Investigating the Relationship between Event-Related

Potentials and Response Kinematics

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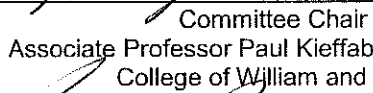The College of William and Mary
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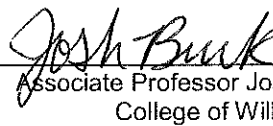
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ABSTRACT

Movement is one of the most important functions of our nervous system. Recent research has shown that cognitive and perceptual functions ranging from our perception of others' emotions to the planning of goal-directed behaviors depends critically on brain areas once thought to be primarily motor in nature. Given the important role our motor system plays in understanding and interacting with the world around us, it is surprising that the majority of cognitive neuroscience research using electroencephalogram (EEG) has focused primarily on perception and cognition irrespective of its relationship(s) to the execution of movement. One possible explanation for this is that EEG and event-related potential (ERP) studies typically rely on simplistic motor responses and ERP averaging techniques that do not afford an analysis of these dynamic relationships. Combining a novel method for tracking dynamic cursor movement and single-trial EEG analysis, the current study addressed this limitation in the field via assessment of younger and older adults' goal-directed movements during a task-set switching procedure. Our results demonstrate that ERPs conventionally interpreted with respect to cognition and perception are in fact related to the kinematics of motor responses.

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The evolutionary development of a nervous system is a prerogative

exclusive to actively moving creatures (Llinás, 2001). Support for this claim is

evidenced by the early life of the sea squirt (Dennett, 1991; Llinás, 2001;

Glenberg, Jaworksi, Rischal, & Levin, 2007). The sea squirt begins life as an

actively moving tadpole-like creature with a rudimentary nervous system. After

finding a habitable rock or piece of coral, the sea squirt binds itself to the site,

never to move again. Shortly after attaching itself, the sea squirt begins to digest

its own nervous system, seemingly unneeded without the impetus for action.

Examples like this have led some theorists to believe that the primary purpose of

a central nervous system is to facilitate interaction with our environment

(Glenberg et al., 2007; Wolpert, Doya, & Kawato, 2003). However, effective

responses to environmental demands require the brain to optimally integrate

perceptual and motor processes.

Although a great deal of cognitive neuroscience research has been

directed at examining the perceptual, cognitive, and motor functions of the brain,

far fewer, have been directed at the relationships between these

perceptual/cognitive functions and the behaviors (i.e., actions) they are purported

to support. This is especially true of research using electroencephalogram (EEG),

the vast majority of which characterizes perceptual and cognitive processes

irrespective of their relationship(s) to motor output. To the extent that the

principle function of our brain is to support our capacity to flexibly and efficiently

respond to a dynamic environment, it is critical that cognitive neuroscience research address these important questions about the translation between perception and responses. The primary aim of the present research was to determine how single-trial EEG dynamics are related to timing and/or properties of behavioral responses.

Perception, Cognition, and Action

Traditional cognitive theories of the relationship between perceptual processes and motor response typically frame response selection and/or motor control as distinct processes that are engaged subsequent to perception (Creem-Regehr & Kunz, 2010). From this perspective, the path from perception to action can be described as a serial process wherein perceptual processes use sensory information to build internal representations of objects in the external world (Cisek, 2007; Marr, 2010). These representations are then passed to other cognitive systems where they are integrated with current goals and past experiences in order to plan and select a subsequent motor response (Johnson-Laird, 1988; Newell & Simon, 1972).

In contrast with the traditional, serial view of the translation from perception to action, some investigations using both neuroimaging and neurophysiology techniques suggest that perception and response do not always adhere to discrete, modular processing stages (Cisek & Kalaska, 2010; Gallese, Craighero, Fadiga, & Fogassi, 1999). Moreover, several recent lines of evidence have demonstrated that brain regions once thought to be exclusively involved in

motor functions support and interact with perceptual and cognitive processes (Bernard & Mittal, 2014; Cabeza & Nyberg, 2000; Doya, 2000).

For example, over the past few decades many researchers have begun theorizing about the non-motor functions of the cerebellum and basal ganglia (Alexander, DeLong, & Strick, 1986; Bernard & Mittal, 2014; Leiner, Leiner, & Dow, 1989). Traditionally, it was believed that the functional significance of these two cortical regions was restricted to the control and coordination of movement (Middleton, 2000). However, a large number of functional-imaging and case studies have found cerebellum and basal ganglia activation to be independently involved in a myriad of non-motor, cognitive and perceptual processes (Ackermann, Mathiak, & Ivry, 2004; Cabeza & Nyberg, 2000; Daum, Beth, & Snitz, 2001; Doya, 2000; Gao et al., 1996).

Furthermore, studies using single-cell recordings of neuronal activity in monkeys have revealed several findings that do not support a serial ordering interpretation of perception, cognition, and response (Alexander & Crutcher, 1990; Crammond & Kalaska, 2000). For instance, when monkeys were required to use abstract rules to make same/different responses by holding or releasing a lever, both premotor cortex (PMC) and prefrontal cortex (PFC) were co-activated during encoding of the rule and response (Wallis & Miller, 2003). Critically, although the rules were represented in both regions, they were encoded earlier and more strongly in the PMC.

Though it has become increasingly evident that a strictly independent conceptualization of motor and perceptual processes is difficult to reconcile,

investigations of their interaction have been relatively restricted to hemodynamic neuroimaging and non-human primate neurophysiology techniques. Little, if any, cognitive neuroscience research using EEG has examined the dynamic interaction between perception and motor processes. One possible explanation for this is that EEG and event-related potential (ERP) studies typically rely on simplistic, non-ecologically valid motor responses (e.g., button presses) that do not afford dynamic assessments of online movements. However, even these simplistic responses occur within the time-course of EEG and ERP waveforms that are typically interpreted as perceptual or cognitive in nature. For instance, investigations utilizing Go/No-go and flanker tasks typically report average response time(s) that overlap with N2 and P3 component waveforms (Donkers & van Boxtel, 2004; Roberts, Rau, Lutzenberger, & Birbaumer, 1994; Tillman & Wiens, 2011). Thus, these ERP waveforms likely contain neural information generated by both perceptual and motor processes. Furthermore, even response-related ERP components (e.g., the lateralized readiness potential (LRP)) that are commonly interpreted as reflecting motor preparation have been demonstrated to overlap with non-motor, perceptual processing (Eimer, 1998).

In order to gain a better understanding of the temporal and functional relationship between traditional EEG and ERP measures of cognitive function and behavioral responses, it is necessary to use a dynamic measure of motor execution that is amenable to measurement of response characteristics that can be related to the recorded EEG data. Kinematic analysis of movement profiles is one promising approach to address this problem.

Kinematics

Kinematics (i.e., the motion of objects as a function of time and the derivatives of displacement (e.g., velocity, acceleration, fluency) afford numerous advantages when studying behavioral responses compared to traditional paradigms used in EEG and ERP studies. Whereas typical EEG tasks are restricted to motor planning and execution inferences from discrete response times, kinematics permit a quantitative measurement of the continuous parameters of the response. In addition, there are several lines of empirical evidence demonstrating the utility of kinematics in the study of perception-response interactions, as well as abundant behavioral data establishing their suitability for distinguishing between various levels of motor functioning (Knoblich & Flach, 2001; Parsons, 1994; Pozzo, Papaxanthis, Petit, Schweighofer, & Stucchi, 2006; Schroter et al., 2003; Paolo Viviani & Stucchi, 1992; Viviani & Stucchi, 1989). Taken together, kinematics provide a promising solution to the aforementioned limitations of traditional EEG tasks. However, their effective application to the study of perceptual-motor integration requires the development of new approaches to EEG analysis.

In studies of cognition and perception, EEG data is typically analyzed using the event-related potential (ERP) method. ERPs are electrical potentials generated by the brain in response to some internal or external event (e.g., stimuli, responses, etc.; Luck, 2012). Because ERPs are typically smaller in amplitude than the co-occurring EEG, some sort of averaging is required to

isolate the event-related waveform. The problem with the traditional ERP method is that by averaging over trials, much of the dynamic event-related signal is lost.

Trial-level EEG Analysis

The predominant approach to EEG analysis has focused on reducing the complexity of EEG data by averaging data segments time-locked to a set of experimental events assumed to evoke consistently similar neural responses (Makeig & Onton, 2009). Theoretically, three types of oscillatory activity contribute to the event-related EEG signal time-locked to a set of experimental events (Dickter & Kieffaber, 2014): (1) phase and time-locked evoked oscillatory activity (EOA) generated by an experimental event, (2) spontaneous oscillatory activity not generated by an experimental event, and (3) induced oscillatory activity (IOA) that is correlated with an experimental event, but not phase-locked to the event. Averaging across data segments removes EEG signals unrelated to time-locked events via phase cancellation. By reducing oscillatory activity to a single statistical parameter (e.g., a mean), we lose the dynamic, induced oscillatory information contained in the original data (Makeig, Debener, Onton, & Delorme, 2004). Critically, because the planning and execution of motor responses varies in time from trial to trial, the conventional averaging process also precludes the ability to investigate the neural correlates of response processes, which is a significant hurdle to the study of perception-motor integration. One alternative approach is to analyze the data at the single-trial level. By looking at event-related EEG at the trial-level, we can determine how

both evoked and induced activity is related to the kinematic properties of a movement.

Kinematics, EEG, and Aging

It has been posited that age-related neural slowing results in an overall decline in the cognitive and motor functioning of older adults (Birren, 1974; Ketcham, Seidler, Van Gemmert, & Stelmach, 2002; Salthouse, 1985). This is evidenced by a large body of experimental research demonstrating that older adults are slower on a wide variety of cognitive and motor tasks (Birren & Fisher, 1995; Seidler et al., 2010). Research on age-related kinematic differences between healthy younger and older adults supports these findings. For instance, compared to younger adults, older adults are slower in initiating and executing motor responses, have lower peak velocities and accelerations, are more dysfluent, and spend a greater proportion of movement time in terminal guidance (Contreras-Vidal, Teulings, & Stelmach, 1998; Ketcham, Seidler, Van Gemmert, & Stelmach, 2002; Tucha et al., 2006). This is important because these motor deficits might be reflected in EEG measures. Several lines of evidence from EEG research suggest this may be the case. For instance, while EEG indices of older adults sensory and perceptual processing appear to be intact, it has been demonstrated that task-related behavioral slowing might be the result of dysfunctional motor and cognitive processing rather than a peripheral nervous system impairment (Falkenstein, Yordanova, & Kolev, 2006; Yordanova, 2004). However, over-reliance on traditional EEG and ERP analyses and serial processing interpretations of motor response have made it difficult to determine

how cognitive and motor processing actually contribute to behavioral slowing. By using trial-level EEG analysis and behavioral kinematics, it might be possible to elucidate these relationships.

The Present Study

Motivated by the aforementioned methodological limitations described in the preceding paragraphs, the aim of the present study was to investigate a procedure for disassociating perceptual, cognitive, and motor processing using single-trial EEG analyses. To achieve this, we used a novel method designed to simultaneously assess dynamic cursor movements and EEG during a cued task-set switching procedure. By using online cursor movements, rather than discrete button presses, we can extract the kinematic measures associated with behavioral responses. Combining these kinematic variables with trial-level analyses, we will determine how the relationships between cognitive and perceptual processing and the parameters of motor responses may be altered during normal cognitive aging.

Method

Participants

Nineteen college-aged adults (15 females; $M = 21.21$, $SD = 4.98$) and 18 healthy older adults (11 females; $M = 74.47$, $SD = 6.71$) were assessed in the present study. Younger adults were recruited from a university research pool at the College of William & Mary and received course credit for their participation. Older adults were community-dwelling citizens and received monetary compensation. The study was conducted with the understanding and consent of

each participant in accordance with the guidelines set forth by the Institutional

Review Board.

Participants were screened for eligibility using the Mini Mental State

Exam (MMSE) (Folstein, Folstein, & McHugh, 1975) and a health-history

questionnaire to exclude those with cognitive impairment or any history of

neurological or movement disorders. A MMSE score of 27 was set as the

minimum inclusion cutoff for participation in the study (O'Bryant et al., 2008). The

average MMSE score for older adults was 29.65 (SD = .67) and 29.38 (SD = .97)

for younger adults. Both older (M = 16.56, SD = 3.29) and younger (M = 14.16,

SD = .96) adults reported many years of education. No participants self-reported

a neurological or psychiatric disorder. All participants had normal or corrected-to-

normal vision with normal color vision and indicated a right hand preference on

the Edinburgh Handedness Inventory (Oldfield, 1971).

Materials and Procedures

Eligible participants were fitted with an electrode cap and then completed

a cued task-set switching procedure. The task was presented on a computer

monitor in an electronically shielded booth using E-Prime (Psychology Software

Tools, Inc., Pittsburg, PA). A schematic of the task is presented in Figure 1.

Analyses of the behavioral and ERP correlates of cue and stimulus processing

with respect to conflict processing and task-set switching are detailed elsewhere

(Kieffaber, Kruschke, Cho, Walker, & Hetrick, 2012). On each task trial,

participants were instructed to make cued judgments concerning target stimuli

according to three potential cues (the word SIZE, SHAPE, or COLOR). Target

stimuli consisted of figure-pairs that varied in size (small/large), shape (square/circle) within a trial, and color (red/blue) across trials. On shape and size cued trials, participants were instructed to determine if the corresponding target stimuli figure-pair was "Same" or "Different" on the cued dimension. On color-cued trials, participants were instructed to determine if the corresponding target stimuli were "Red" or "Blue". Cues were displayed for 800ms followed by a 700ms cue-target interval before the figure-pair target stimuli appeared. Target figure-pairs remained until a response was recorded. Responses were made by moving a mouse cursor from a home position at the bottom center of the screen to one of two response positions at the left and right of the target figure-pair. The response positions were indicated by black squares with white Different/Red labels (left) and Same/Blue (right) (see Figure 1). Responses were recorded as soon as the mouse cursor entered any part of the response position (no click required). Response labels did not vary across trials. Accuracy feedback was immediately given after a response was recorded and remained until the mouse cursor was returned to the bottom center "Home" position. Returning to the home position initiated a 1500ms inter-trial interval. Task-set cue rules changed randomly between trials with switch (cue switch) and repeat (cue same) trials equiprobable. Size, shape, and color cues were evenly distributed across blocks. Participants completed three blocks with 120 trials each with self-administered breaks between blocks.

Behavioral Measures

Participant responses were measured by continuously sampling the x-y coordinates of the mouse cursor at 200 Hz (i. e., every 5 ms). Two measures were recorded on a trial-by-trial basis. Movement initiation was defined from velocity profiles using the optimal algorithm of Teasdale, Bard, Fleury, Young, and Proteau (1993). The algorithm located the sample (S1) where the velocity time series first exceeded 10% of the peak velocity (PV; e.g., the point of maximum velocity of the movement) of the time series. It then worked backwards from this point until it found the first sample (S2) in the velocity time series less than or equal to PV/10-PV/100. The standard deviation of the time series between sample S1 and sample S2 was then calculated. The movement initiation sample was the first sample less than or equal to S2-SD (Ketcham et al., 2002). The second measure, movement duration, was defined as the elapsed time between movement initiation and movement completion. A movement was considered completed when the mouse cursor entered any part of the boundary of one of the marked response positions.

