fluctuation more than 70µV were removed from the analysis in the account for the artifact. For the remaining trials, DC shift correction was performed by subtracting the mean activity of the whole trial from the respective trial. The baseline activity was corrected similarly by subtracting the mean of activity during fixation time from the corresponding trial (Gratton et al., 1988).

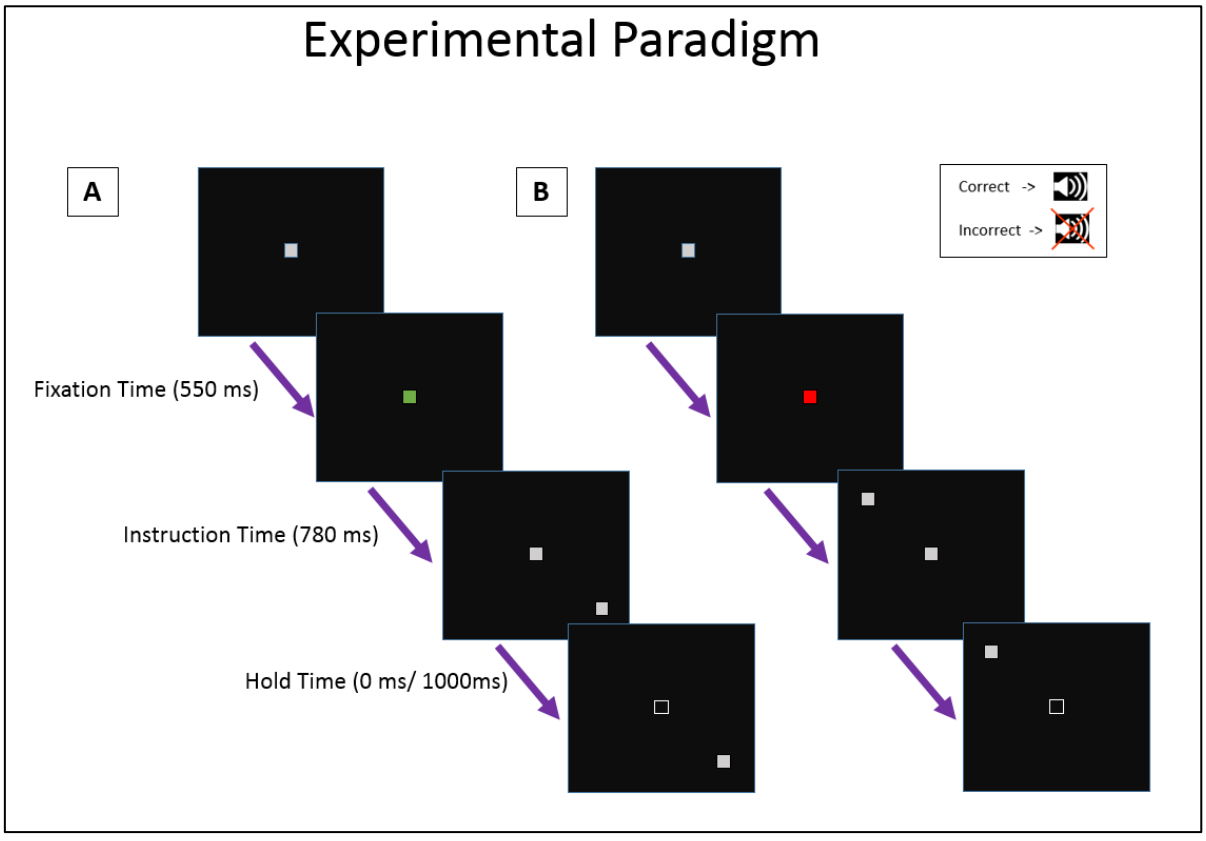

Figure 1: Experimental paradigm – The experimental paradigm for A) fast velocity and B) slow velocity is shown above figure. A fixation period of 550 ms is indicated by grey fixation box. Then the indication about velocity is represented by color of fixation box. This instruction stays for 780 ms on screen. After instruction time a target appears on the screen and depending on hold time (0 ms or 1000 ms) a go cue is given which is indicated by empty fixation box.

2.5 Reaction Time and Movement Time:

The reaction time is defined as the duration between go cue and hand movement beginning. Hence the calculation of hand movement beginning becomes an important parameter. The hand movement beginning was calculated as following. First, the time stamp, when the velocity reached 10% of maximum velocity for that trial, was extracted and used as a marker from which to estimate the time point when the velocity was not significantly different from the baseline fluctuation. This time point was considered as the beginning of hand movement. The movement time was defined as the duration between hand movements begin and time when a hand reaches the target.

2.6 LRP Analysis:

The lateralized potential for a given location was calculated as the differential EEG activity on the contralateral electrode compared to its counterpart on the ipsilateral side. Lateralized Readiness Potential (LRP) is a special case of lateralized activity over motor cortex and aligned on the movement onset.

A trial was low-pass filtered (4 Hz and below) using a Butterworth fourth order filter to calculate the LRP (Van Vugt et al., 2014). Since in this experiment, the task required movement of only one hand (dominant), LRPs are calculated only for the dominant hand, and hence the formula used in this analysis was as follows,

$$LRP = (C3 - C4)_{\text{dominant hand}}$$

A similar analysis was used to calculate the lateralized potential of other pairs of electrode channels (e.g., F3/F4, FC1/FC2, CP1/CP2, P3/P4). Grand averages were calculated by averaging individual data for a specific condition and then averaging across subjects.

The LRP analysis was done on the stimulus-locked waveform called S-LRP and the response-locked waveform called LRP-R. LRP peaks were computed as the maximum negative activity during ± 500 ms of hand onset. If the second highest peak comes before the time of highest peak and has an amplitude greater than 60% of the maximum peak, then the second peak is considered as the peak of LRP. The beginning

of LRP during reaction time was computed by calculating the time when the LRP signal was 30% of its peak activity (Miller et al., 1998) and using that time to estimate the first point where the slope of LRP was less than -0.005 μV/ms. The rationale behind this approach was to ensure that the estimated onset to be insensitive to the baseline level which could vary across conditions. Hence we used the fixed instantaneous slope criteria as an LRP. LRP slopes were calculated using the best linear fit between LRP onset and LRP offset.

2.7 Power Analysis:

All the power analysis was done using the Chronux toolbox (Bokil et al., 2010). Spectrograms were constructed using the *mtspecgramc* function in Chronux using a multi-taper algorithm. [Thompson, 1982]. A moving window of 500 ms and a step size of 25 ms was used for the analysis. These values are chosen depending on the signal length and to maximize time-frequency resolution.

The event-related spectral power was computed for alpha (8 Hz - 12 Hz), lower beta (12 Hz - 22 Hz), upper beta (22 Hz – 30 Hz) and gamma (30-70 Hz) bands. These powers were normalized with respect to average baseline powers for each subject (k) at each time point (t) of the signal and averaged across all the subjects (Tzagarakis et al., 2010). The relative powers were calculated using the following method:

$$P_{t,k}(dB) = 10 \log_{10} \frac{P_{t,k}}{B_k} \qquad k \in \{\alpha, \text{lower } \beta, \text{upper } \beta, \gamma\}$$

2.8 Jackknife Resampling:

Most statistical test demands for the distributional assumptions of sample and population. These assumptions may not meet when the sample size is small, or the sample distribution is not normal. In these situations, resampling methods may be used. Resampling is the method of drawing repeated samples from the original. This method ignores the distributional assumptions. Hence it is a non-parametric method of statistical inference. There are many ways by which resampled data can be obtained such as bootstrapping method, jackknife method, and Monte-Carlo simulation.

The classical method for calculating the standard error may not work in the EEG studies as individual subjects LRP contain more noise than the grand averaged data. Common criteria cannot be applied for calculation of the parameters as some subjects may not satisfy them. The jackknife method of resampling is widely used in the LRP studies (Jentzsch et al., 2007; Miller et al., 1998; Ulrich and Miller, 2001; Xu et al., 2015). In the Jackknife resampling method EEG data is first resampled using jackknife resampling, i.e., the i^{th} sample is computed by taking grand averages of all subjects except the i^{th} subject. Hence we get the resampled data for all the subjects. Further, the standard error of this sample is calculated by following formula

$$S_d = \sqrt{\frac{(N-1)\sum_{i=1}^{N}(D_{-i} - \bar{J})}{N}}$$

Where N is the number of samples, D_{-i} is the parameter value taken average for all subjects except i^{th}, J is the parameter value calculated from the grand average.
Once the standard error is calculated, the statistical test is performed using this jackknife error estimation. For example, t-value in t-test is calculated as,

$$t_J = \frac{D}{S_d}$$

Alternatively, similar analysis can be done be passing the resampled parameters for all subjects to the t-test or ANOVA and changing the t-values by dividing it by (N – 1) or F-values by dividing it by $(N-1)^2$. Unlike the general method of standard error, this method compares the variation in parameter across a subset of the total sample. In the present study, the statistical tests involving jackknife-resampling is mentioned by F_c. Otherwise, the normal statistical tests are used.