Kinematic Measures

Kinematic variables corresponding to variations in the first derivative (i.e., velocity), second derivative (i.e., acceleration), and third derivative (i.e., jerk) of the mouse cursor as a function of time were organized into four categories corresponding to the (1) speed, (2) guidance, (3) decision time, and (4) fluency underlying the cursor displacement on each trial. Maximum and mean absolute velocity and acceleration were measured to assess the peak and overall speed

of cursor movements, respectively. Total movement duration and the acceleration- deceleration asymmetry ratio were used to measure guidance. The asymmetry ratio differentiates the proportion of the total movement duration spent in the deceleration phase (e.g., terminal guidance) from the acceleration phase. Prolonged periods of terminal guidance are indicated by acceleration ratios less than 0.5, and represent the period of time to peak velocity divided by the total movement duration (Bellgrove, Phillips, Bradshaw, & Gallucci, 1998; Nagasaki, 1989). Decision time was defined as the time from target onset to the time of movement onset (e.g., movement start time). The number of inversions of velocity (NIV) and average normalized jerk (ANJ) were measured to determine the fluency of the cursor movements. Automatic, fluid movements are characterized by smaller numbers of inversions of velocity (Tucha et al., 2006). Supernumerary velocity and acceleration fluctuations correspond to additional increases and decreases in speed caused by lack of control (Danna, Paz-Villagrán, & Velay, 2013). Because jerk, the change of acceleration, differs greatly with the length and duration of a movement, jerk was normalized and averaged to correct for variations in movement size and time according to Teulings, Contreras-Vidal, Stelmach, & Adler, 1997. Normalized jerk is minimal in smooth movements and is used to compare acceleration control between movements of different sizes and lengths (Contreras-Vidal et al., 1998). Smaller ANJ scores indicate smoother movements.

Sampled x-y coordinates were filtered with a second-order, dual-pass Butterworth filter using a 10 Hz low-pass cutoff (Ketcham et al., 2002; Phillips &

Triggs, 2001). Cursor displacement data were then differentiated thrice using a three-point central finite difference algorithm to compute velocity, acceleration, and jerk.

EEG Recordings and Data Analysis

Electrophysiology data were recorded continuously at 2000 samples per second using a high-impedance DBPA-1 Sensorium bio-amplifier (Sensorium Inc., Charlotte, VT) with an analog high-pass filter of 0.01 Hz and a low-pass filter of 500 Hz (four-pole Bessel). Recordings were made using fabric caps with 74 Ag-AgCl sintered electrodes (Electrode Arrays, El Paso, TX) while participants were seated in an electronically shielded booth. EEG recordings were made using a forehead ground electrode and an average common reference at the tip of the nose. Horizontal and vertical eye movements were recorded from perioccular electrodes positioned at the lateral canthi and from electrodes positioned on the superior and inferior orbits (centered with the pupil), respectively. All impedances were adjusted to within 0-20 kΩ at the start of the recording session.

EEG data were analyzed off-line using EEGLAB (Delorme & Makeig, 2004). Raw data were visually inspected to remove channels with extreme artifacts and identify bad data segments. The continuous EEG data were corrected for ocular artifacts using independent components analysis (ICA; Jung et al., 2000) and smoothed with a band-pass, zero phase-shift Butterworth filter between .2 and 30Hz. The data were then segmented using ERPLAB (Lopez-

Calderon & Luck, 2014) and individual segments containing voltages exceeding 300 µV were removed.

Data segments were defined with respect to either target onset (-200 – 1000 ms) or movement initiation (-1000 – 2000 ms). Data segments time-locked to target onset were baseline corrected between -200 and 0 ms. Data segments time-locked to movement initiation were baseline corrected using the mean of the full interval between -1000 and 2000ms.

Data reduction was accomplished using group-wise ICA to re-describe the multi-channel EEG data in terms of a small number of components. Separate ICA decompositions were applied to the target onset and movement initiation data. Because of the potential for redundancy in the data following target onset and prior to response initiation, subsets of the segmented data were used for the ICAs. For those segments time-locked to target onset, only data between 200 ms prior to target onset and 100 ms prior to movement initiation were submitted to the ICA decomposition. For those segments time-locked to the movement initiation, only data between 100ms prior to movement initiation and 200ms following the completion of the movement were submitted to the ICA decomposition. Each of the two sets of spatial filters resulting from the ICA decompositions were then applied to the original data segments.

In order to reduce computational demands and in the interest of parsimony, the 65-channel data were reduced to 15 principal dimensions using PCA prior to the ICA analysis. Of the resulting 15 independent components, only

those required to account for more than 90% of variance in the data were selected for further analysis.

Relationships between EEG amplitude and kinematic variables were evaluated using "ERP images". An ERP image is a representation of ERP amplitude (color) over time (X-axis) and trials (Y-axis). When the trials are sorted along the Y-axis with respect to some measured behavior (e.g., velocity, response latency), patterns in the ERP image can reveal characteristics of the relationship(s) between EEG amplitude and that behavior (Makeig et al., 2004). In the present research, ERP images with 200-trial smoothing were generated for each of the ICA components, for the complete sample and separately for young and older adults and sorted in ascending order with respect to the timing of movement initiation and mean velocity of the response.

For each of the ICA components and analyzed kinematic variables a univariate 2 (Age) X 2 (Quantile) ANVOA was used to evaluate mean differences at each time point in the smoothed, single-trial data. A correction for the False Discovery Rate (Bejamini & Yekutieli, 2001) was used to address the inflated risk of Type I error. In addition, "significant" results were defined as those associated with an effect size (eta-squared) greater than or equal to .14, indicating a "large" effect. The results of these analyses are presented along with the ERP image analyses, however, because they are similar to those of a conventional ERP analysis they will not be discussed further.

Recall that the foremost concern with conventional averaging approaches to ERP analysis (including the univariate analyses just described) is that they

are incapable of characterizing EEG activity that is evoked by external (e.g., target onset) or internal (e.g., movement onset) events that are not phase-locked across trials. Furthermore, there remains considerable debate in the literature about how to quantify temporally dynamic EEG activity in single trials (Makeig et al., 2004). For present purposes, features (i.e., peaks and troughs) of the single trial (smoothed) EEG data were characterized using a peak-centered moving window. First, a window (e.g., 100ms to 200ms) was defined for each feature (e.g., P1, N1, etc.) identified in the ERP images. Next, a "spread" (e.g., 20ms) was defined in accordance with each feature. Finally, the maximum/minimum amplitude was identified within the window. The latency of the feature on each trial was measured as the latency of the maximum/minimum amplitude and the amplitude of the feature on each trial was measured as the mean amplitude over the "spread" of the feature surrounding the peak/trough. Each of the peak/trough amplitude and latency measures for each of the identified EEG features was then analyzed to determine if it reflected three types of potential neural processes: (1) sensory and perceptual, (2) perceptual and cognitive, or (3) cognitive and motor.

Concerning features associated with target-locked events, a feature was considered to reflect a sensory and perceptual process if it was unrelated to the kinematic sorting variables. Next, a feature was considered to indicate a perceptual and cognitive process if the amplitude, but not latency, of the feature was related to the kinematic sorting variable. Lastly, a feature was considered to reflect a cognitive and motor process if the latency, plus or minus the amplitude, was related to the kinematic sorting variable.

In regards to features associated with movement onset time-locked events, features occurring prior to the movement initiation were considered to reflect sensory and perceptual processes if correlated in latency with the Target onset, but not with the kinematic sorting variable. Features that were present following movement initiation were interpreted using the same criteria as the target-locked features.

Results

Behavioral Data

The experimental design permits comparisons between three levels of task switching (e.g., repeat, attention switch, and response switch) and four levels of task conflict (e.g., no conflict, attentional conflict, response conflict, and all conflict). Switch (3) by conflict (4) by age (2) mixed model ANOVAs were employed to determine if accuracy rates and reaction times (RT) were affected by age, task-switching, or conflict.

The following behavioral results are largely consistent with prior literature on task-set switching and conflict processing (see Kieffaber et al., 2012), and are provided here only in the interest of transparency. Because the primary aim of the present research is to evaluate relationships between EEG and kinematics, the results regarding switching, conflict, and age will not be discussed further.

Accuracy. The analysis of accuracy indicated only a main effect of conflict, $F(3, 105) = 21.94$, $p < .001$. Post-hoc paired-samples t-tests with Bonferroni correction (alpha= .008) for multiple comparisons revealed an expected trend in accuracy rates across types of conflict. Results revealed no

accuracy rate differences between "no conflict" ($M = 99\%$; $SD = .02$) and "attentional conflict" ($M = .98\%$; $SD = .04$) trial types, $t(36)= 1.93$, $p > .05$, but did indicate greater accuracy on "no conflict" trials when compared to "response conflict" trials ($M = 95\%$; $SD = .05$), $t(36)= 4.93$, $p < .008$, and "all conflict" trials ($M = 93\%$; $SD = .07$), $t(36)= 5.59$, $p < .008$. There were higher accuracy rates on "attentional conflict" trials compared to "response conflict" trials, $t(36)= 3.53$, $p < .008$, and "all conflict" trials, $t(36)= 5.34$, $p < .008$. Finally, accuracy rates were lower on "all conflict" trials compared to "response conflict" trials, $t(36)= 3.09$, $p < .008$. This pattern demonstrates that, as expected, accuracy rates decrease as conflict demands increase. Overall accuracy was not affected by age $F(1, 35) = 2.82$, $p > .05$, and was high for both young ($M = 96\%$; $SD = .05$) and old ($M = 93\%$; $SD = .06$) adults.

      Reaction times. The analysis of reaction times indicated several statistically significant main effects and interactions. A main effect of task-switching revealed significant RT switch costs, $F(2, 70) = 16.54$, $p < .001$. Post-hoc paired-samples t-tests with Bonferroni correction (alpha= .016) for multiple comparisons indicated that RTs were shorter on "repeat" trials ($M = 1352.96$; $SD = 368.44$) than "attention switch" trials ($M = 1392.4$; $SD = 378.38$), $t(36)= -2.55$, $p < .016$, and that RTs were shorter on "attention switch" trials than "response trials" ($M = 1352.96$; $SD = 368.44$), $t(36)= -2.72$, $p < .016$. These findings indicate that, as expected, greater task-switching demands result in increases in RT costs.

      There was also a statistically significant main effect of conflict, $F(3, 105) = 13.62$, $p < .001$. Post-hoc paired-samples t-tests with Bonferroni correction

(alpha= .008) for multiple comparisons revealed that RTs were shorter on "no conflict" trials (M = 1329.51; SD = 373.21) than "response conflict" trials (M = 1417.78; SD = 382.91), $t(36)$= -5.5, p < .008, and "all conflict" trials (M = 1446.7; SD = 392.77), $t(36)$= -5.96, p < .008. Furthermore, RTs were shorter on "attentional conflict" trials (M = 1378.35; SD = 409.08) than "all conflict" trials, $t(36)$= -3.57, p < .008. No other pairwise comparisons were statistically significant. These results indicate that as conflict demands increase, so do RT costs.

A switch by conflict interaction was also statistically significant, $F(36, 210)$ = 3.08, p < .05. Three switch (repeat, attention switch, and response switch) by conflict (no conflict, attentional conflict, response conflict, and all conflict) repeated measures ANOVAs were employed to analyze the simple main effects. The first analysis revealed there were significant RT costs associated with the different types of conflict on "repeat" trials, $F(3, 108)$ = 35.79, p < .001. Post-hoc paired-samples t-tests with Bonferroni correction (alpha= .008) for multiple comparisons indicated increased RTs costs consistent with expected differences between conflict processing demands. Results revealed shorter RTs on "no conflict" trials (M = 1261.76; SD = 354.27) than "attentional conflict" trials (M = 1316.82; SD = 385.48), $t(36)$= -3.19, p < .008, followed by shorter RTs on "attentional conflict" trials than "response conflict" trials (M = 1381.67; SD = 378.9), $t(36)$= -3.78, p < .008. Lastly, results indicated there were shorter RTs on "response conflict" trials than "all conflict" trials (M = 1451.58; SD = 382.33), $t(36)$= -3.01, p < .008. The second analysis indicated there were no significant

RT costs associated with the different types of conflict on "attention switch" trials, $F(3, 108) = 1.19$, $p > .05$.

The third analysis showed there were significantly significant RT costs associated with the different types of conflict on "response switch" trials, $F(3, 108) = 4.67$, $p > .05$. Post-hoc paired-samples t-tests with Bonferroni correction (alpha= .008) for multiple comparisons indicated that RTs were shorter on "no conflict" trials ($M = 1372.68$; $SD = 413.47$) than on "response conflict" trials ($M = 1478.97$; $SD = 413.26$), $t(36)= -3.64$, $p < .008$, and on "all conflict" trials ($M = 1485.98$; $SD = 438.11$), $t(36)= -3.03$, $p < .008$. No other pairwise comparisons were statistically significant.

Finally, there was a statistically significant age (e.g., old and young) by switch interaction, $F(2, 70) = 4.31$, $p < .001$. Three one-way ANOVAs with Bonferroni correction (alpha= .016) for multiple comparisons were used to examine differences between older and younger adults across the different levels of task-switching. Results indicated that RTs of older adults ($M = 1606.12$; $SD = 327.34$) were longer than younger adults ($M = 1113.12$; $SD = 213.41$) on "repeat" trials, $F(1, 35) = 29.78$, $p < .016$. Findings also indicated that RTs of older adults ($M = 1635.56$; $SD = 331.2$) were longer than younger adults ($M = 1162.04$; $SD = 260$) on "attentional switch" trials, $F(1, 35) = 23.54$, $p < .016$. Finally, results indicated that RTs of older adults ($M = 1718.14$; $SD = 351.11$) were longer than younger adults ($M = 1164.61$; $SD = 253.2$) on "response switch" trials, $F(1, 35) = 30.5$, $p < .016$. No other main effects or interactions of the age by switch by conflict omnibus repeated mixed measures ANOVA were statistically significant.

Kinematic Data

One-way ANOVAs with Bonferroni correction (alpha= .005) for multiple comparisons were used to examine differences between older and younger adults on kinematic measures. Due to low frequency of incorrect responses for both younger (M = 7.79; SD = 7.73) and older adults (M = 7.22; SD = 7.86), F(1, 35) = 0.49, p > .05, all reported analyses of kinematic variables are limited to data collected on correct trials.

Speed. There was a significant effect for mean velocity, F(1, 35) = 23.39, p < .005, with older adults demonstrating slower overall responses (M = 3.31; SD = 1.07) than younger adults (M = 4.97 ms; SD = 1). Mean acceleration was also significant, F(1, 35) = 21, p < .005, indicating overall acceleration was greater for younger adults (M = 0.34; SD = 0.12) than older adults (M = 0.18; SD = 0.09). Older adults had significantly smaller peak velocities (M = 6.54; SD = 1.82) than younger adults (M = 9.49; SD = 2), F(1, 35) = 23.55, p < .005, as well as smaller peak accelerations (M = .46; SD = .18) than younger adults (M = .74; SD = .21), F(1, 35) = 19.66, p < .005.

Guidance. A significant effect was demonstrated for the asymmetry ratio, F(1, 35) = 9.48 p < .005, indicating that older adults (M = 0.51; SD = 0.06) demonstrated more difficulty in the terminal guidance of their responses compared to younger adults (M = 0.56; SD = 0.05).

Fluency. There was a significant effect for NIV, F(1, 35) = 15.1, p < .005, indicating that younger adults (M = 3.33; SD = .47) demonstrated more control and automatization of responses compared to older adults (M = 4.27; SD = 1.27).

ANJ was also significant, $F(1, 37) = 14.72$, revealing that older adults ($M = 30.82$;

$SD = 13.45$) showed less smooth responses than younger adults ($M = 18.76$;

$SD = 4$).

      Decision time. There was a significant effect for decision time, $F(1, 35) =$

31.56, $p < .005$, demonstrating that older adults ($M = 1168.02$ ms; $SD = 265.1$

ms) took longer to initiate responses than younger adults ($M = 752.3$ ms; $SD =$

194.2 ms).

Electrophysiological Analysis

      The separate ICA decompositions applied to the target onset and

movement initiation data indicated that six and five components accounted for

more than 90% of the variance, respectively. Topographical maps and grand

averaged ERPs of these components are presented in Figure 2 and Figure 3. In

the interest of parsimony, we limited component ERP image analyses to two

measured kinematic variables, movement initiation time and mean velocity of

response. Pearson product-moment correlations were employed to determine if

the features (e.g., peaks and troughs) of the component ERP images were

related to the kinematic variables. "Significant" correlations between the

amplitude and latency of features and kinematic measures were defined as those

with a value greater than or equal to .7 (i.e., >50% variance accounted for),

indicating a "large" effect. Time windows used to characterize the component

ERP image features were identified using the complete sample ERP image

sorted by movement initiation time. Conventional ERP labeling was used to

describe the peaks and troughs identified in the component ERP images.

Target Onset Data

Data segments time-locked to target onset spanned a -200 to 1000 ms interval and were baseline corrected between -200 and 0 ms. The ICA decomposition of the data segments reflects a subset of data between 200 ms prior to target onset and 100 ms prior to movement initiation.

Component 1 and 2. ERP images for components 1 and 2 are presented in Figure 4 and Figure 5, respectively. The scalp topography for component 1 was characterized by a central positivity. Two time windows were used to characterize the P1 (100 – 300 ms) and P2 (300 – 800 ms) features of the ERP images. No relationships between the amplitude or latency of the features and the kinematic measures were statistically significant.

Component 2 was characterized by a medial prefrontal negative scalp topography. Three time windows were used to characterize the P1 (100 – 200 ms), N1 (250 – 600), and N2/P2 (600 – 1900 ms) features of the ERP images. Results for the ERP image features sorted by movement initiation time indicated several statistically significant relationships. Peak amplitude of the N1 feature was positively related to the timing of movement initiation for older adults, r (3325) = .71, $p < .001$, but negatively related to movement initiation for younger adults, r (3636) = -.31, $p < .001$. Peak amplitude of the N2 feature was also positively related to the timing of movement initiation for older adults, r (3325) = .82, $p < .001$, but inversely related to movement initiation for younger adults, r (3636) = -.61, $p < .001$. In addition, the latency of the N2 feature was positively related to the timing of movement initiation for both younger, r (3636) = .87, p

< .001, and older adults r (3325) = .73, p < .001. No relationships between the amplitude or latency of the features and the mean velocity of the response were statistically significant.

Component 3 and 4. ERP images for components 3 and 4 are presented in Figure 6 and Figure 7, respectively. Component 3 was characterized by a posterior negative scalp topography. Three time windows were used to characterize the P1 (0 – 100 ms), N1 (130 – 200), and N2/P2 (320 – 1900 ms) features of the ERP images. Results for the ERP image features sorted by movement initiation time indicated several statistically significant relationships. Peak amplitude of the N1 feature was positively related to the timing of movement initiation for both younger, r (3636) = .72, p < .001, and older adults r (3325) = .85, p < .001. Peak amplitude of the N2 feature was also positively related to the timing of movement initiation for both younger, r (3636) = .81, p < .001, and older adults r (3325) = .36, p < .001. In addition, peak amplitude of the P2 feature was also positively related to the timing of movement initiation for both younger, r (3636) = .75, p < .001, and older adults r (3325) = .58, p < .001. No relationships between the amplitude or latency of the features and the mean velocity of the response were statistically significant.

The scalp topography for component 4 was characterized by a parieto-central positivity. Two time windows were used to characterize the P1 (50 – 120 ms) and N1/P2 (320 – 1900 ms) features of the ERP images. Results for the ERP image features sorted by movement initiation time indicated several statistically significant relationships. Peak amplitude of the N1 feature was

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positively related to the timing of movement initiation for both younger, r (3636) = .79, $p < .001$, and older adults r (3325) = .63, $p < .001$. In addition, the latency of the P2 feature was positively related to the timing of movement initiation for both younger, r (3636) = .86, $p < .001$, and older adults r (3325) = .62, $p < .001$. No relationships between the amplitude or latency of the features and the mean velocity of the response were statistically significant.

Component 5 and 6. ERP images for components 5 and 6 are presented in Figure 8 and Figure 9, respectively. Component 5 was characterized by a parietally distributed negative scalp topography. Three time windows were used to characterize the P1 (70 – 130 ms), N1 (140 – 210), and P2 (300 – 1900 ms) features of the ERP images. Results for the ERP image features sorted by movement initiation time indicated that the peak amplitude of the P2 feature was positively related to the timing of movement initiation for both younger, r (3636) = .73, $p < .001$, and older adults r (3325) = .12, $p < .001$. No relationships between the amplitude or latency of the features and the mean velocity of the response were statistically significant.

The scalp topography of component 6 was characterized by a lateralized parietal positivity and negativity. Two time windows were used to characterize the P1 (120 – 200 ms) and N1 (330 – 1900) features of the ERP images. No relationships between the amplitude or latency of the features and the kinematic measures were statistically significant.

Movement Onset Data

Data segments time-locked to movement initiation spanned a -1000 to 2000 ms interval and were baseline corrected using the mean of the full interval between -1000 and 2000 ms. The ICA decomposition of the data segments reflects a subset of data between 100 ms prior to movement initiation and 200 ms following the completion of the movement. In the interest of interpretability, ERP images sorted with respect to movement initiation time were plotted in reverse in order to reflect target onset latencies.

Component 1 and 2. ERP images for components 1 and 2 are presented in Figure 10 and Figure 11, respectively. The scalp topography for component 1 was characterized by a fronto-central positivity. One time window was used to characterize the N1 (-1000 – 0) baseline feature of the ERP images and two time windows were used to characterize the P1 (-200 – 300 ms) and P2 (400 – 1500 ms) features localized around and after the time-locked movement initiation event. Results for the ERP image features sorted by target onset latency indicated several statistically significant relationships. Peak amplitude of the N1 feature was positively related to the timing of the target onset for both younger, r (3636) = .77, $p < .001$, and older adults r (3325) = .21, $p < .001$. In addition, peak latency of the N1 feature was positively related to the timing of the target onset for both younger, r (3636) = .89, $p < .001$, and older adults r (3325) = .68, $p < .001$. Peak amplitude of the P2 feature was also positively related to the timing of the target onset for both younger, r (3636) = .73, $p < .001$, and older adults r

(3325) = .4, *p* < .001. No relationships between the amplitude or latency of the features and the mean velocity of response were statistically significant.

The scalp topography of component 2 was characterized by a posterior negativity. One time window was used to characterize the P1 (-1000 – 0) baseline feature of the ERP images and two time windows were used to characterize the N1 (0 – 130 ms) and P2 (200 – 1300 ms) features localized around and after the time-locked movement initiation event. Results for the ERP image features sorted by target onset latency indicated the peak amplitude of the P1 feature was positively related to the timing of the target onset for both younger, *r* (3636) = .77, *p* < .001, and older adults *r* (3325) = .42, *p* < .001. No relationships between the amplitude or latency of the features and the mean velocity of response were statistically significant.

Component 3, 4, and 5. ERP images for components 3, 4, and 5 are presented in Figure 12, Figure 13, and Figure 14, respectively. The scalp topography for component 3 was characterized by a medial prefrontal negativity. One time window was used to characterize the N1 (-1000 – 200) baseline feature of the ERP images and one time window was used to characterize the N1 (250 – 1300 ms) feature after the time-locked movement initiation event. No relationships between the amplitude or latency of the features and the sorting variables were statistically significant.

The scalp topography for component 4 was characterized by a parieto-central negativity. One time window was used to characterize the P1/N1 (-1000 – 0) baseline features of the ERP images and two time windows were used to

characterize the P2 (150 – 400 ms) and N2 (500 – 1100 ms) features after the time-locked movement initiation event. Results for the ERP image features sorted by target onset latency indicated several statistically significant relationships. Peak amplitude of the P1 feature was positively related to the timing of the target onset for both younger, r (3636) = .87, $p < .001$, and older adults r (3325) = .34, $p < .001$. In addition, peak latency of the N1 feature was positively related to the timing of the target onset for both younger, r (3636) = .87, $p < .001$, and older adults r (3325) = .34, $p < .001$. Results for the ERP image features sorted by mean velocity of response also indicated several statistically significant relationships. Peak amplitude of the P1 feature was positively related to the mean velocity of the response for both younger, r (3636) = .84, $p < .001$, and older adults r (3325) = .59, $p < .001$. The peak latency of the P2 feature was positively related to the mean velocity of response for both younger, r (3636) = .67, $p < .001$, and older adults r (3325) = .78, $p < .001$. Lastly, the peak amplitude of the N2 feature was positively related to the mean velocity of response for younger adults, r (3636) = .73, $p < .001$, but negatively related to the mean velocity of response for older adults, r (3325) = -.72, $p < .001$.

The scalp topography of component 5 was characterized by a lateralized parietal positivity and negativity. One time window was used to characterize the P1 (-1000 – 0) baseline feature of the ERP images and one time window was used to characterize the N1 (0 – 1300 ms) feature after the time-locked movement initiation event. No relationships between the amplitude or latency of the features and the sorting variables were statistically significant.

Discussion

The primary aim of the present research was to investigate a procedure for disassociating perceptual, cognitive, and motor processing using single-trial EEG analyses. By extracting the kinematic properties of dynamic responses, we have demonstrated the usefulness of this procedure for achieving these goals. In addition, we have shown that perceptual and motor processes do not always adhere to discrete modular stages in EEG. Furthermore, we have provided evidence that these processes might be altered in normal cognitive aging.

One particularly interesting outcome of the analysis was the stark similarity between the two ICA decompositions despite the fact that the analyses were trained on non-overlapping subsets of the target and movement-locked data segments, the results indicated highly correlated components with nearly identical topographical distributions (see Figure 15). In order to facilitate a parsimonious interpretation of the component ERP image findings, discussion of the ERP images time-locked to target onset and movement initiation will be grouped according to their topographies.

Posterior Negativity

The scalp topography of component 3 (target onset) and component 2 (movement onset) were both characterized by a posterior negativity maximal over the occipital cortex. Features of the target-locked component 3 ERP image sorted by movement initiation time revealed a P1 feature that was unrelated to the timing of movement initiation, suggesting it reflected a sensory or perceptual process. The amplitude of the N1 feature that followed the P1 was positively

related to the timing of response initiation for both younger and older adults, indicating it reflected a perceptual or cognitive process. We interpret these features as being analogous to the P1/N1 visual evoked components that reflect stimulus processing in an averaged ERP. This interpretation is supported by several studies demonstrating that N1 amplitude is an index of attentional discrimination and is characterized by a parietal negativity that peaks around 150 ms (Mangun, 1995). Furthermore, N1 amplitude increases as task demands increase, resulting in longer reaction times (Vogel & Luck, 2000). Thus, our finding that N1 amp is positively related to response initiation time is consistent with this interpretation.

Concerning features of the movement-locked component 2 ERP image sorted by movement initiation, the baseline P1 amplitude that is positively related to the timing of stimulus onset most likely reflects the visual evoked P1/N1 features seen in the stimulus-locked component ERP image. Given that no features of the target or movement-locked ERP images were related to the mean velocity of the response, we interpret these components as primarily reflecting sensory, perceptual, and cognitive processes that are unrelated to the kinematic qualities of the response. These components seemed to be involved in the visual processing and discrimination of the target stimulus. The relationship between the N1 component and faster movement initiation might reflect the quality of visual and discrimination processing rather than any sort of perceptual-motor integration or overlap.

Medial Prefrontal Negativity

The scalp topography of component 2 (target onset) and component 3 (movement onset) were both characterized by a negativity maximal over medial prefrontal cortex. Features of the target-locked component 2 ERP image sorted by movement initiation time revealed a P1 feature that was unrelated to the timing of movement initiation, suggesting it reflected a purely sensory or perceptual process. The amplitude of the N1 and N2 features that followed the P1 were positively related to the timing of response initiation for older adults, but negatively related to movement initiation time in younger adults, indicating they reflected a perceptual or cognitive process. Furthermore, the latency of the N2 feature was also positively related to the timing of response initiation, suggesting it was related to both cognitive and motor processes. We interpret these findings as reflecting executive control and motor planning.

It is well established that the prefrontal cortex (PFC) plays an important role in "top-down" executive control of goal-directed behavior (for a review, see Ridderinkhof, van den Wildenberg, Segalowitz, & Carter, 2004). PFC control is required when simple, automatic stimulus-responses mappings are insufficient for organizing and responding to current goals or task demands (Miller & Cohen, 2001; Potts, Martin, Burton, & Montague, 2006). It is theorized that the PFC exerts this control by maintaining internal representations of the rules and action plans needed to respond to task-relevant goals, and then providing a biasing signal that organizes and selects the most appropriate response from those internal representations (Potts et al., 2006). There is extensive evidence

demonstrating that processes controlled by the PFC, such as inhibition and motor planning, decline as we age (West, 1996). Although the current analyses do not afford a conclusive interpretation, we conjecture that the N1/N2 feature differences between older and younger adults may reflect slower or more dysfunctional cognitive control and response selection processes in older adults.

Concerning features of the target-locked component 2 and movement-locked component 3 ERP images sorted by movement initiation and mean velocity of response, no features were related to the kinematic measures. Thus, only the target-locked features sorted by movement initiation time seem to reflect any sort of cognitive and motor processes.

Parietal Positivity/Negativity

The scalp topography of component 4 for target onset was characterized by a parietal positivity whereas component 4 for movement onset had a parietal negativity distribution. Features of the target-locked component 4 ERP image sorted by movement initiation time revealed a P1 feature that was unrelated to the timing of movement initiation, suggesting it reflected a purely sensory or perceptual process. The amplitude of the N1 feature that followed the P1 was positively related to the timing of response initiation for both younger and older adults, indicating it reflected a perceptual or cognitive process. The latency of the P2 post-movement initiation feature was positively related to the timing of movement initiation for both younger and older adults, suggesting this feature reflected both cognitive and motor processes. Features of the target-locked

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component 4 ERP image were not related to the mean velocity of the subsequent movement.