Chapter 3: Results

Through this experiment, I endeavor to study two important movement related parameters. In the first part, I attempt to elucidate the neural correlates of a kinematics representation (specifically velocity) in the event-related potentials (ERP) during the preparation time i.e. the time before the movement onset. The second part of my thesis concerns an ERP analysis of reaction times to determine whether response time can be predicted from the ERP signals and its relation to established computational models of RT. For this analysis, the electrodes of interest were F3/F4, FC1/FC2, C3/C4, CP1/CP2, P3/P4 and Fz, FCz, Cz, CPz, and Pz. These electrodes span the frontal, frontocentral, central, centroparietal, and parietal regions involved in different aspect of movement planning.

3.1 Neural Correlates of Velocity:

First, the movement duration was computed to see that the subjects were performing the task correctly i.e. for the fast velocity trials the movement duration should be short and for slow velocity trials the movement duration must be long. Each session is divided into four trial conditions the fast velocity with 0 ms hold time (Fast-0), the slow velocity with 0 ms hold time (Slow-0), the fast velocity with 1000 ms hold time (Fast-1), and slow velocity for 1000 ms hold time (Slow-1). The movement durations for four trial conditions Fast-0, Slow-0, Fast-1, Slow-1 were 121 ± 6 ms, 685 ± 122 ms, 127 ± 6 ms and 700 ± 15 ms, respectively (Figure 2A). A 2-way ANOVA revealed that movement durations fast velocity trials were significantly shorter than slow velocity trials, $F(1, 36) = 3036.38$, $p < 0.001$. Hence I confirmed that the fast and slow velocity trials were performed correctly by subjects.

Second, I checked whether the reaction time (RT) was modulated across four trial conditions. The reaction time (averaged across all subjects) for trial conditions Fast-0, Slow-0, Fast-1, and Slow-1 were 386 ± 11, 447 ± 15, 272 ± 13 and 309 ± 19 ms,

respectively (Figure 2B). The reaction time for fast velocity was faster than slow velocity trials, $F(1, 36) = 11.09$, $p = 0.002$. However, within group analysis revealed that no significant correlations between velocity and RT ($r_{Fast} = -0.334$, $p_{Fast} = 0.143$; $r_{Slow} = -0.242$, $p_{Slow} = 0.303$). Thus, for subsequent across group ERP analysis, I normalized the RT differences, but for within-group analysis, normalization was not required as analysis failed to reveal any correlation between kinematics and RTs within a group.

Consistent with a large body of literature, I also replicated the hold time effect, which predicts the greater extent of preparatory activity i.e. longer hold time, therefore, faster RTs. Thus, the reaction time for trials with no hold time had slower RTs than trials with 1000 ms hold time, $F(1, 36) = 70.09$, $p < 0.001$ (Figure 2B). However there was no interaction between velocity and hold time conditions, $F(1, 36) = 0.67$, $p = 0.4184$. The additive factor method (AFM) by Sternberg (Sternberg, 1969), suggest that if the two experimental conditions affect at least single common processing stage, the interaction between these two factors should be seen. According to this model, the hold time and velocity may not be affecting the common stages in the process of response preparation.

Next part of the analysis involved the inspection of velocity signature in EEG signals. For this analysis, the timeline of each trial was divided into instruction time (when the velocity instruction was given), hold time (when the target position was shown) and reaction time. The analysis was carried out on the grand average.

a) Time Domain:

Very few studies have reported the velocity representation in ERP. Hence I wanted to see if there is an explicit ERP signature in the LRP. The analysis was done on single channel's activity as well as lateralized activity.

The velocity information was given at the start of instruction time. Hence one would expect to see the velocity related preparation during instruction time. However, the differences in fast and slow velocity were not found in any channel activity and lateralized activity. The corresponding statistics was performed on the average activity during 150-350 ms of fast and slow velocity trials and is shown in Table 1. Similarly, no significant difference was observed during hold time for fast and slow trials. To quantify this, the

average activity during hold time for fast and slow velocity was considered. The statistics confirmed that there was no effect of velocity during hold time (Table 1).

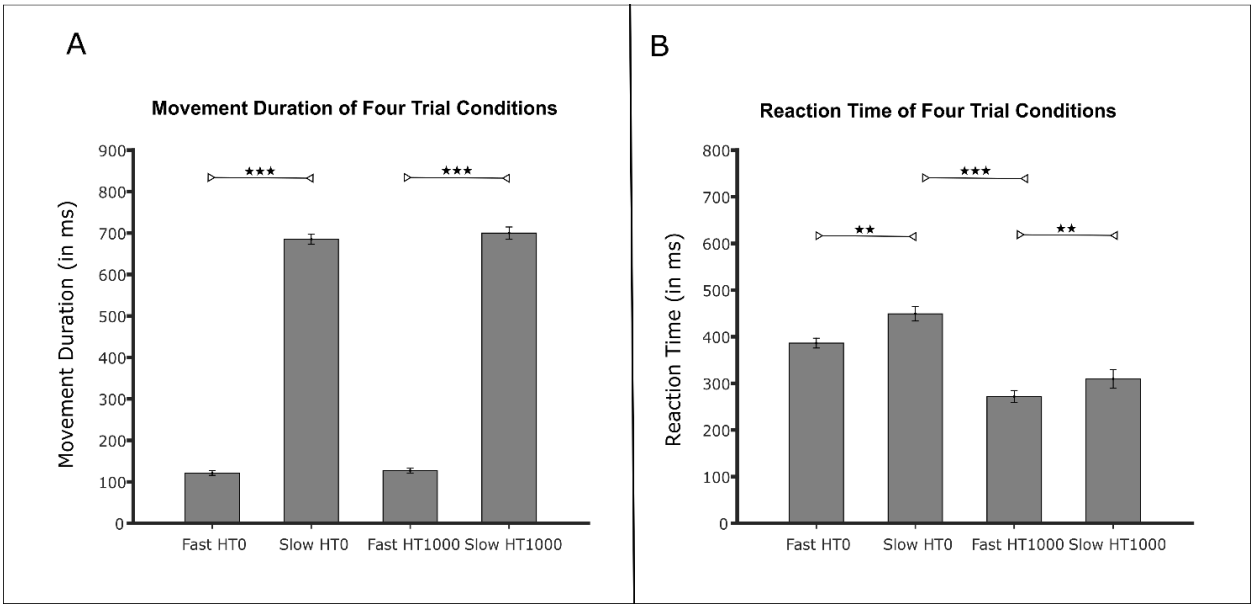

Figure 2: Behavioral Results - Behavioral results of A) movement duration and B) reaction time for fast velocity with 0 ms hold time, slow velocity with 0 ms hold time, fast velocity with 1000 ms hold time, slow velocity with 1000 ms hold time conditions. The timings are shown for the average across all subjects with

The velocity effect was not observed in the single channel activity hence I further analyzed whether the lateralized readiness potentials (LRP) shows the velocity preparation during reaction time. As mentioned in the introduction, the response selection processes occur before the LRP onset, and the motor programing stage is represented after LRP onset. Hence, the LRPs were examined with two alignments i.e. go stimulus-locked LRP (S-LRP) and response-locked LRP (LRP-R). The LRPs were quantified by LRP onset, LRP peak and the slope of LRP from onset to peak. The N-way ANOVA on these S-LRP parameters revealed that LRP onset, LRP peaks, and LRP slopes were not significantly different for fast and slow velocity conditions, onset: $F_c(1, 30) = 0.966$, $p = 0.334$; peak: $F_c(1, 30) = 0.08$, $p = 0.780$); slope: $F_c(1, 30) = 0.41$, $p = 0.527$). The corresponding result is shown in figure 3A. This result suggests that the velocity does not modulate the S-LRP (which is used as a proxy for response selection process). The next step was to look at the velocity effect on LRP-R. The LRP-R was quantified by four factors

LRP onset, LRP peak, the slope^P from LRP onset to peak, and slope^R from LRP onset to response onset. The N-way ANOVA on the means showed no main effect of velocity on any of the five factors, onset: $F_c(1, 30) = 0.6258$, $p = 0.435$; peak: $F_c(1, 30) = 0.044$, $p = 0.835$; slope^P: $F_c(1, 30) = 0.238$, $p = 0.629$; slope^R: $F_c(1, 30) = 0.348$, $p = 0.560$. Hence we conclude from this part of analysis that there were no velocity signatures in the time domain (ERP and LRP components) of EEG signal.

b) Frequency Domain:

The velocity did not correlate with a time domain signal hence the next question was to see whether velocity is encoded in the frequency domain. I did the time-frequency analysis on the lateralized potentials at F3/F4, FC1/FC2, C3/C4, CP1/CP2, and P3/P4 electrode locations because the lateralized potential is known to represent motor preparation. For this analysis, the frequencies were divided into four bands, i.e., the alpha band (8-12 Hz), the lower beta band (12-22 Hz), the upper beta band (22-30 Hz), and gamma band (30-70 Hz). The time-frequency spectrograms are shown in figure 4. From the figures, we can see that the relative power of alpha and beta band decreases during movement planning and movement execution. These trend in power is consistent with the previous literature (Pfurtscheller and Lopes, 1999). Although these band power are thought to be related to movement planning and execution, I did not see any effect of velocity on these powers (table 2).