The features of the component 4 ERP image sorted by mean velocity of response revealed several interesting findings related to sensory-motor integration/processing. For instance, the latency of the P1 feature that occurred after movement initiation was positively related to the mean velocity of the executed movement. On trials where older and younger adults moved quickly, this P1 feature occurred earlier suggesting it was related to both cognitive and motor processing. Interestingly, the amplitude of the N1 feature that followed the P1 was also positively related to the mean velocity, suggesting it was only related to cognitive and perceptual processing. Thus, these processes seem to be occurring in a continuous, or parallel manner rather than strictly serially. These findings may reflect processes of evidence accumulation and/or decisional certainty.

Given that the P1 feature occurred sooner and was followed by smaller N1 amplitude when responses were faster overall, we interpret the latency of the P1 as reflecting a degree of decisional certainty/evidence accumulation and the amplitude of the N1 as reflecting a degree of decisional uncertainty. Several lines of recent evidence support this interpretation (Cisek, 2007; Cisek & Kalaska, 2010). For instance, it has been shown that the brain prepares a motor response while it is accumulating the evidence to make a decision and once that evidence reaches some threshold, the action is executed (Paul Cisek & Kalaska, 2010; Gold & Shadlen, 2007; Shadlen, Kiani, Hanks, & Churchland, 2008).

Limitations

Due to the large number of components identified by the ICA decompositions, as well as the inclusion of an aging cohort, kinematic and EEG analyses were limited. Even so, we have demonstrated the usefulness of kinematics and single-trial analysis for investigating relationships between EEG measures and motor responses. In addition, statistical limitations (i.e., large degrees of freedom) made it difficult to determine if statistically significant correlation differences between older and younger adults were meaningfully different (e.g., large effect size). However, it seems reasonable to assume that several of our large correlation differences do indicate that the perceptual, cognitive, and motor processing of older adults, as reflected in the single-trial analyses, are altered in normal cognitive aging.

Furthermore, high performance on the task-set switching procedure, coupled with the aforementioned data reduction problems, made it difficult to investigate how task switching and conflict processing contributed to perception-motor relationships in the single-trial analyses. In the future, by further optimizing our analysis approach, we can investigate how high and low conflict processing was related to the single-trial EEG dynamics and properties of behavioral responses.

Conclusions

In conclusion, the present findings suggest that properties of motor response are reflected in EEG and may be altered in normal cognitive aging. Furthermore, we have provided novel evidence demonstrating the usefulness of

trial-level EEG analysis for disassociating perceptual, cognitive, and motor processes. Future research should continue to investigate how perception and motor relationships are reflected in dynamic EEG by using advanced image analyses and kinematic methods. For instance, displacement data can be collected using digitizing tablets and a stylus pen (Caligiuri, Teulings, Dean, Niculescu III, & Lohr, 2010). One benefit to using digitizing tablets is that they afford measurement of force control and pen pressure, which could provide indices of gross motor control. The familiarity of a stylus pen might be especially useful when studying clinical populations when task difficulty is a concern. Furthermore, several digital imaging techniques might be particularly useful for characterizing dynamic EEG data.

Blob detection is a method for extracting pixel "blobs", or subsections of a digital image that are similar and clustered together (see Shneier, 1983). This method could be a powerful way to extract, characterize, and analyze the dynamic trial-level EEG features. In addition, trial-level data could represented in 3-dimensions and object-based image analysis could be used to characterize not only the spectral and temporal qualities of the image but also their shapes and relationships (see Blaschke, 2010).

In conclusion, given the important relationships between perceptual and motor processes demonstrated in the present research using dynamic measures of motor response and single-trial analysis, it is critical that cognitive neuroscience research using EEG begins to address these important questions about the translation between perception and responses.

References

Ackermann, H., Mathiak, K., & Ivry, R. B. (2004). Temporal Organization of
    "Internal Speech" As a Basis for Cerebellar Modulation of Cognitive
    Functions. *Behavioral and Cognitive Neuroscience Reviews*, *3*(1), 14–22.
    http://doi.org/10.1177/1534582304263251

Alexander, G. E., & Crutcher, M. D. (1990). Neural representations of the target
    (goal) of visually guided arm movements in three motor areas of the
    monkey. *Journal of Neurophysiology*, *64*(1), 164–178.

Alexander, G. E., DeLong, M. R., & Strick, P. L. (1986). Parallel Organization of
    Functionally Segregated Circuits Linking Basal Ganglia and Cortex.
    Annual Review of Neuroscience, *9*(1), 357–381.
    http://doi.org/10.1146/annurev.ne.09.030186.002041

Bellgrove, M. A., Phillips, J. G., Bradshaw, J. L., & Gallucci, R. M. (1998).
    Response (Re-)Programming in Aging: A Kinematic Analysis. *The
    Journals of Gerontology Series A: Biological Sciences and Medical
    Sciences*, *53A*(3), M222–M227. http://doi.org/10.1093/gerona/53A.3.M222

Bernard, J. A., & Mittal, V. A. (2014). Cerebellar-motor dysfunction in
    schizophrenia and psychosis-risk: the importance of regional cerebellar
    analysis approaches. *Frontiers in Psychiatry*, *5*, 160.
    http://doi.org/10.3389/fpsyt.2014.00160

Birren, J. E., & Fisher, L. M. (1995). Aging and Speed of Behavior: Possible
    Consequences for Psychological Functioning. *Annual Review of*

Psychology, *46*(1), 329–353.

http://doi.org/10.1146/annurev.ps.46.020195.001553

Blaschke, T. (2010). Object based image analysis for remote sensing. *ISPRS Journal of Photogrammetry and Remote Sensing*, *65*(1), 2–16. http://doi.org/10.1016/j.isprsjprs.2009.06.004

Cabeza, R., & Nyberg, L. (2000). Imaging Cognition II: An Empirical Review of 275 PET and fMRI Studies. *Journal of Cognitive Neuroscience*, *12*(1), 1–47. http://doi.org/10.1162/08989290051137585

Caligiuri, M. P., Teulings, H.-L., Dean, C. E., Niculescu III, A. B., & Lohr, J. B. (2010). Handwriting movement kinematics for quantifying extrapyramidal side effects in patients treated with atypical antipsychotics. *Psychiatry Research*, *177*(1–2), 77–83. http://doi.org/10.1016/j.psychres.2009.07.005

Cisek, P. (2007). Cortical mechanisms of action selection: the affordance competition hypothesis. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *362*(1485), 1585–1599. http://doi.org/10.1098/rstb.2007.2054

Cisek, P., & Kalaska, J. F. (2010). Neural Mechanisms for Interacting with a World Full of Action Choices. *Annual Review of Neuroscience*, *33*(1), 269–298. http://doi.org/10.1146/annurev.neuro.051508.135409

Contreras-Vidal, J. L., Teulings, H., & Stelmach, G. (1998). Elderly subjects are impaired in spatial coordination in fine motor control. *Acta Psychologica*, *100*(1-2), 25–35. http://doi.org/10.1016/S0001-6918(98)00023-7

Crammond, D. J., & Kalaska, J. F. (2000). Prior information in motor and premotor cortex: activity during the delay period and effect on pre-movement activity. *Journal of Neurophysiology*, *84*(2), 986–1005.

Creem-Regehr, S. H., & Kunz, B. R. (2010). Perception and action. *Wiley Interdisciplinary Reviews: Cognitive Science*, *1*(6), 800–810. http://doi.org/10.1002/wcs.82

Danna, J., Paz-Villagrán, V., & Velay, J.-L. (2013). Signal-to-noise velocity peaks difference: a new method for evaluating the handwriting movement fluency in children with dysgraphia. *Research in Developmental Disabilities*, *34*(12), 4375–4384. http://doi.org/10.1016/j.ridd.2013.09.012

Daum, I., Beth, E., & Snitz, H. A. (2001). Neuropsychological deficits in cerebellar syndromes. *International Review of Psychiatry*, *13*(4), 268–275. http://doi.org/10.1080/09540260127527

Delorme, A., & Makeig, S. (2004). EEGLAB: an open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *Journal of Neuroscience Methods*, *134*(1), 9–21. http://doi.org/10.1016/j.jneumeth.2003.10.009

Donkers, F. C. L., & van Boxtel, G. J. M. (2004). The N2 in go/no-go tasks reflects conflict monitoring not response inhibition. *Brain and Cognition*, *56*(2), 165–176. http://doi.org/10.1016/j.bandc.2004.04.005

Doya, K. (2000). Complementary roles of basal ganglia and cerebellum in learning and motor control. *Current Opinion in Neurobiology*, *10*(6), 732–739. http://doi.org/10.1016/S0959-4388(00)00153-7

Eimer, M. (1998). The lateralized readiness potential as an on-line measure of

central response activation processes. *Behavior Research Methods,*

Instruments, & Computers, *30*(1), 146–156.

http://doi.org/10.3758/BF03209424

Falkenstein, M., Yordanova, J., & Kolev, V. (2006). Effects of aging on slowing of

motor-response generation. *International Journal of Psychophysiology*,

59(1), 22–29. http://doi.org/10.1016/j.ijpsycho.2005.08.004

Folstein, M. F., Folstein, S. E., & McHugh, P. R. (1975). "Mini-mental state."

Journal of Psychiatric Research, *12*(3), 189–198.

http://doi.org/10.1016/0022-3956(75)90026-6

Gao, J.-H., Parsons, L. M., Bower, J. M., Xiong, J., Li, J., & Fox, P. T. (1996).

Cerebellum Implicated in Sensory Acquisition and Discrimination Rather

Than Motor Control. *Science*, *272*(5261), 545–547.

http://doi.org/10.1126/science.272.5261.545

Gold, J. I., & Shadlen, M. N. (2007). The Neural Basis of Decision Making.

Annual Review of Neuroscience, *30*(1), 535–574.

http://doi.org/10.1146/annurev.neuro.29.051605.113038

Jung, T.-P., Makeig, S., Humphries, C., Lee, T.-W., McKeown, M. J., Iragui, V., &

Sejnowski, T. J. (2000). Removing electroencephalographic artifacts by

blind source separation. *Psychophysiology*, *37*(2), 163–178.

http://doi.org/10.1111/1469-8986.3720163

Ketcham, C. J., Seidler, R. D., Van Gemmert, A. W. A., & Stelmach, G. E. (2002).

Age-Related Kinematic Differences as Influenced by Task Difficulty,

Target Size, and Movement Amplitude. *The Journals of Gerontology Series B: Psychological Sciences and Social Sciences*, *57*(1), P54–P64. http://doi.org/10.1093/geronb/57.1.P54

Kieffaber, P. D., Kruschke, J. K., Cho, R. Y., Walker, P. M., & Hetrick, W. P. (2012). Dissociating Stimulus-Set and Response-Set in the Context of Task-Set Switching. *Journal of Experimental Psychology: Human Perception and Performance*. http://doi.org/10.1037/a0029545

Knoblich, G., & Flach, R. (2001). Predicting the Effects of Actions: Interactions of Perception and Action. *Psychological Science*, *12*(6), 467–472. http://doi.org/10.1111/1467-9280.00387

Leiner, H. C., Leiner, A. L., & Dow, R. S. (1989). Reappraising the cerebellum: What does the hindbrain contribute to the forebrain? *Behavioral Neuroscience*, *103*(5), 998–1008. http://doi.org/10.1037//0735-7044.103.5.998

Llinás, R. R. (2001). *I of the vortex: from neurons to self* (1st ed). Cambridge, Mass: MIT Press.

Lopez-Calderon, J., & Luck, S. J. (2014). ERPLAB: an open-source toolbox for the analysis of event-related potentials. *Frontiers in Human Neuroscience*, *8*. http://doi.org/10.3389/fnhum.2014.00213

Makeig, S., Debener, S., Onton, J., & Delorme, A. (2004). Mining event-related brain dynamics. *Trends in Cognitive Sciences*, *8*(5), 204–210.

Mangun, G. R. (1995). Neural mechanisms of visual selective attention. *Psychophysiology*, *32*(1), 4–18.

Marr, D. (2010). *Vision: a computational investigation into the human representation and processing of visual information*. Cambridge, Mass: MIT Press.

Middleton, F. (2000). Basal ganglia and cerebellar loops: motor and cognitive circuits. *Brain Research Reviews*, *31*(2-3), 236–250. http://doi.org/10.1016/S0165-0173(99)00040-5

Miller, E. K., & Cohen, J. D. (2001). An integrative theory of prefrontal cortex function. *Annual Review of Neuroscience*, *24*, 167–202. http://doi.org/10.1146/annurev.neuro.24.1.167

Nagasaki, H. (1989). Asymmetric velocity and acceleration profiles of human arm movements. *Experimental Brain Research*, *74*(2). http://doi.org/10.1007/BF00248865

Newell, A., & Simon, H. A. (1972). *Human problem solving*. Englewood Cliffs, N.J: Prentice-Hall.

O'Bryant, S. E., Humphreys, J. D., Smith, G. E., Ivnik, R. J., Graff-Radford, N. R., Petersen, R. C., & Lucas, J. A. (2008). Detecting Dementia With the Mini-Mental State Examination in Highly Educated Individuals. *Archives of Neurology*, *65*(7). http://doi.org/10.1001/archneur.65.7.963

Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia*, *9*(1), 97–113. http://doi.org/10.1016/0028-3932(71)90067-4

Parsons, L. M. (1994). Temporal and kinematic properties of motor behavior reflected in mentally simulated action. *Journal of Experimental*

Psychology: Human Perception and Performance, *20*(4), 709–730. http://doi.org/10.1037/0096-1523.20.4.709

Phillips, J. G., & Triggs, T. J. (2001). Characteristics of cursor trajectories controlled by the computer mouse. *Ergonomics*, *44*(5), 527–536. http://doi.org/10.1080/00140130121560

Potts, G. F., Martin, L. E., Burton, P., & Montague, P. R. (2006). When Things Are Better or Worse than Expected: The Medial Frontal Cortex and the Allocation of Processing Resources. *Journal of Cognitive Neuroscience*, *18*(7), 1112–1119. http://doi.org/10.1162/jocn.2006.18.7.1112

Pozzo, T., Papaxanthis, C., Petit, J. L., Schweighofer, N., & Stucchi, N. (2006). Kinematic features of movement tunes perception and action coupling. *Behavioural Brain Research*, *169*(1), 75–82. http://doi.org/10.1016/j.bbr.2005.12.005

Ridderinkhof, K. R., van den Wildenberg, W. P. M., Segalowitz, S. J., & Carter, C. S. (2004). Neurocognitive mechanisms of cognitive control: The role of prefrontal cortex in action selection, response inhibition, performance monitoring, and reward-based learning. *Brain and Cognition*, *56*(2), 129–140. http://doi.org/10.1016/j.bandc.2004.09.016

Roberts, L. E., Rau, H., Lutzenberger, W., & Birbaumer, N. (1994). Mapping P300 waves onto inhibition: Go/No☐Go discrimination. *Electroencephalography and Clinical Neurophysiology/Evoked Potentials Section*, *92*(1), 44–55. http://doi.org/10.1016/0168-5597(94)90006-X

Schröter, A., Mergl, R., Bürger, K., Hampel, H., Möller, H.-J., & Hegerl, U. (2003). Kinematic Analysis of Handwriting Movements in Patients with Alzheimer’s Disease, Mild Cognitive Impairment, Depression and Healthy Subjects. *Dementia and Geriatric Cognitive Disorders*, *15*(3), 132–142. http://doi.org/10.1159/000068484

Seidler, R. D., Bernard, J. A., Burutolu, T. B., Fling, B. W., Gordon, M. T., Gwin, J. T., … Lipps, D. B. (2010). Motor control and aging: Links to age-related brain structural, functional, and biochemical effects. *Neuroscience & Biobehavioral Reviews*, *34*(5), 721–733. http://doi.org/10.1016/j.neubiorev.2009.10.005

Shneier, M. (1983). Using Pyramids to Define Local Thresholds for Blob Detection. *IEEE Transactions on Pattern Analysis and Machine Intelligence*, *PAMI-5*(3), 345–349. http://doi.org/10.1109/TPAMI.1983.4767397

Teulings, H.-L., Contreras-Vidal, J. L., Stelmach, G. E., & Adler, C. H. (1997). Parkinsonism Reduces Coordination of Fingers, Wrist, and Arm in Fine Motor Control. *Experimental Neurology*, *146*(1), 159–170. http://doi.org/10.1006/exnr.1997.6507

Tillman, C. M., & Wiens, S. (2011). Behavioral and ERP indices of response conflict in Stroop and flanker tasks: Response conflict in Stroop and flanker tasks. *Psychophysiology*, *48*(10), 1405–1411. http://doi.org/10.1111/j.1469-8986.2011.01203.x

Tucha, O., Mecklinger, L., Thome, J., Reiter, A., Alders, G. L., Sartor, H., …

　　　Lange, K. W. (2006). Kinematic analysis of dopaminergic effects on skilled

　　　handwriting movements in Parkinson's disease. *Journal of Neural*

　　　Transmission, *113*(5), 609–623. http://doi.org/10.1007/s00702-005-0346-9

Viviani, P., & Stucchi, N. (1989). The effect of movement velocity on form

　　　perception: geometric illusions in dynamic displays. *Perception &*

　　　Psychophysics, *46*(3), 266–274.

Viviani, P., & Stucchi, N. (1992). Biological movements look uniform: Evidence of

　　　motor-perceptual interactions. *Journal of Experimental Psychology:*

　　　Human Perception and Performance, *18*(3), 603–623.

　　　http://doi.org/10.1037/0096-1523.18.3.603

Vogel, E. K., & Luck, S. J. (2000). The visual N1 component as an index of a

　　　discrimination process. *Psychophysiology*, *37*(2), 190–203.

Wallis, J. D. (2003). From Rule to Response: Neuronal Processes in the

　　　Premotor and Prefrontal Cortex. *Journal of Neurophysiology*, *90*(3), 1790–

　　　1806. http://doi.org/10.1152/jn.00086.2003

West, R. L. (1996). An application of prefrontal cortex function theory to cognitive

　　　aging. *Psychological Bulletin*, *120*(2), 272–292.

　　　http://doi.org/10.1037/0033-2909.120.2.272

Wolpert, D. M., Doya, K., & Kawato, M. (2003). A unifying computational

　　　framework for motor control and social interaction. *Philosophical*

　　　Transactions of the Royal Society B: Biological Sciences, *358*(1431), 593–

　　　602. http://doi.org/10.1098/rstb.2002.1238

Yordanova, J. (2004). Sensorimotor slowing with ageing is mediated by a

functional dysregulation of motor-generation processes: evidence from

high-resolution event-related potentials. *Brain, 127*(2), 351–362.

http://doi.org/10.1093/brain/awh042
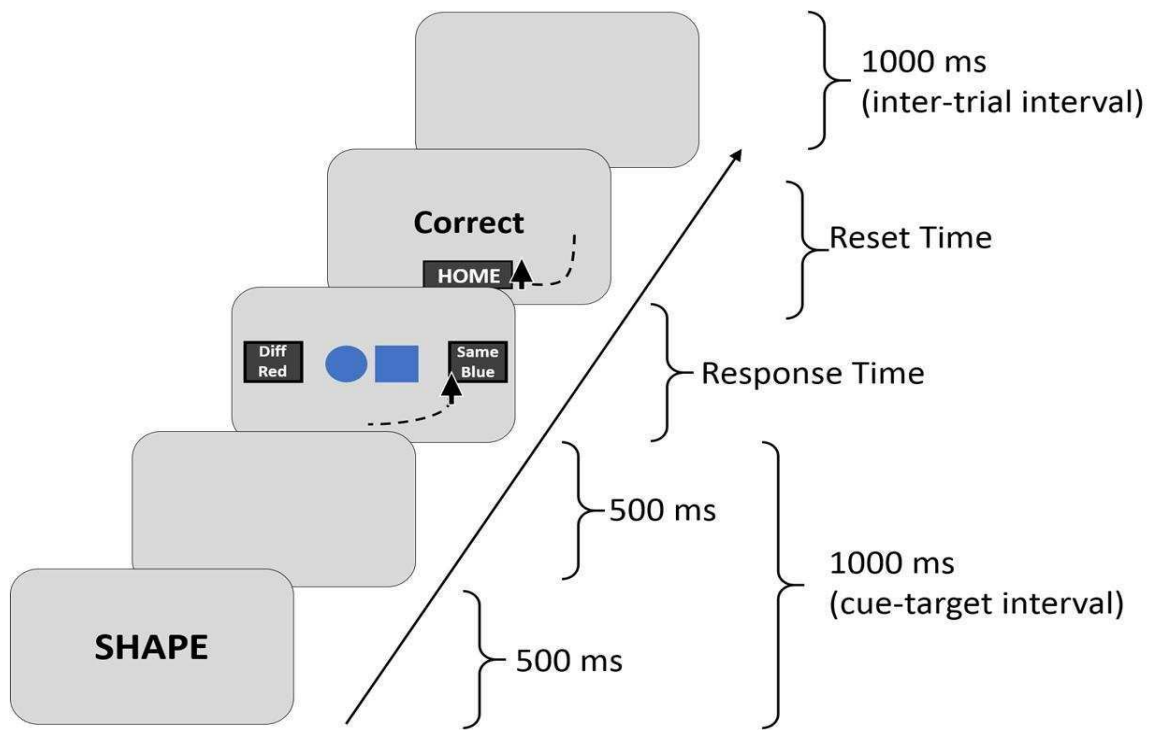
Figure 1. Schematic of task-set switching trial (Kieffaber et al., 2012).
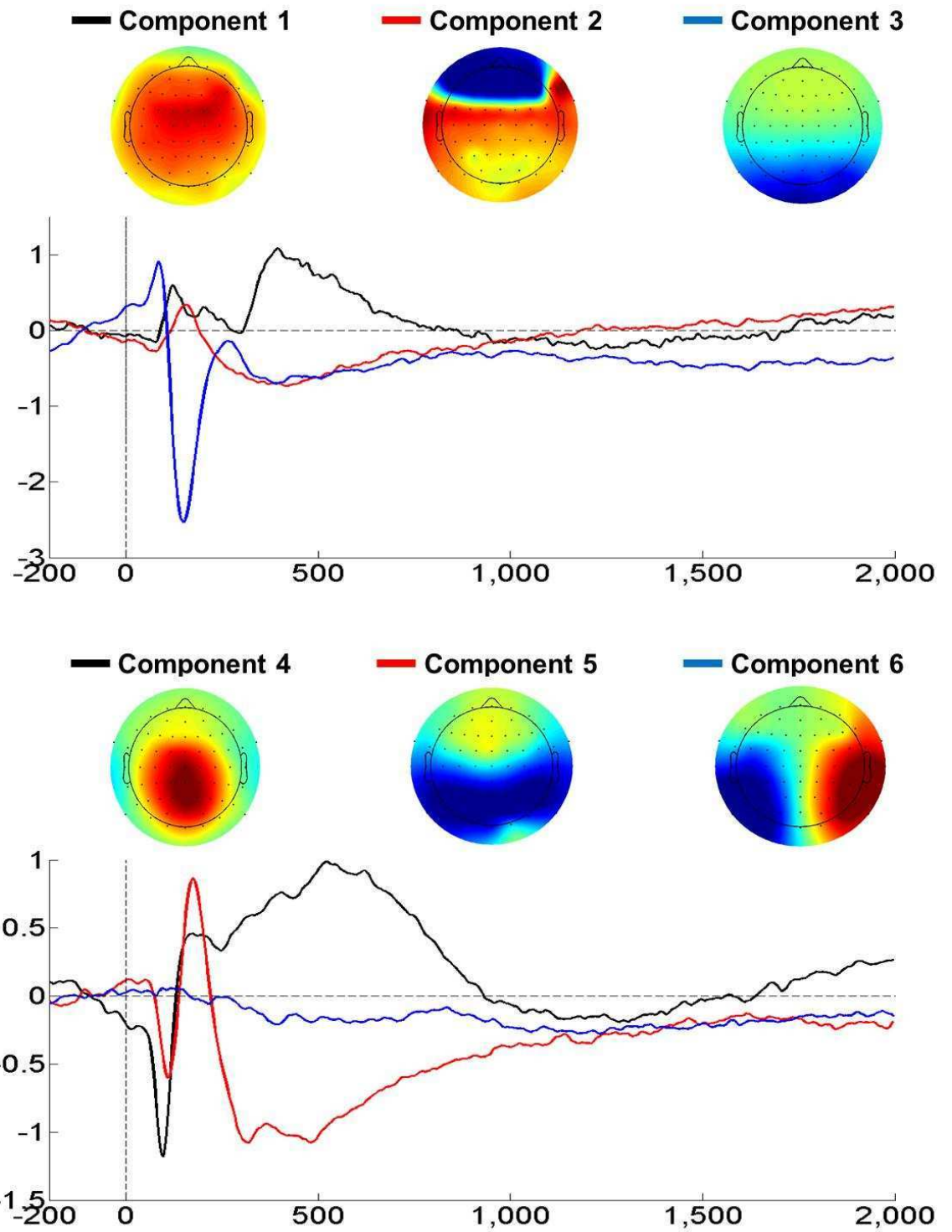
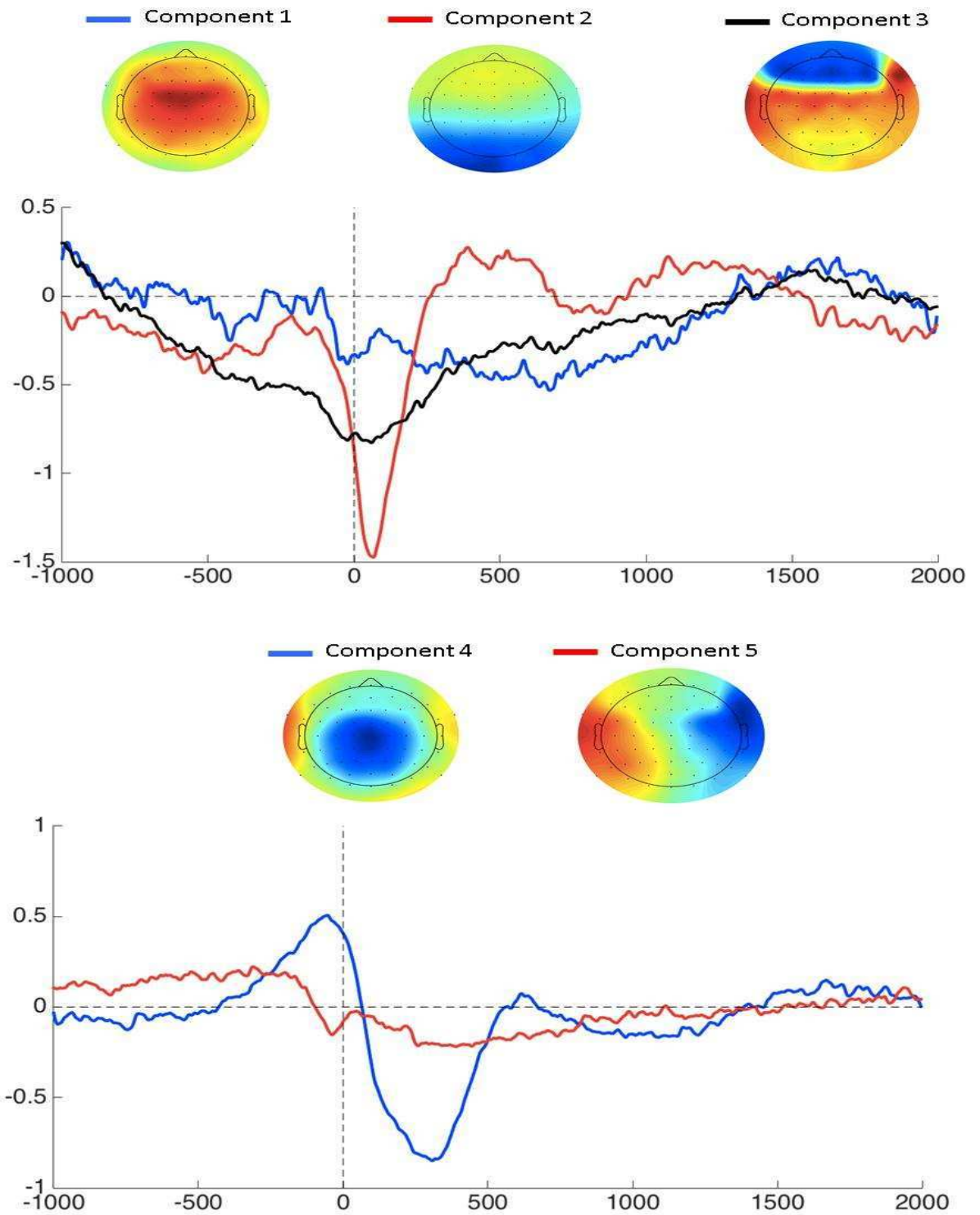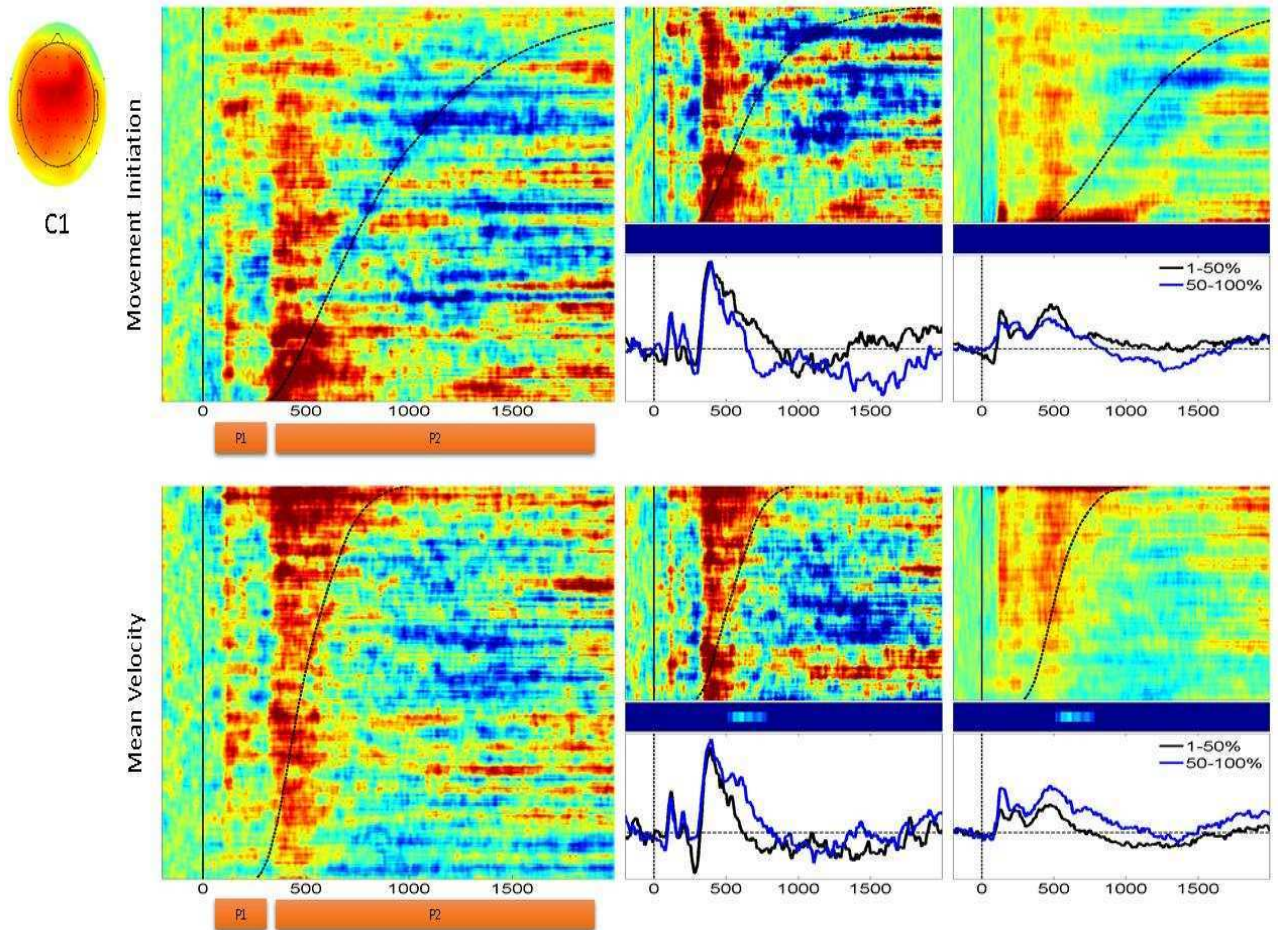*Figure 2*. Target onset component topographies and grand averaged ERPs.