The study by Aoki et. al., showed the correlation of gamma band power and target selection (kinematics) in the memory-guided task (Aoki et al., 1999). These study motivated me to investigate if the gamma band power was correlated with another kinematic parameter - velocity. The power of gamma band (in the parietal area) as a function of movement-locked time is shown in figure 5. The figure indicates that the gamma power for fast velocity and slow velocity diverge before movement. The quantification of this was done as follows: The maximum number of bins (step size 25 ms) before movement onset are calculated for which the average gamma band power for was significantly different for fast and slow velocity. The similar analysis was done for other lateralized channels (figure 6). The time point (with respect to movement onset) for

which the mean power difference was significant for lateralized channels FC, C, CP, and P were are -99 ms, 76 ms, -74 ms, -99 ms respectively. The corresponding statistics for FC, C, CP, and P are as follows in the same order, $F(1, 37) = 4.69$, $p = 0.0369$; $F(1, 37) = 4.33$, $p = 0.044$; $F(1, 37) = 2.198$, $p = 0.0405$; $F(1, 37) = 4.08$, $p = 0.0508$; $F(1, 37) = 4.33$, $p = 0.0444$.

This result indicates that velocity differences were observed in the gamma band. Moreover, these differences occur earlier in parietal and fronto-parietal electrodes than central electrodes (motor cortex).

In conclusion, we found that there was no association between ERP and velocity in the time domain. In the frequency domain, unlike the control subjects, the gamma band power showed differences for different velocities, and this difference was temporally earlier in parietal and fronto-central electrodes. These differences remained during the execution phase as well.

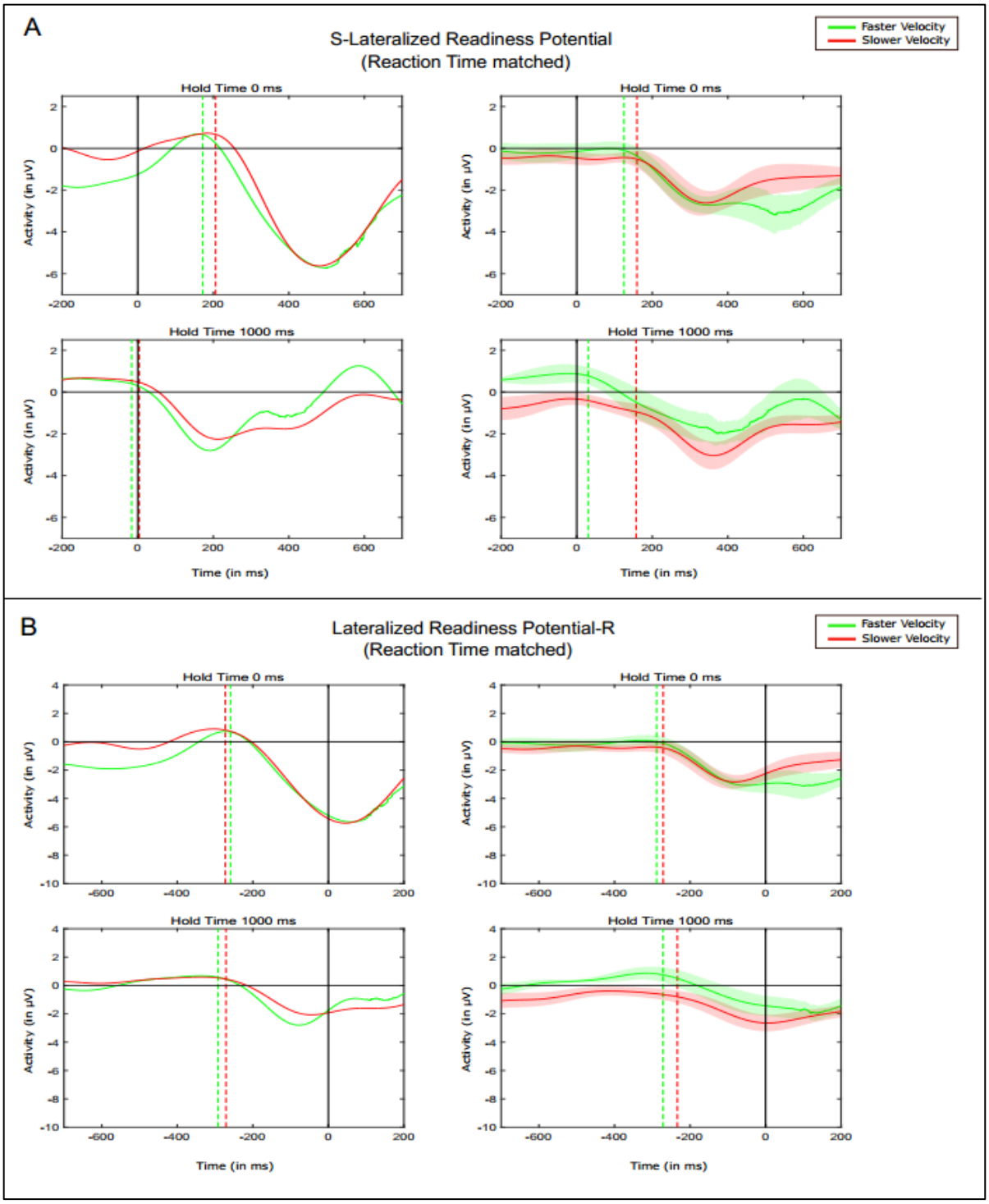

Figure 3: Effect of Velocity on lateralized readiness potentials - Lateralized readiness potential for reaction time matched trials with 0 ms hold time, and 1000 ms hold time. A) Stimulus-locked LRP and B) Response-locked LRP where left panel shows representative subjects data and right panel shows grand averaged data across all subjects. The verticle dashed line shows the late LRP onset for fast velocity (green) and slow velocity (red).

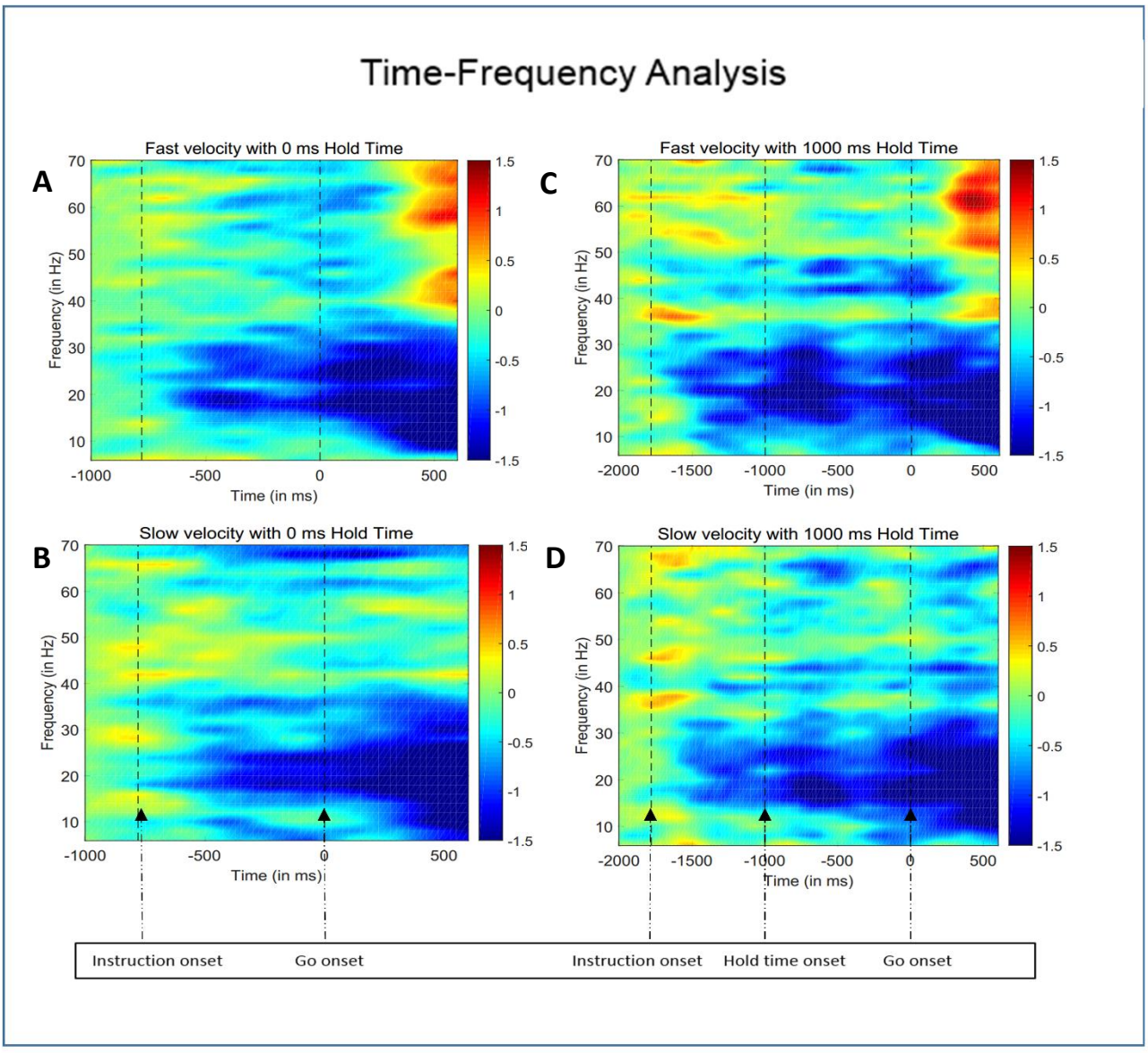

Figure 4: The power spectrogram for four different trial conditions – The overall frequency analysis for four different trial conditions – A) Fast velocity with 0 ms hold time B) Slow velocity with 0 ms hold time, C) Fast velocity with 1000 ms hold time, and D) Slow velocity with 1000 ms hold time. The vertical dashed lines indicate the timings of stimulus given to subjects.