Figure 3. Movement onset component topographies and grand averaged ERPs.

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Figure 4. ERP images and quantile ERPs for component 1 time-locked to target onset. The first ERP image in each row (reading from left to right) reflect the complete sample (trials for both young and old), and the second (young) and third (old) ERP images reflect the trials for younger and older adults separately. Orange bars underneath the complete set ERP images reflect the features of the image. Below the subsets of ERP images are quantile ERPs representing median splits of the sorting variable. The colored rows above the quantile ERPs of the younger adults reflect the 2 (Age) X 2 (Quantile) ANVOA mean amplitude differences. The top reflects the main effect of age, the middle row reflects the main effect of the sorting variable, and the third row reflects the age x sorting variable interaction. The colored rows above the quantile ERPs of the older adults are reflect the effect sizes of the mean amplitude differences (red being a large effect and blue being a smaller effect).
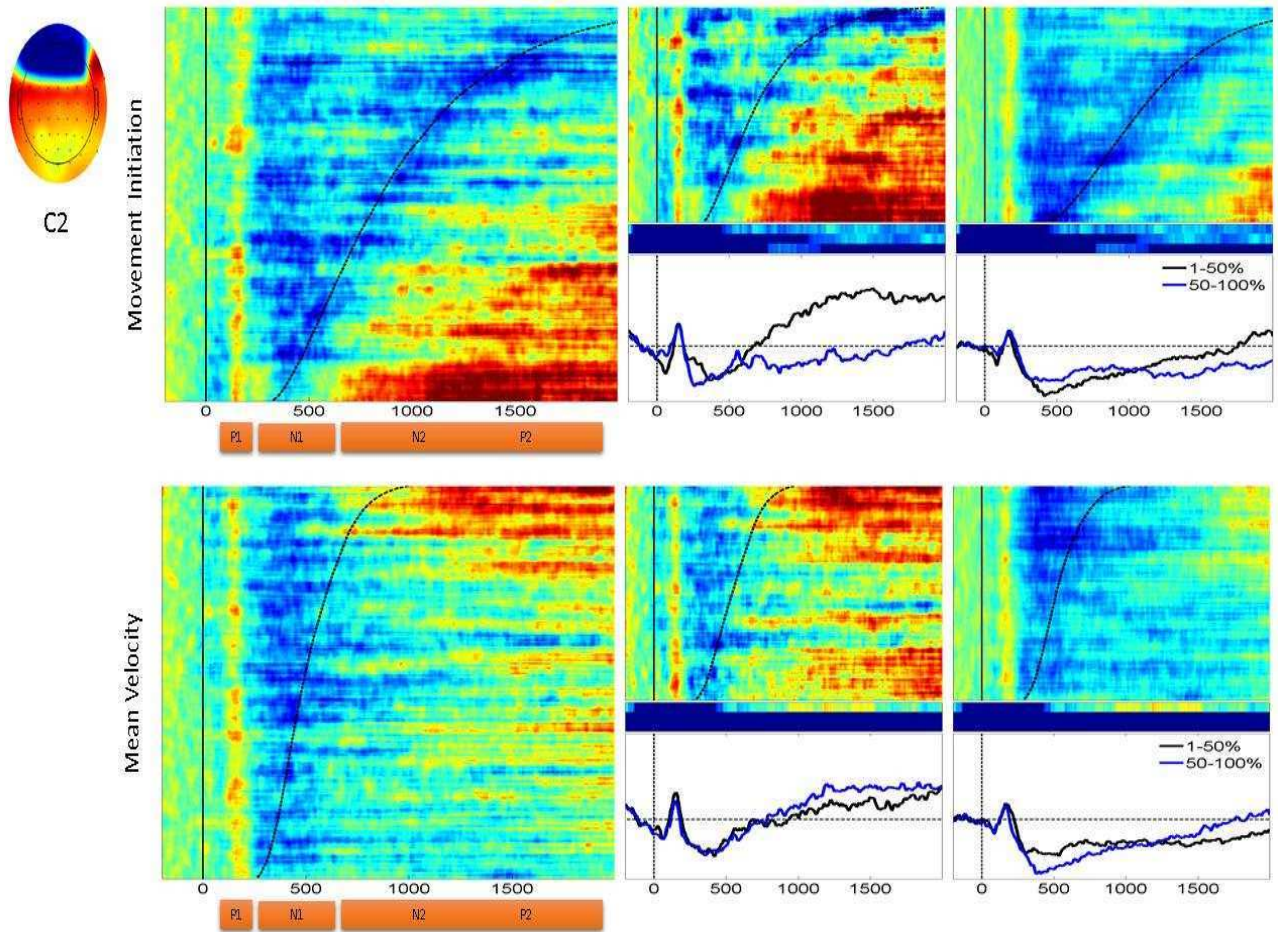
Figure 5. ERP images and quantile ERPs for component 2 time-locked to target onset.
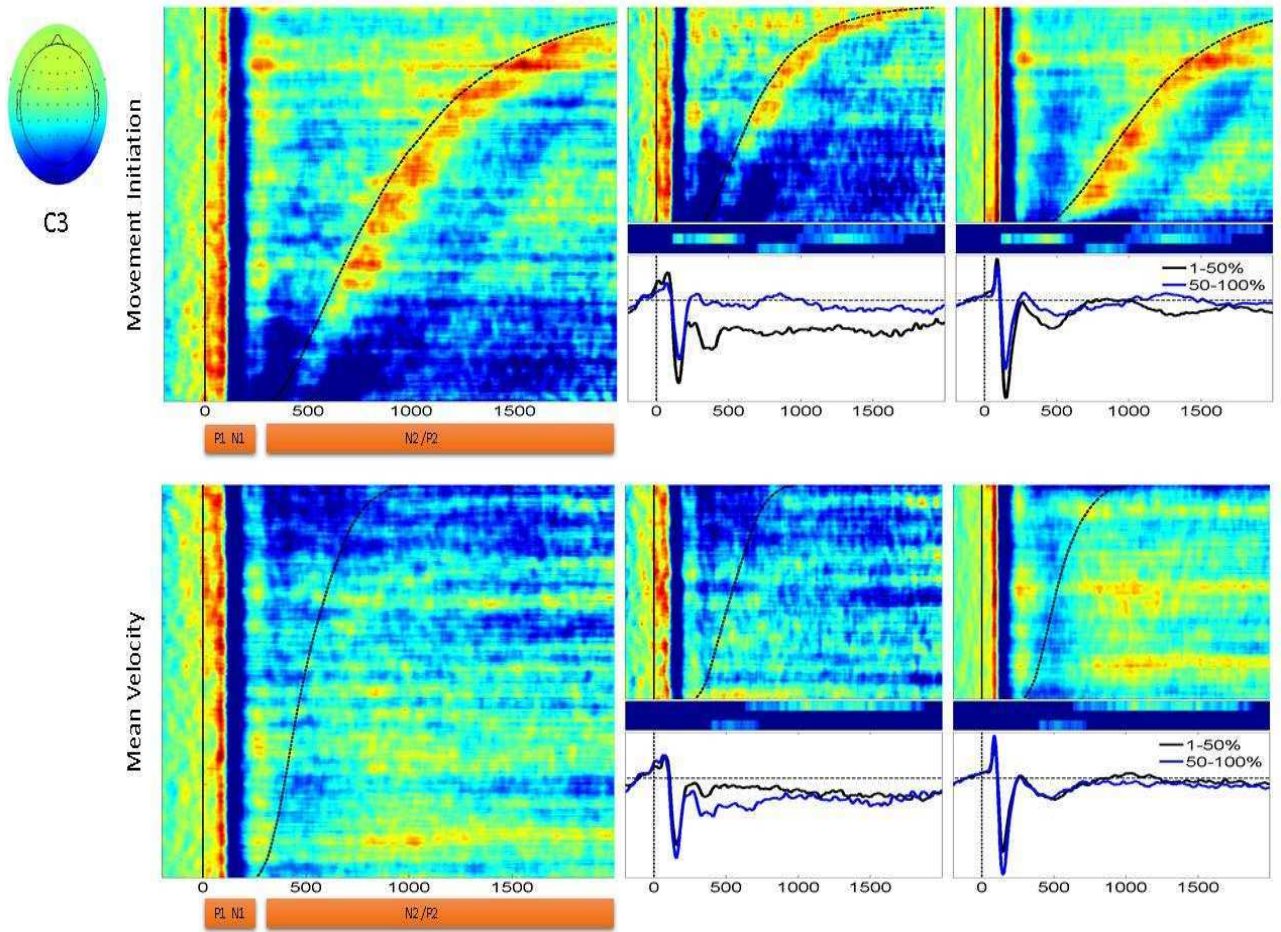
Figure 6. ERP images and quantile ERPs for component 3 time-locked to target onset.
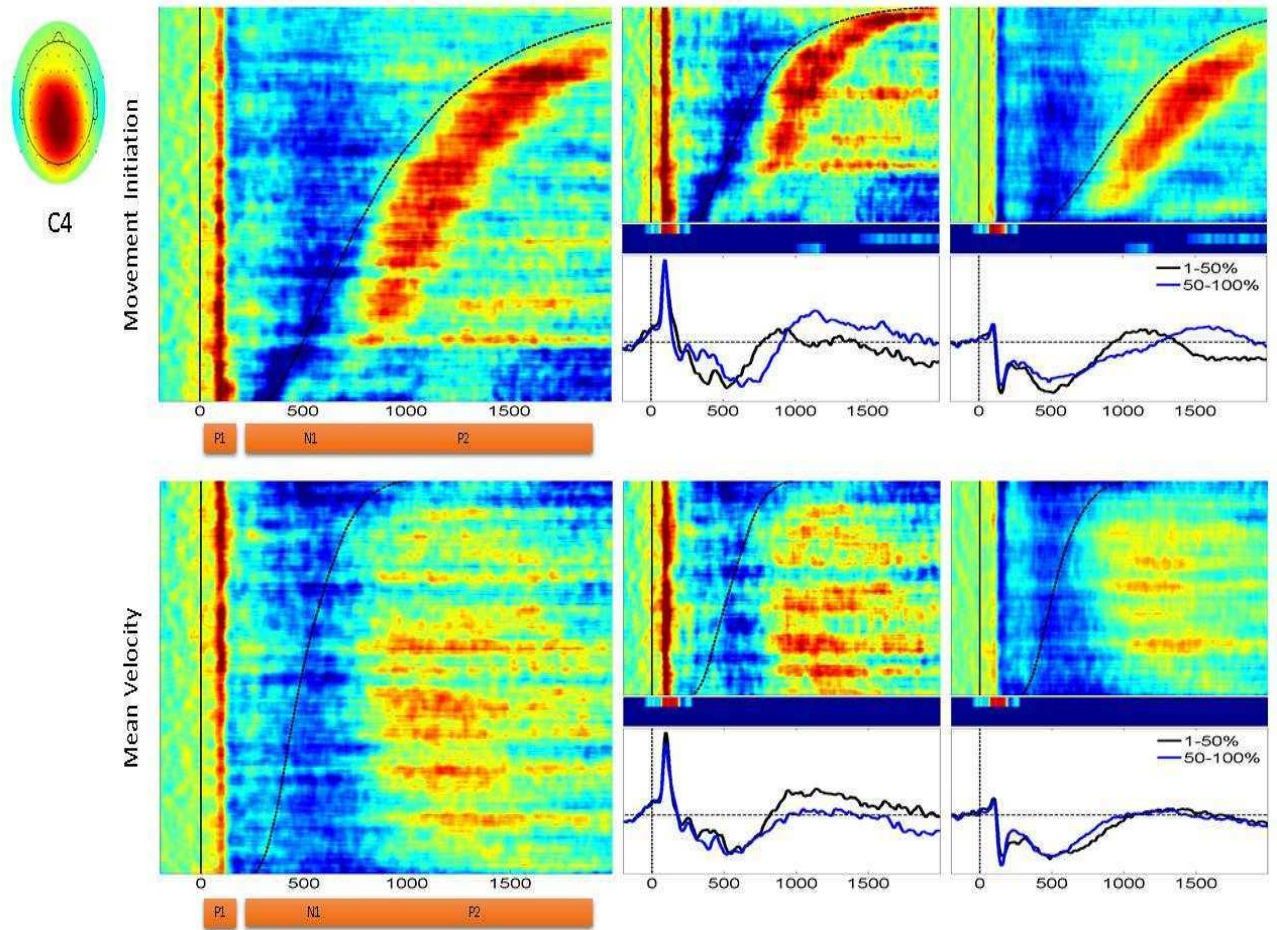
Figure 7. ERP images and quantile ERPs for component 4 time-locked to target onset.
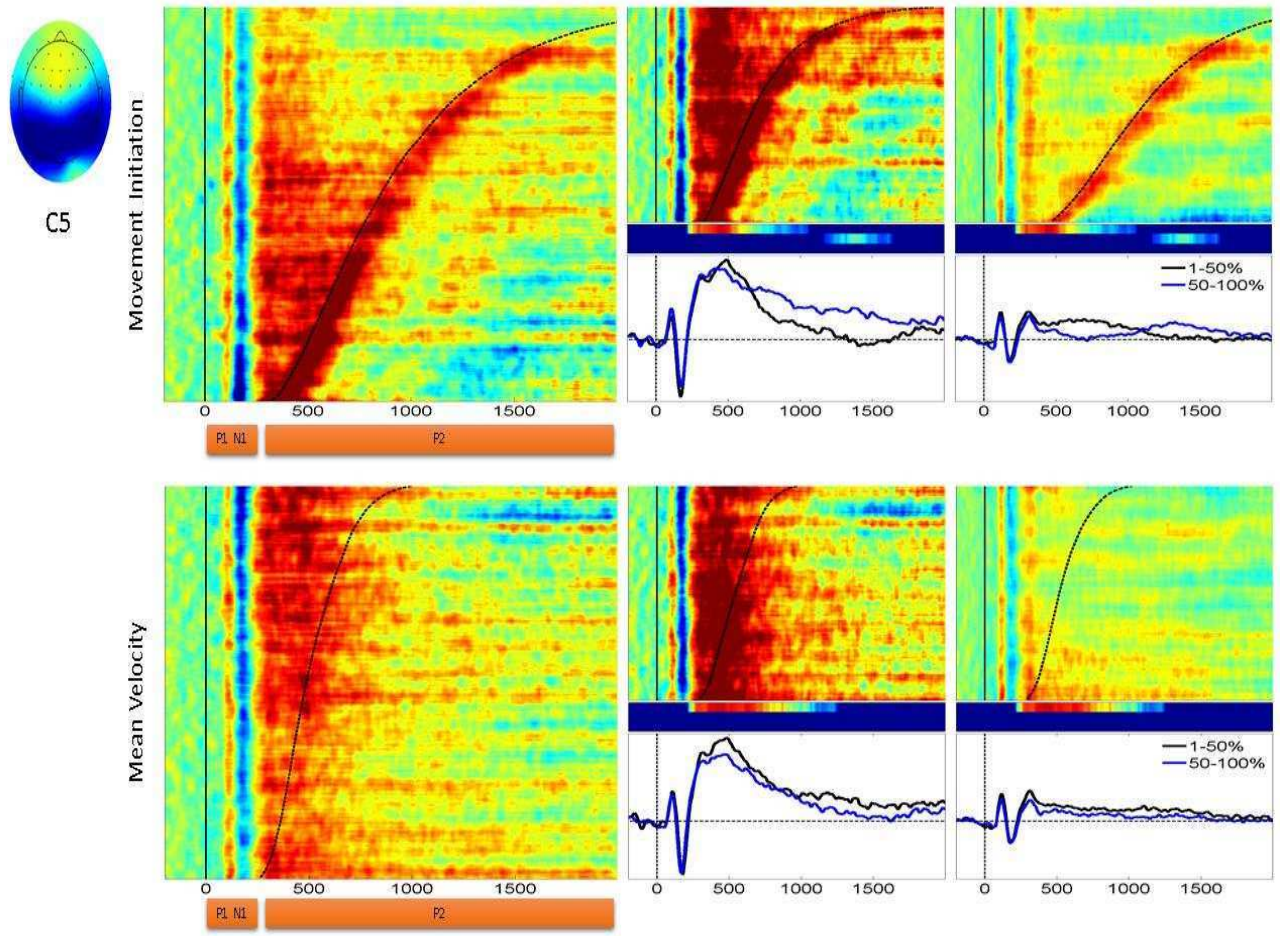
Figure 8. ERP images and quantile ERPs for component 5 time-locked to target onset.
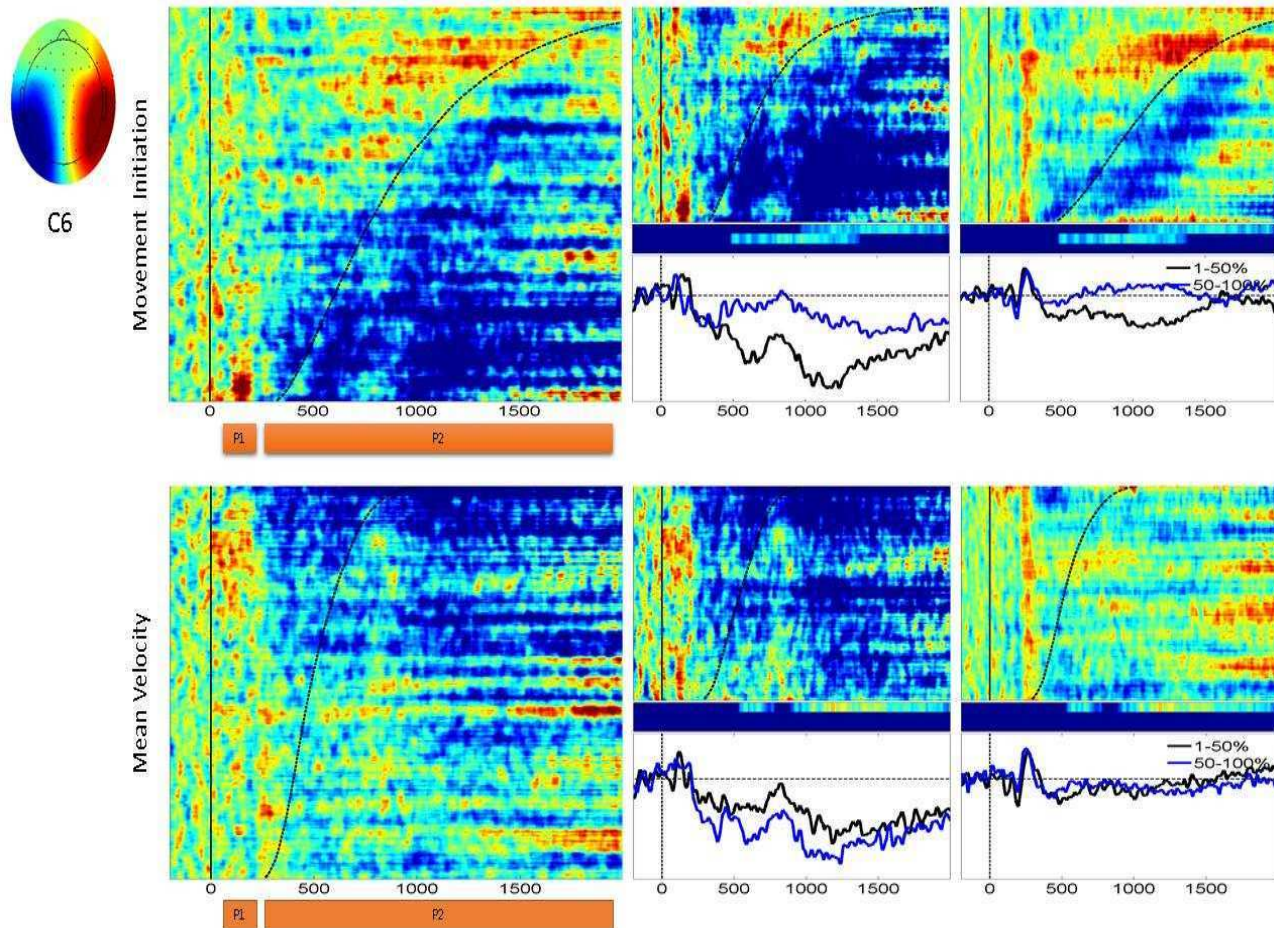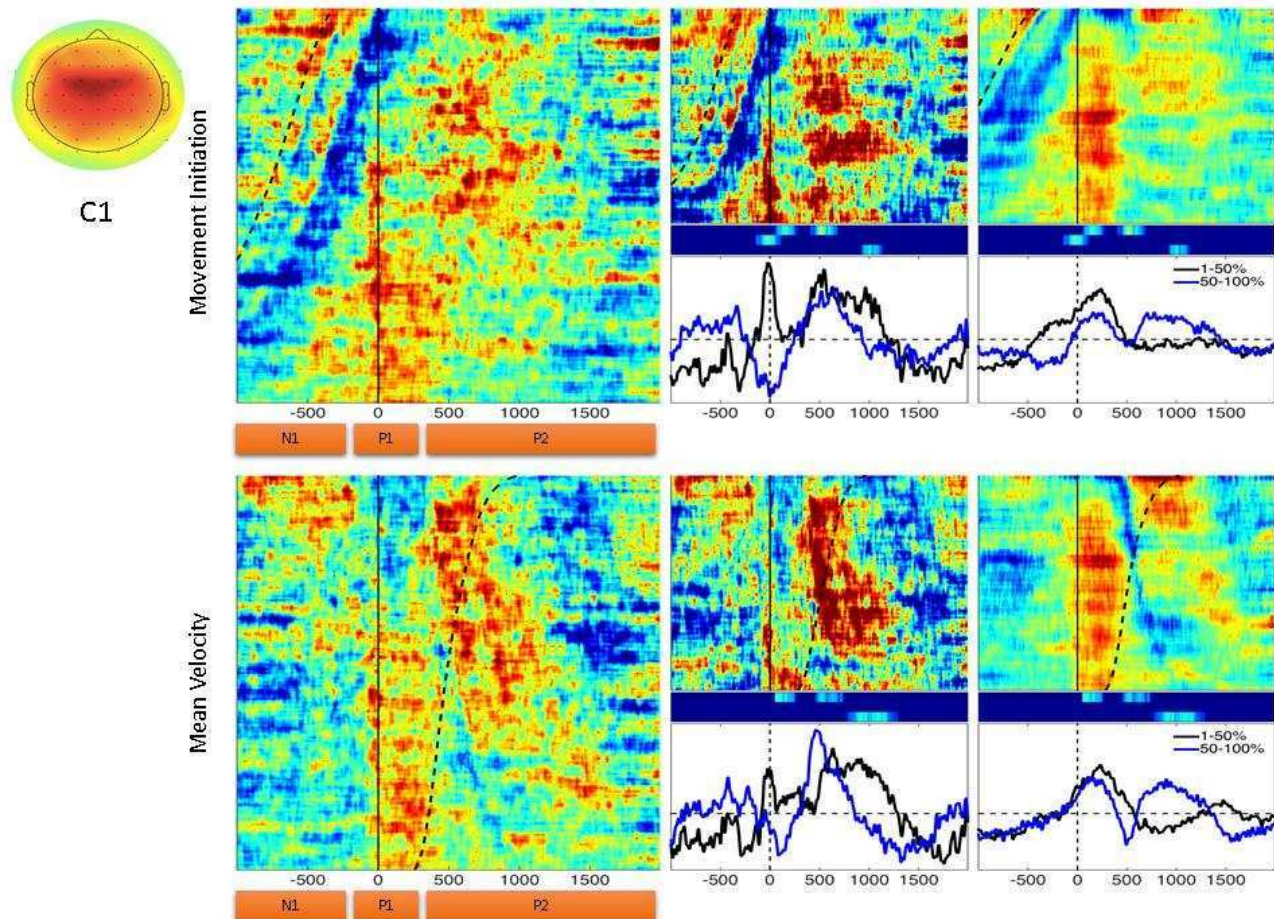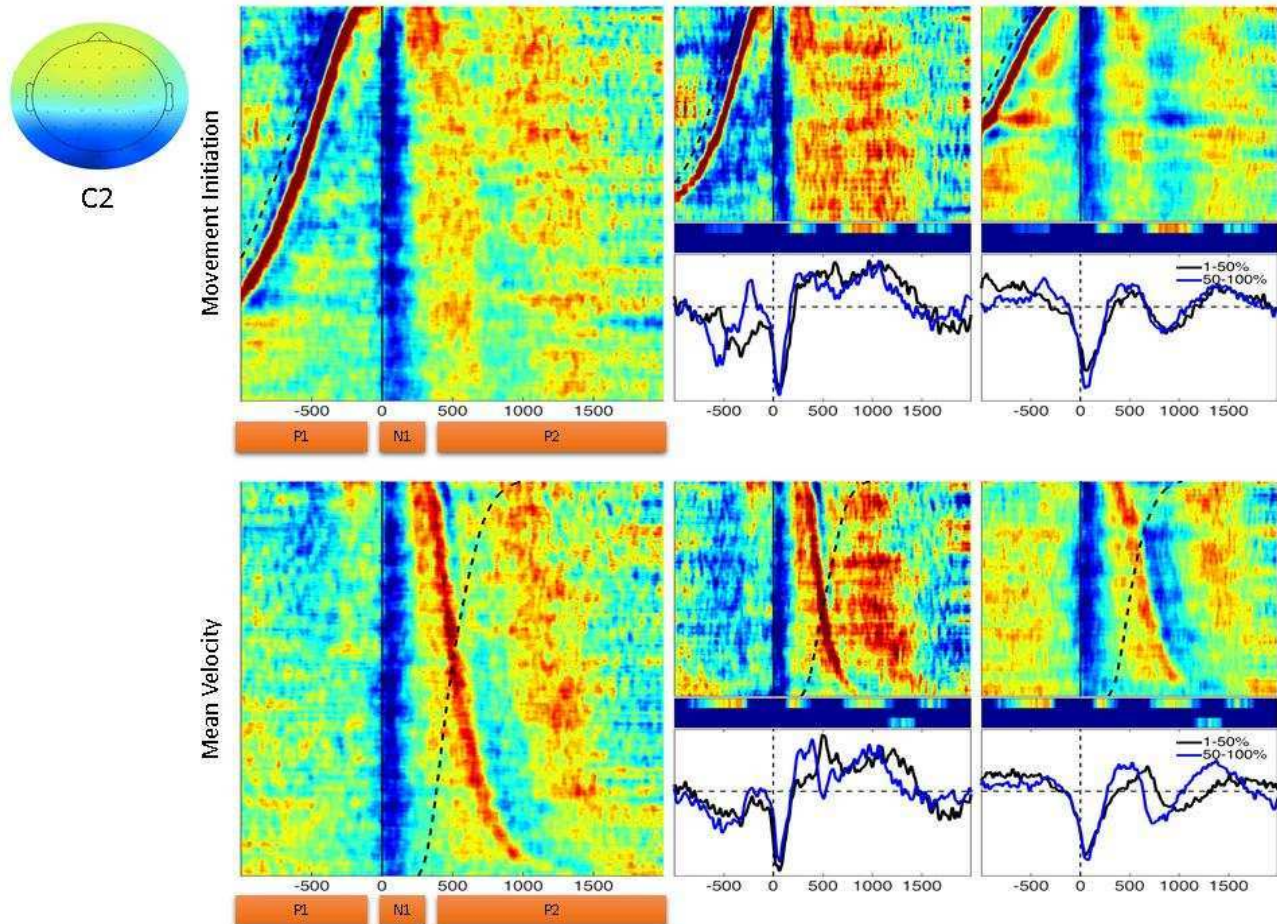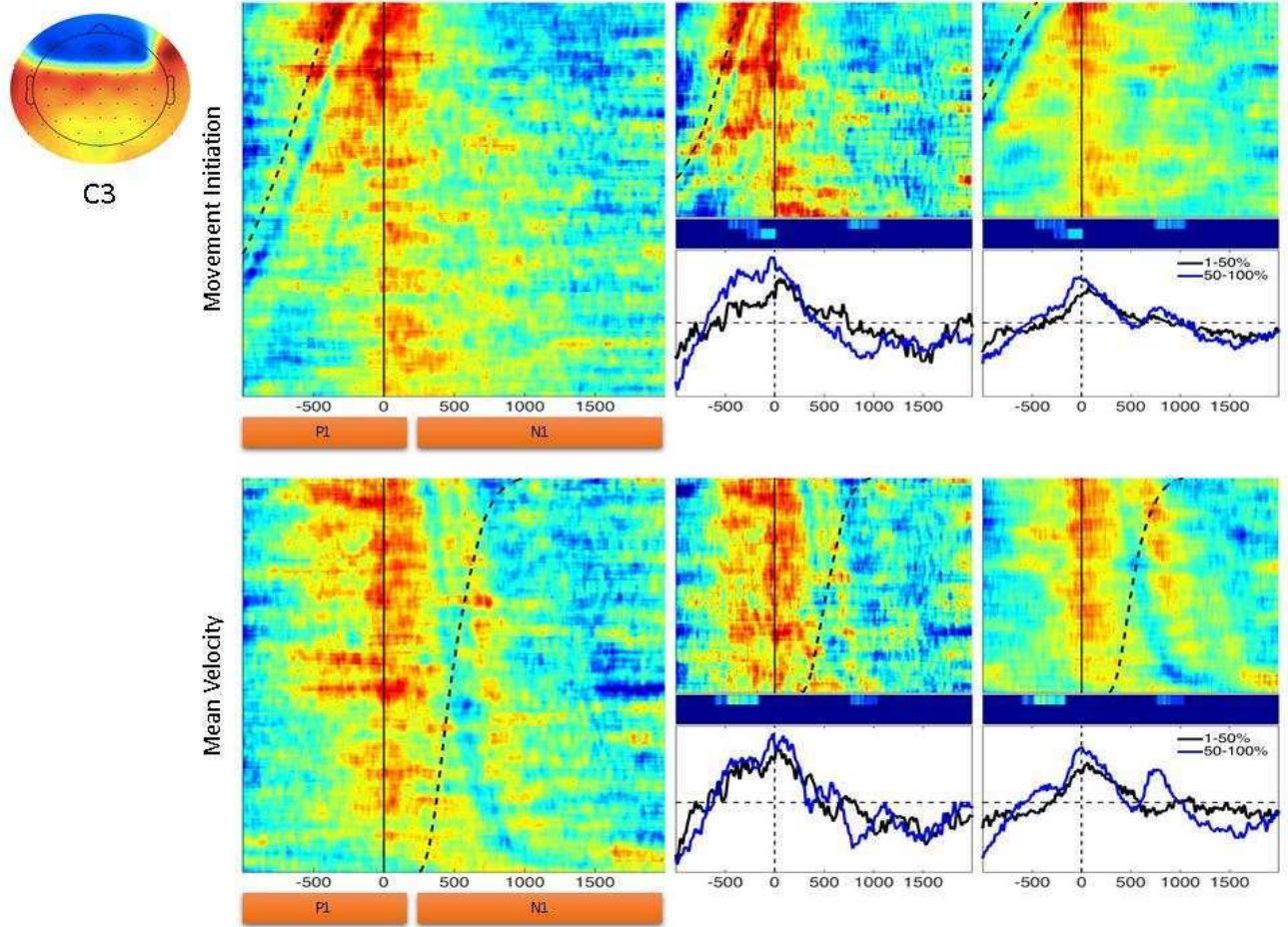
Figure 9. ERP images and quantile ERPs for component 6 time-locked to target onset.