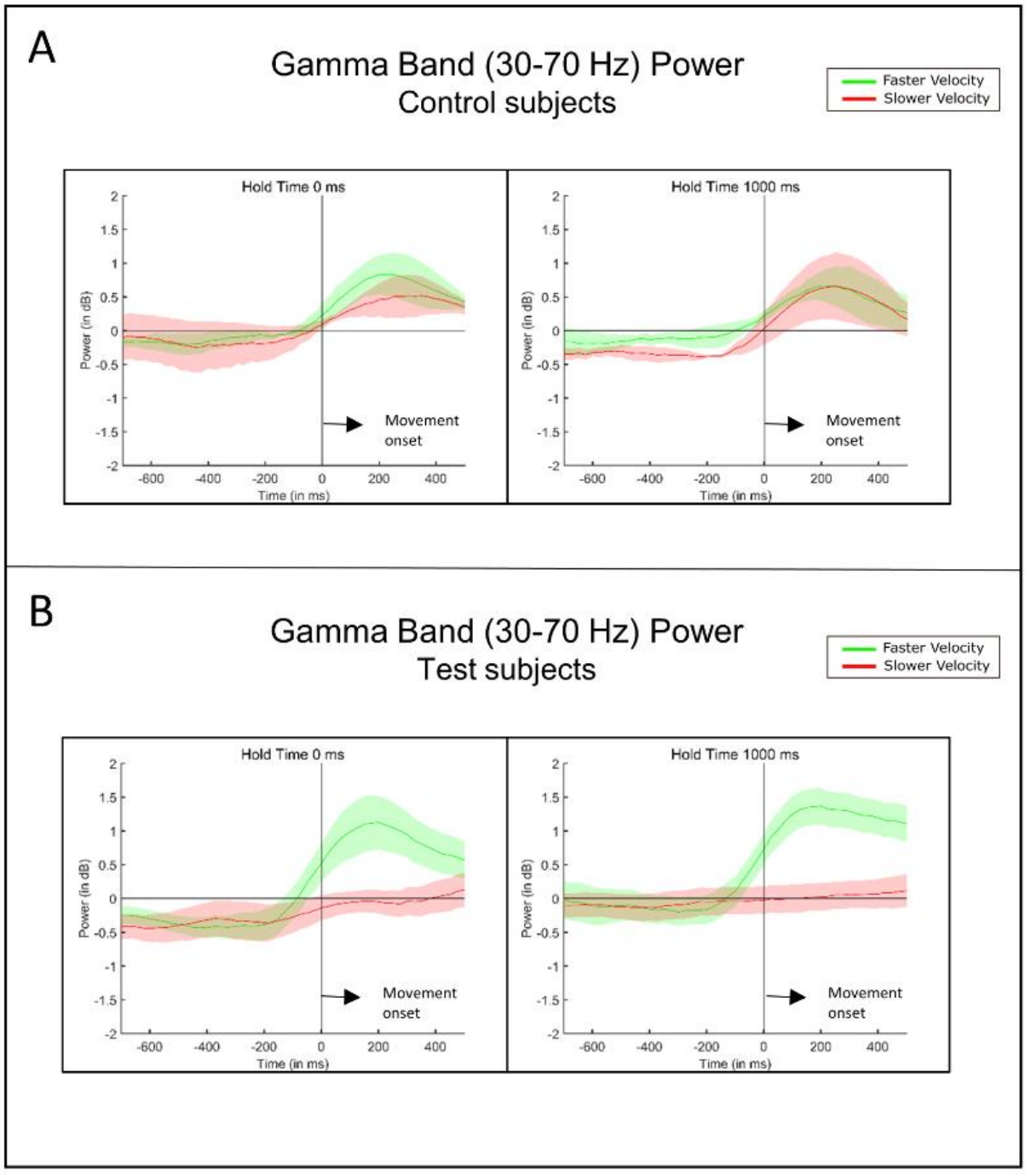

Figure 5: Variation in the relative power of gamma band – The figure shows the modulation in gamma power around movement onset in parietal area (P3/P4). The signal is grand averaged and aligned on movement onset. A) Gamma power variation in control subjects and B) test subjects. The green trace represents faster velocity trials and red trace represents slower velocity trials.

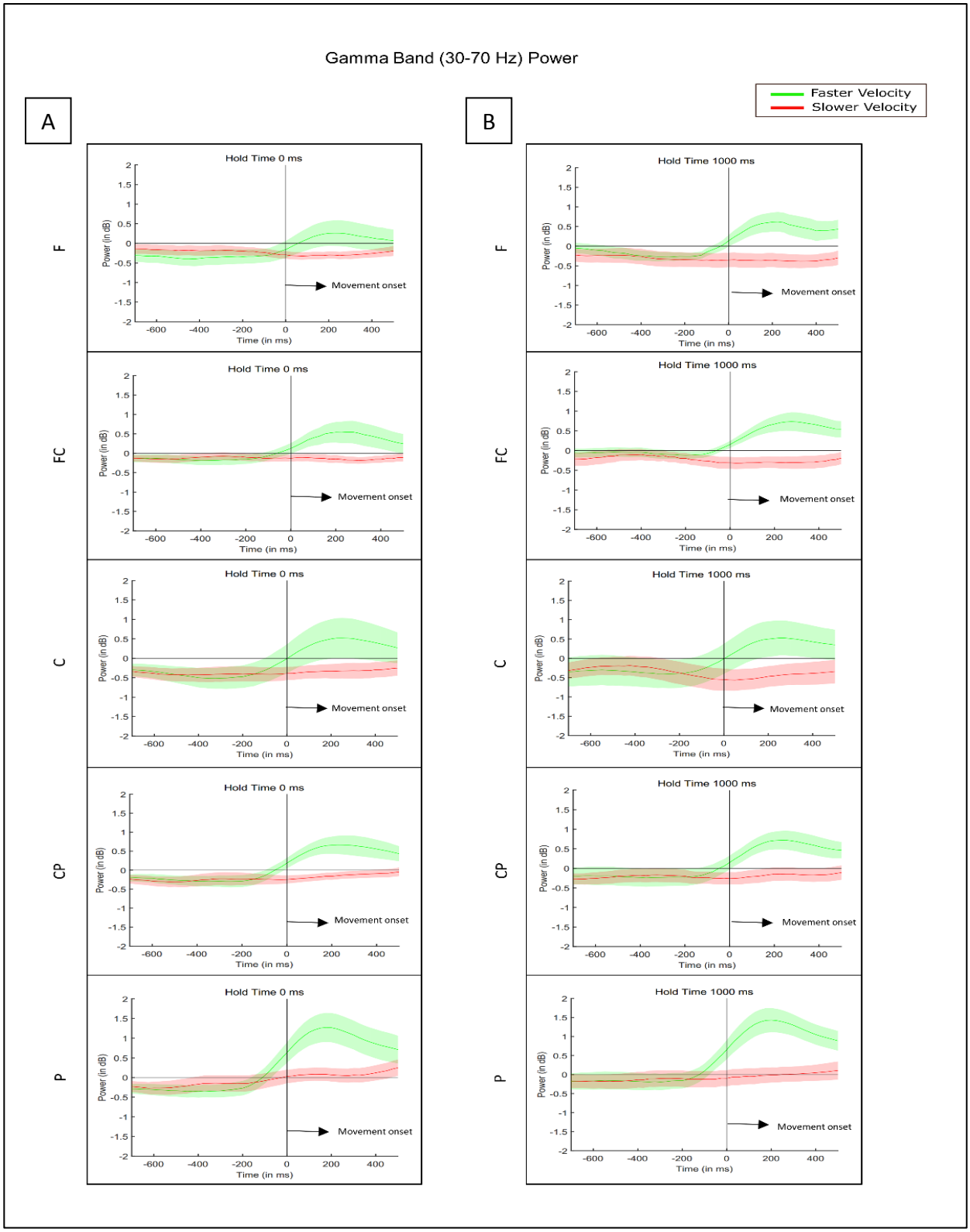

Figure 6: The chronology of velocity representation in gamma band- The gamma power variation for fast (green) and slow (red) velocities. (A) The left panel represents trials with no hold time, and (B) right panel represents trials with 1000 ms hold time. The plots are shown for five electrode positions (F, FC, C, CP, and P) where green color indicates for fast velocity trial and red color for slow velocity trials

Table 1: Comparison of velocity differences on mean of ERPs – The statistics for velocity during instruction time and hold time for single and lateralized channels.

Interval	Instruction Time (150 ms – 350 ms)		Hold Time	
Criteria	Velocity		Velocity	
	F (1,18)	p	F (1,18)	p
F3	0.022	0.884	1.270	0.275
F4	0.009	0.924	1.903	0.185
FC1	0.290	0.597	0.385	0.543
FC2	0.139	0.713	0.640	0.434
C3	0.026	0.873	0.642	0.433
C4	0.001	0.971	2.173	0.158
CP1	0.001	0.970	0.001	0.982
CP2	0.016	0.900	2.138	0.161
P3	0.153	0.700	1.955	0.179
P4	0.027	0.871	3.556	0.076
Lateralized F	0.713	0.410	0.939	0.353
Lateralized FC	0.749	0.399	0.259	0.621
Lateralized C	0.041	0.842	0.944	0.352
Lateralized CP	0.019	0.893	0.068	0.798
Lateralized P	0.006	0.940	0.039	0.847

Table 2: Comparison of velocity differences on mean of frequency powers – The statistics for fast and slow velocities in movement preparation time for alpha, beta, and gamma frequencies

Interval	Instruction Time					
Frequency	Alpha (8-12 Hz)		Lower Beta (12-22 Hz)		Higher Beta (12-22 Hz)	
Criteria	Velocity		Velocity		Velocity	
	F (1,36)	p	F (1,36)	p	F (1,36)	p
Lateralized F	0.004	0.953	0.045	0.833	0.252	0.619
Lateralized FC	0.018	0.895	0.279	0.601	0.336	0.566
Lateralized C	0.130	0.720	0.393	0.535	0.302	0.586
Lateralized CP	0.000	0.996	0.003	0.954	0.008	0.929
Lateralized P	0.013	0.909	0.033	0.857	0.028	0.867

Interval	During Reaction Time					
Frequency	Alpha (8-12 Hz)		Lower Beta (12-22 Hz)		Higher Beta (12-22 Hz)	
Criteria	Velocity		Velocity		Velocity	
	F (1,36)	p	F (1,36)	p	F (1,36)	p
Lateralized F	0.101	0.753	0.194	0.663	0.642	0.428
Lateralized FC	0.541	0.467	0.088	0.768	0.042	0.839
Lateralized C	0.043	0.836	0.006	0.941	0.001	0.979
Lateralized CP	0.209	0.650	0.207	0.652	0.332	0.568
Lateralized P	0.166	0.686	0.222	0.640	0.214	0.647

3.2 Neural Correlates of Temporal Planning:

This part of the thesis concern about the reaction time effect. Two main questions that were addressed in this section: i) could the reaction times be predicted by the ERPs and LRPs, particularly in the context of established computational models of reaction time? ii) How different experimental conditions affect the movement preparation stages during reaction time? To address these two questions, each experimental condition Fast-0, Slow-0, Fast-1, and Slow-1 was bisected into faster reaction time (0-35 percentile of RT distribution) and slower reaction time (65-100 percentile of RT distribution). The statistical analysis (N-way ANOVA) was performed on these RT across four experimental conditions.

a) Reaction Time Effect:

First, I checked whether ERPs of faster and slower RT showed reaction time effect on single channel activity. Qualitatively no difference was observed in any channel. To quantify this the mean of ERPs during reaction time were compared for faster and slower RTs. The corresponding statistical analysis is shown in Table 3.

As explained in the introduction, findings from most studies suggest that the reaction time affects the S-LRP interval (response selection stage) in the motor preparation. However, the task used in these studies was very different from current study as in current study the hold time was given after the task-relevant parameters were presented. Hence I sought to find how does reaction time modulates the LRPs in this task. The LRP analysis was divided into two parts i.e. go stimulus-locked LRP (S-LRP) and response-locked LRPs (LRP-R).

To see whether reaction time affects response selection stages as proposed by previous studies, the LRPs were aligned on the stimulus onset (S-LRP) (Figure 7). These S-LRPs were quantified by four factors namely, LRP onset (duration from go stimulus), LRP peaks, LRP peak times and slope of LRP from onset to peak time.

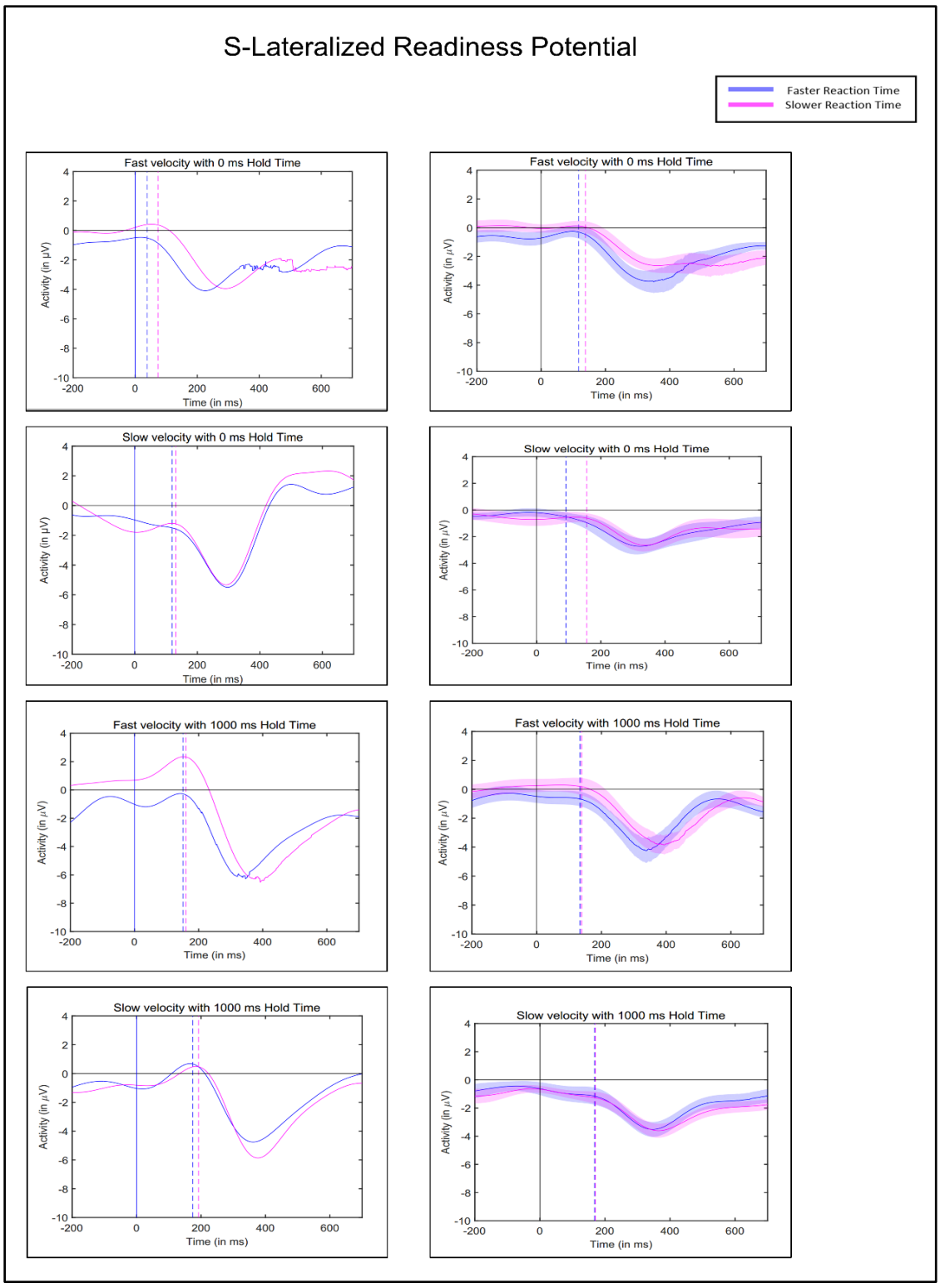

Figure 7: The Effect of reaction time on S-LRP - Stimulus-locked Lateralized readiness potential for four trial conditions. The left panel shows data for representative subject and right panel shows grand averaged data. The verticle dashed line shows the late LRP onset for faster reaction time (blue) and slower reaction time (magenta).

The statistical analysis revealed that these factors did not differ for faster and slower RTs, onset: $F_c(1, 71) = 0.665$, $p = 0.418$; peak: $F_c(1, 71) = 0.578$, $p = 0.45$; peak time: $F_c(1, 71) = 0.471$, $p = 0.495$; slope: $F_c(1, 71) = 0.28$, $p = 0.598$. This result was in contrary to most studies as the S-LRP did not differ for different reaction time.