Figure 10. ERP images and quantile ERPs for component 1 time-locked to movement

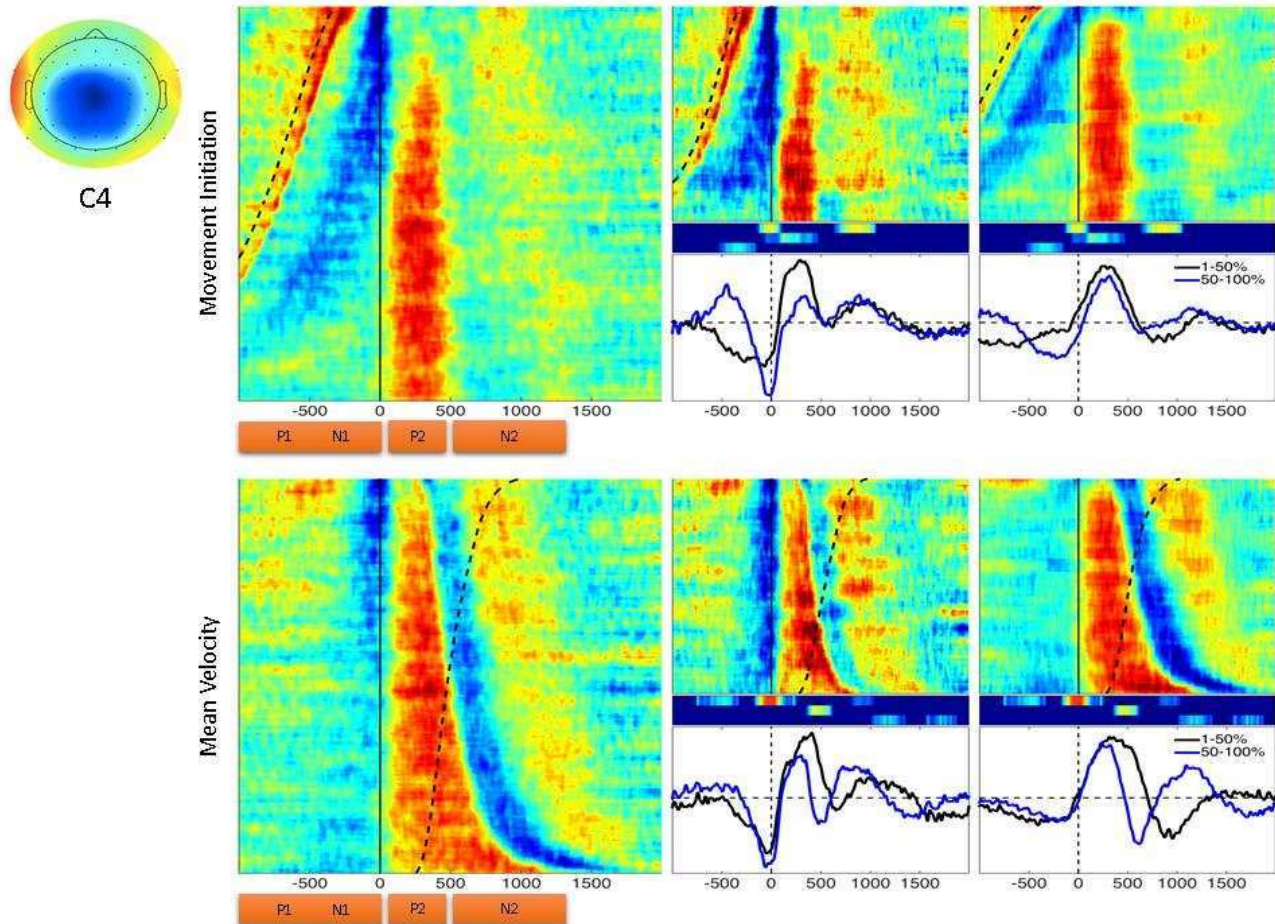onset. ERP images sorted by movement initiation reflect the timing of stimulus onset.

Figure 11. ERP images and quantile ERPs for component 2 time-locked to movement

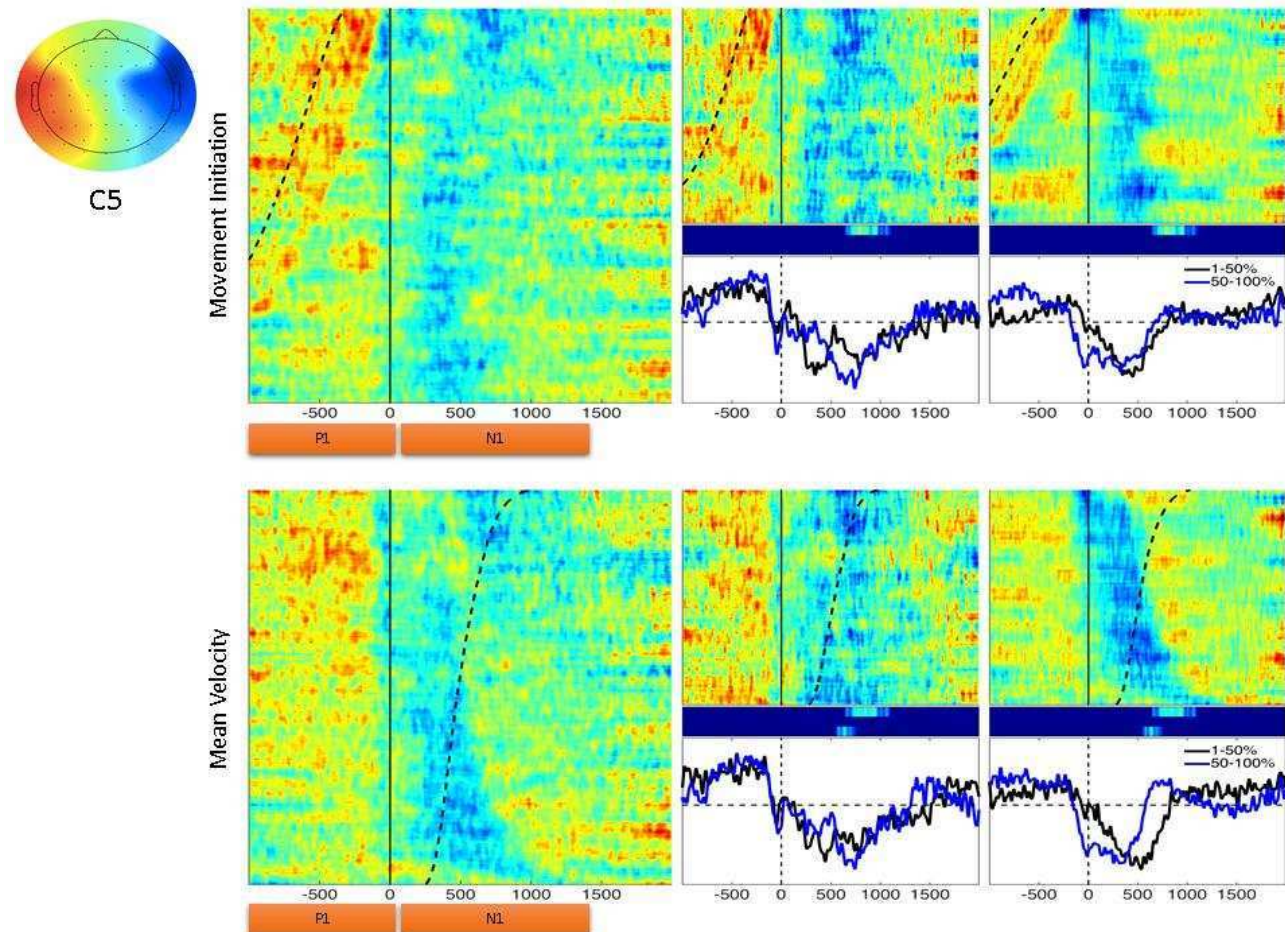onset. ERP images sorted by movement initiation reflect the timing of stimulus onset.

Figure 12. ERP images and quantile ERPs for component 3 time-locked to movement

onset. ERP images sorted by movement initiation reflect the timing of stimulus onset.

Figure 13. ERP images and quantile ERPs for component 4 time-locked to movement

onset. ERP images sorted by movement initiation reflect the timing of stimulus onset.

Figure 14. ERP images and quantile ERPs for component 5 time-locked to movement

onset. ERP images sorted by movement initiation reflect the timing of stimulus onset.
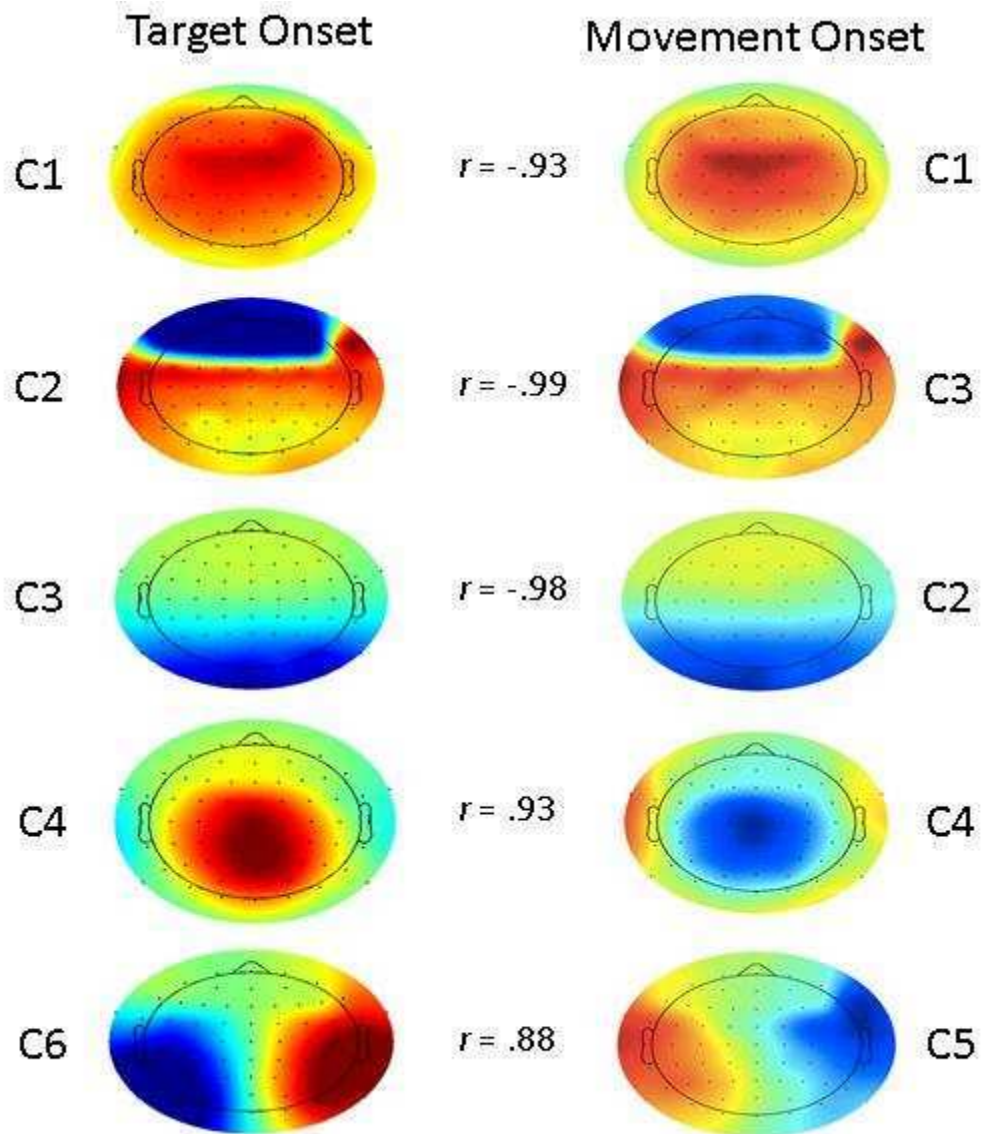
Figure 15. Correlations for ICA weights for both target and movement-locked

components.