Reaction time effect was not reflected in S-LRP. Hence I analyzed the LRP-R (Figure 8). The LRP-R was quantified using five features namely, i.e. LRP onset (duration from response initiation), LRP peaks, slope^P (from onset to peak time), LRP threshold (activity at response initiation) and slope^R (from onset to response initiation). The statistics on this factor indicated that onset latency for faster reaction time was shorter than slower reaction time $F_c(1, 71) = 22.501$, $p < 0.001$ (refer Table 4). The LRP slope^P qualitatively looked different but did not reach the significance level, $F_c(1, 71) = 2.487$, $p = 0.112$ The LRP slope^R was significantly different for different faster and slower reaction time i.e. faster reaction time have steeper slope than slower reaction time condition, $F_c(1, 71) = 4.329$, $p = 0.041$ (Table 5). The other parameters such as LRP peak and LRP threshold did not differ with the reaction time, peak: $F_c(1, 71) = 0.301$, $p = 0.586$; threshold $F_c(1, 71) = 0.260$, $p = 0.618$. Before moving further, I confirmed that these differences in the LRP onset were not due to averaging effect by checking the correlation between LRP-R onset and reaction time (Figure 9). The analysis suggests that the LRP-R and the reaction time are correlated (slope = 0.502, $r = 0.586$, $p < 0.001$). Hence it was confirmed that this LRP-R onset difference was not due to averaging but due to reaction time effect

In conclusion, I found that the reaction time can only be predicted by the LRP-R onset and LRP-R slope. None other parameters of S-LRP and LRP-R reflects reaction time. Hence it can be inferred that in the current task, the variability in reaction time is coming only from the motor programing stages rather than response selection stages.

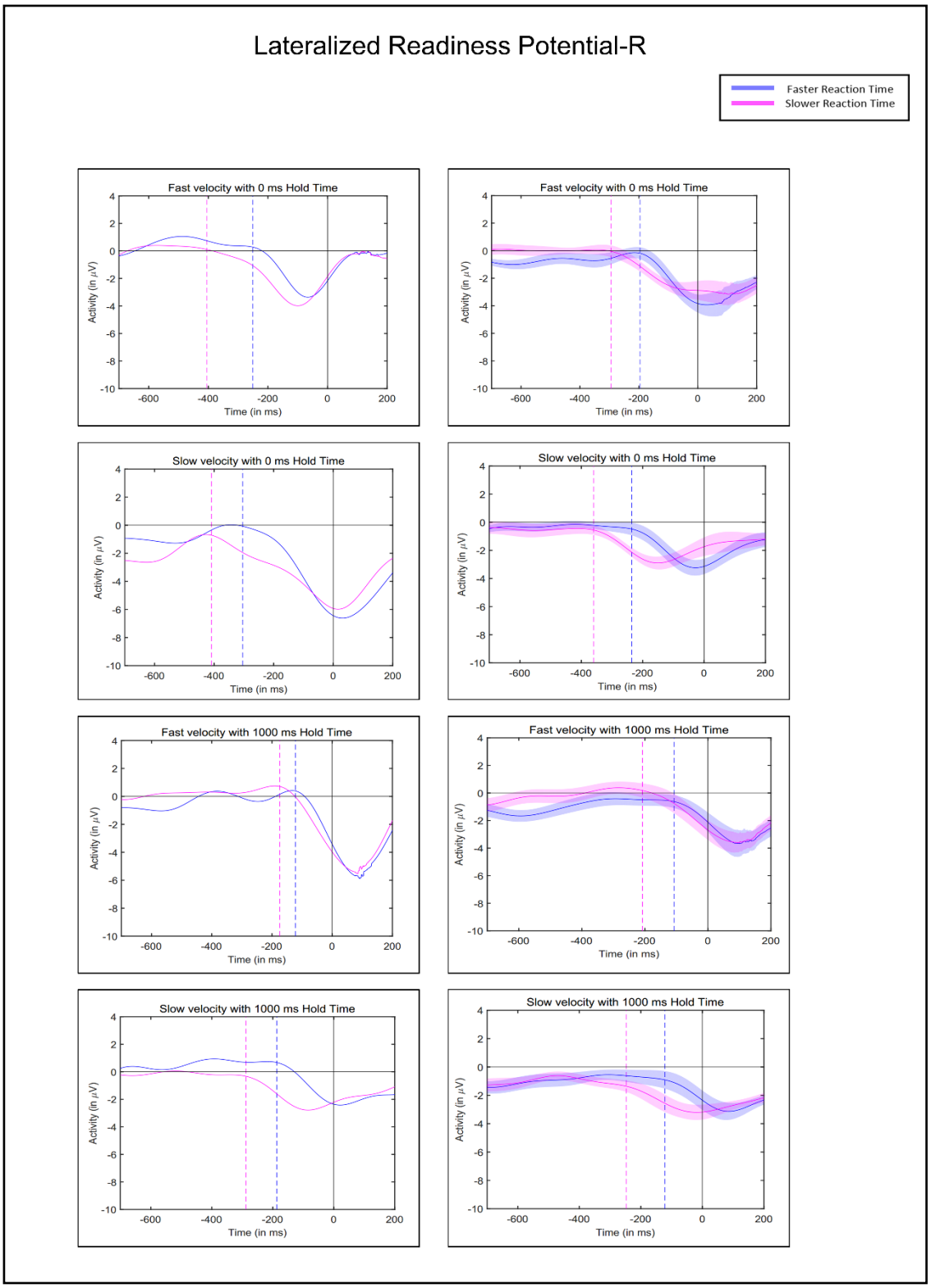

Figure 8: The Effect of reaction time on LRP-R - Response-locked Lateralized readiness potential for four trial conditions. The left panel shows data for representative subject and right panel shows grand averaged data. The verticle dashed line marks late LRP onset for fast reaction times (blue) and slow reaction time (magenta).

Table 3: Comparison of reaction time differences in mean of ERPs – The statistics for reaction times effects before movement onset for single and lateralized channels.

Interval	Reaction Time			
Criteria	Reaction Time		Hold Time	
	F (1,71)	p	F (1,71)	p
F3	0.126	0.724	5.071	0.027
F4	0.043	0.837	2.441	0.123
FC1	0.126	0.724	1.036	0.312
FC2	0.726	0.397	1.011	0.318
C3	0.068	0.795	0.084	0.773
C4	0.036	0.850	0.042	0.837
CP1	0.304	0.583	2.471	0.120
CP2	0.044	0.834	4.268	0.043
P3	0.143	0.707	0.589	0.445
P4	0.127	0.723	2.431	0.123
Lateralized F	0.074	0.787	0.146	0.704
Lateralized FC	0.126	0.724	5.071	0.027
Lateralized C	0.043	0.837	2.441	0.123
Lateralized CP	0.068	0.795	0.084	0.773
Lateralized P	0.126	0.724	1.036	0.312

Table 4: Comparing LRP-R onsets for faster and slower reaction Time - Comparison of mean LRP latency between faster and slower reaction time trials when aligned on movement onset. The onsets were mentioned for all for trial conditions.

LRP latency (in ms)				
		Faster RT	Slower RT	Differences
HT0	Fast	-196.1 ± 12.83	-294.2 ± 24.29	98.1 ± 17.52
	Slow	-235.7 ± 29.55	-360.2 ± 20.86	124.5 ± 25.28
HT1000	Fast	-107.6 ± 18.64	-207.6 ± 54.02	100 ± 50.24
	Slow	-121.67 ± 46.30	-247.22 ± 43.69	125.56 ± 24.15

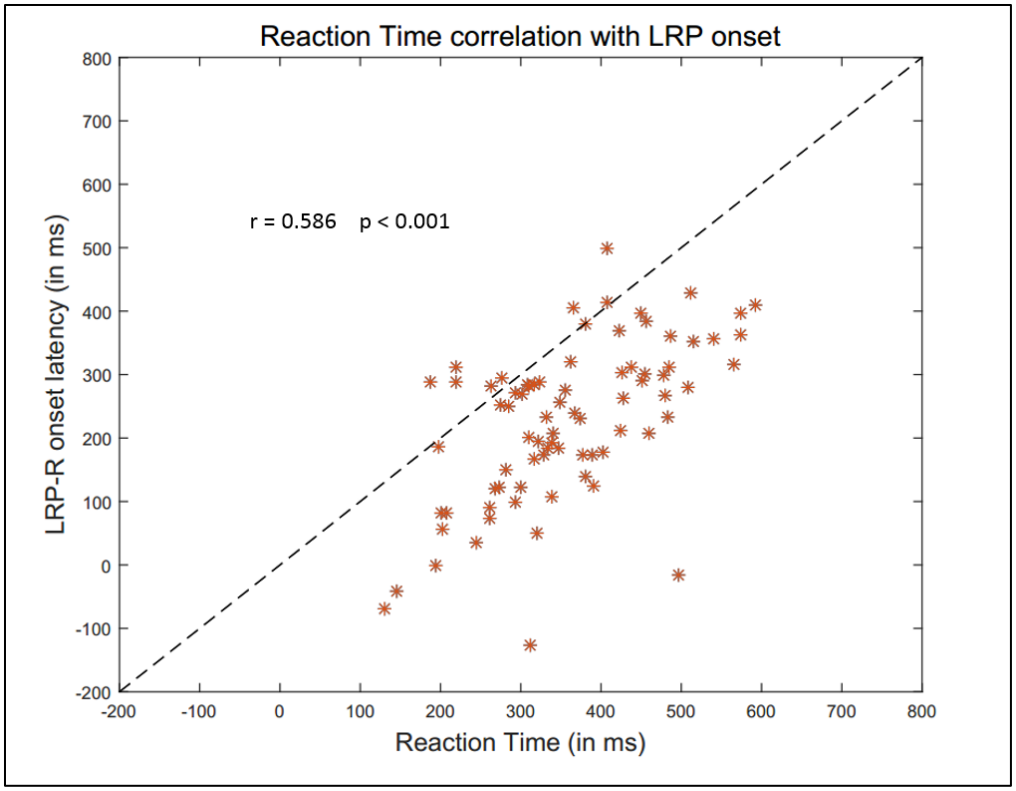

Figure 9: Correlation between reaction time and LRP-R- Onset latency LRP-R for eight trial conditions across all subjects. Two data points are removed because of noisy LRP data

Table 5: Comparing slopes of LRP-R for fast and slow reaction times- The table shows a comparison between faster and slower reaction time trials across four trial conditions.

LRP Slope (offset)				
		Faster RT	Slower RT	Differences
HT0	Fast	-0.0215 + 0.005	-0.0115 + 0.0036	-0.01 + 0.0041
	Slow	-0.0143 + 0.0028	-0.0045 + 0.0024	-0.0098 + 0.0023
HT1000	Fast	-0.0139 + 0.004	-0.0144 + 0.0054	0.0005 + 0.0032
	Slow	-0.0122 + 0.0036	-0.0089 + 0.0025	-0.0033 + 0.0022

b) Hold Time effect:

It has already been shown in the previous section that the reaction time decreases for longer hold time. Hence I wanted to see which part of the movement was getting prepared during hold time. This question was answered by performing LRP analysis. It is shown in the previous section that LRP parameters changes with the reaction time. In order to separate the RT effect from hold time effect, RT-normalized trials might be used. However, this analysis could not be performed as very few trials show the overlap of RT between no hold time and 1000 ms hold time condition. To address this, the four experimental conditions were divided based on RT (similar to reaction time analysis). Hence the hold time comparison was performed in following conditions: Fast velocity and faster RT (Ff), Fast velocity and slower RT (Fs), Slow velocity and faster RT (Sf), and Slow velocity and slower RT (Ss). Such analysis would reduce the variability in LRP parameters caused by reaction time.

The analysis on S-LRP revealed that the LRP onset and slope LRP does not change for no hold time and 1000 ms hold time conditions, onset: $F_c(1, 71) = 0.864$, $p = 0.356$; slope: $F_c(1, 71) = 0.993$, $p = 0.323$. The LRP peak showed difference for hold time conditions but did not reach the significant level, $F_c(1, 71) = 3.373$, $p = 0.071$. The LRPs for corresponding conditions are shown in figure 10.

The analysis on LRP-R showed that the LRP onset was different for no hold time and 1000 ms hold time condition, $F_c(1, 71) = 18.1$, $p < 0.001$. But the other LRP parameters such as peak, slope^P, threshold and slope^R did not change for different hold time, peak: $F_c(1, 71) = 0.042$, $p = 0.839$; slope^P: $F_c(1, 71) = 0.111$, $p = 0.74$; threshold: $F_c(1, 71) = 0.512$, $p = 0.477$; slope^R: $F_c(1, 71) = 0.051$, $p = 0.822$. The corresponding graphs are shown in figure 11.

These results demonstrated that the hold time affects the LRP-R activity but not the S-LRP activity which indicates that the extra preparation time during hold time facilitates the motor preparation process but not the response selection process.

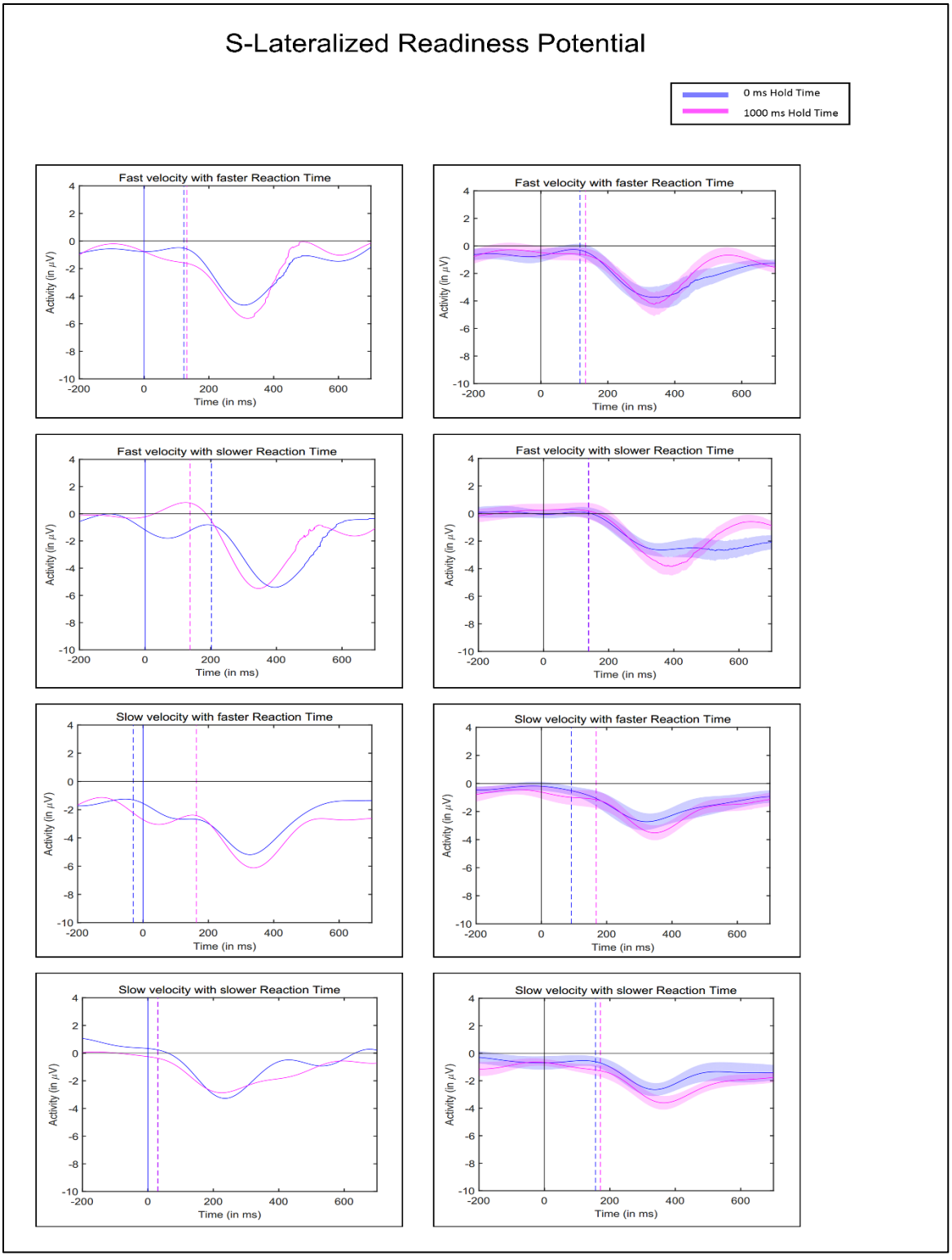

Figure 10: Effect of Hold Time on S-LRP - Stimulus-locked Lateralized readiness potential for four trial conditions. The left panel shows data for representative subject and right panel shows grand averaged data. The verticle dashed line shows the late LRP onset for 0 ms hold time (blue) and 1000 ms hold time (magenta).

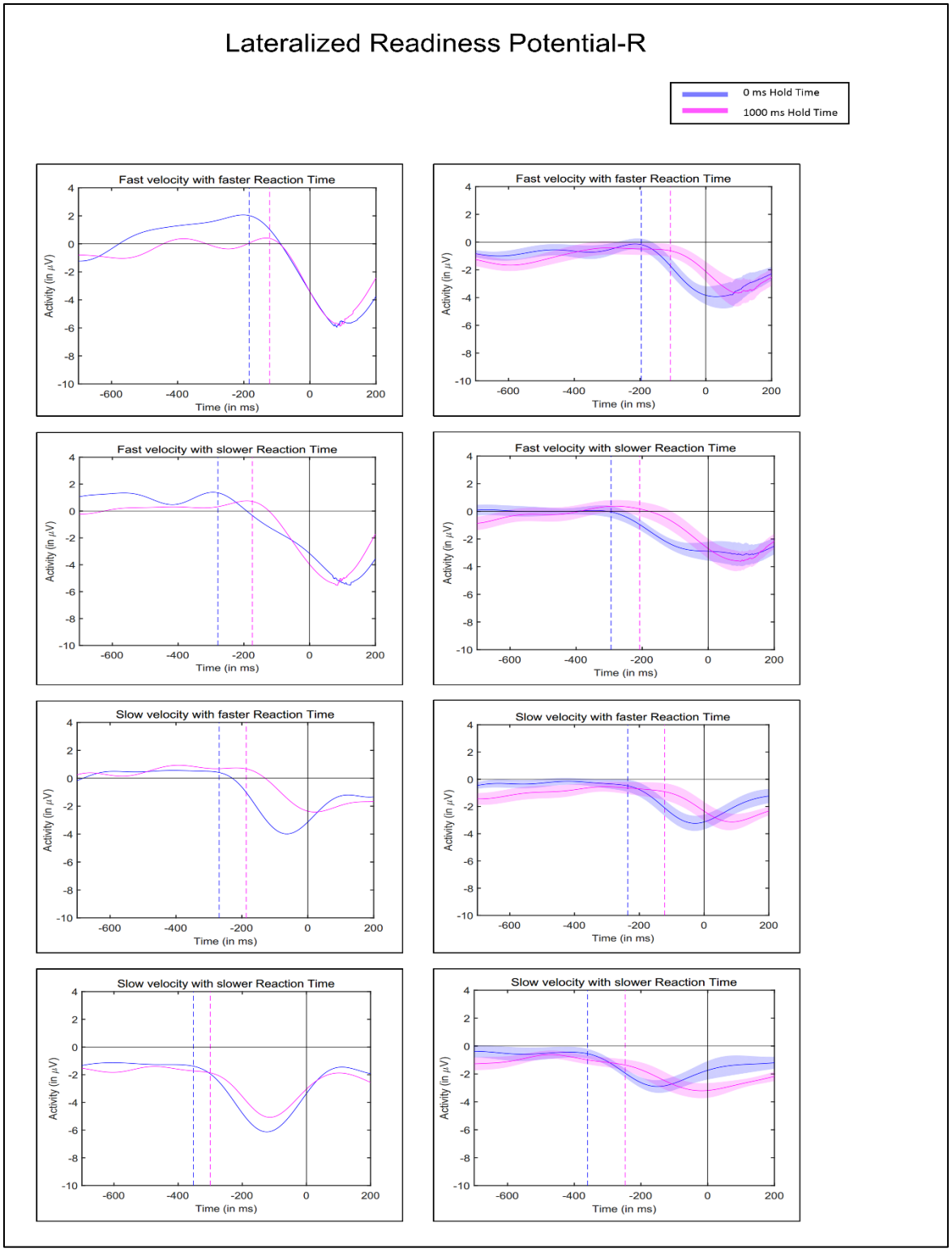

Figure 11: Effect of Hold Time on LRP-R - Response-locked Lateralized readiness potential for four trial conditions. The left panel shows data for representative subject and right panel shows grand averaged data. The verticle dashed line marks late LRP onset for 0 ms hold time condition (blue) and 1000 ms hold time (magenta).

Chapter 4: Discussion

The present study has made an attempt to understand the two important parameters of the movement preparation: 1) Planning of velocity (kinematics) in the movement planning stage and 2) Prediction of reaction time from LRP. I found that the gamma frequency in parietal cortex was modulated with velocity. However, velocities were not represented in ERPs. The second part showed that the reaction time effect is seen in LRP-R onsets but not in S-LRP. Similar to reaction time, hold time effect was observed in LRP-R onsets. These results of are discussed in corresponding sections.

4.1 Planning of Velocity:

A few of the previous EEG studies have attempted to look for the associativity between the velocity of ensuing hand movements and ERPs (Amengual et al., 2014; Kirsch and Hennighausen, 2010). A study by Amengual (2014) found a negative peak in LRP at the time of maximum velocity over the primary motor cortex. However, no study to date has shown a velocity signature in the ERP during the planning stage. A recent paper by L. Xu (Xu et al., 2015) has reported that the response-locked lateralized readiness potential had distinct onsets for different movement duration in the foreperiod task. The similar result was found in the current study i.e. LRP-R onsets were different for different velocity. However, in their study, no attempt was made to normalize for reaction time differences that we have observed in this study. Hence the differences reported by them may be confounded by differences in RT which were normalized in this study. After the RT normalization, there were no differences in LRP onsets, suggesting that the differences in the LRP not be due to the velocity. No other time components show any differences in the ERPs and LRPs.

In the frequency domain, many of the studies have modeled the velocity using linear regression on multiple frequency bands (Bradberry et al., 2010; Kim et al., 2014; Yang et al., 2015b; Yeom et al., 2013; Yuan et al., 2010). These studies have reported that the

alpha and beta frequency band were associated with the velocity. The present study analyses the frequency band fluctuation of lateralized potentials instead on fluctuation observed in single channels. Although the current study also finds the decrease in alpha and beta bands powers during the planning and execution phase, no differences in their powers as a function of velocity was found. On the other hand, I found that the gamma band showed different power for both the fast and slow velocity approx. 99 ms before the movement onset. Interestingly, this difference in power was observed in FC, C, CP, and P lateralized channels with different latency. The latency was maximum for parietal and fronto-central channels (-99 ms), then centro-parietal channel (-49 ms) and least for the central electrode (75 ms) which showed the difference after movement onset. Taken together, these results suggest that a kinematic representation is first observed over fronto-parietal cortex, which is later transmitted to the primary motor cortex. In this context it is interesting to note that Kalaska (Kalaska et al., 1990) reported that the kinematic parameters were correlated with the neuronal firing in parietal are 5, but only the dynamic parameters were encoded in primary motor cortex. A more recent study by Padoa-Scioppa et al., (Padoa-Schioppa et al., 2002) showed kinematic to dynamic transformation in signals within the supplementary motor area which likely to correspond the FC1 and FC2 electrodes in this study. In congruence with these reports, the current study confirms that the kinematic (velocity) parameter is encoded in the parietal area. Since there is an anatomical projection from parietal area to premotor area, the encoded kinematic parameters may reach the premotor area. To the best of my knowledge, this is the first time such a chronometry has been documented in the EEG literature.

4.2 Temporal Effect on LRP:

The presents study has looked at the two components of the temporal effects: reaction time and hold time. With respect to RT effects, a study by Gratton (Gratton et al., 1988) showed that the LRP activity at the time of response initiation did not change with reaction time. This suggests that LRP shows some accumulation, which after reaching a threshold initiates the movement. A similar effect is found in the present study. Other studies (Hackley et al., 2007; Mordkoff and Grosjean, 2001) on reaction time have found

that the for different reaction times the S-LRP onset was distinct, but there was no effect on LRP-R. From these results, the study claimed that the reaction time affected the response selection stage of movement planning. The present study shows that the reaction time differences observed on LRP-R but not on the S-LRP, which is contrary to the reports mentioned above. These results suggest that the reaction time affected the motor programming stage instead of preceding response selection stage. This contradiction may have occurred because of the task differences. Since previous studies had used a foreperiod task where they give a hold time before the stimulus onset, and the stimulus contained the instruction about the task. Hence the RT effect on S-LRP (response selection) was expected as the task-related decisions are only made after stimulus onset. However, in the present study, the information about the task was already provided to the subjects and then a hold time was given. Moreover, no distinct response related decision was made during RT. Hence I observed the onset differences on LRP-R (motoric programming) for distinct reaction time.

For no hold time condition I observed that although the threshold was constant across RT, the slopes and onsets were different. Thus aligned on movement onset, I observed that for long RT the LRP onsets were more distant to movement than short RT. Also, the slopes were steeper for short RT than long RT. These basic signatures are consistent with the LATER model. Similar signatures have been observed in FEF for eye movements but never have been demonstrated for hand movements. However, for 1000 ms hold time, I observed that the LRP did not follow the LATER model. While the onsets were different for different RTs, the slopes and threshold did not change with RTs. The differences in the hold time seen in LRP suggests that either the LATER model should not to be generalized across different hold times or all the variability associated with RT is due to the decision of where to go which is reflected only in the onset of the LRP signal and not its slope. Thus in 0 ms hold time, the variability in RT can be attributed to LRP, however, at a large enough hold time all the variability cannot be attributed to only LRP.

In addition to RT, I also used the long and short hold time to address the basis of the well-known effect which posits that longer hold time leads to faster RTs. The studies on hold time (Hackley et al., 2007; Masaki et al., 2004; Xu et al., 2015) have shown that

the distinct S-LRP onsets were observed for different hold times. However, the LRP-R onset did not get affected by the hold time. From these results, they claim that the additional preparation during hold time facilitates the response selection process.

Contrary to the result mentioned above, the present study showed that with different hold time the LRP-R onset differs instead of LRP-S. These results also follow the study by Gethmann (Müller-Gethmann et al., 2000) that showed when the advance information about the movement direction during hold time shows different onsets for S-LRP and LRP-R. The differences might have occurred because of the hold time given in different stages. In the previous studies, the hold time was provided before then the information about the movement was given at the time of go stimulus. Hence the hold time differences were evident on S-LRP onset (response selection stage). Because no information was available about the movement parameter, hold time could not facilitate the motor programming stage. In our task, the hold time was provided after the complete information about movement parameters were given. Hence one would expect to see the effect of hold time at the motor programming stage as hold time may have facilitated the motor preparation.

Results from the current study and the previous studies point to the fact that the effect of hold time on response selection or motor programing stage is task dependent. If the hold time is given without relevant task information, it will facilitate response selection process. If hold time is given after complete task-relevant information is provided, it will facilitate the motor programming stage.

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