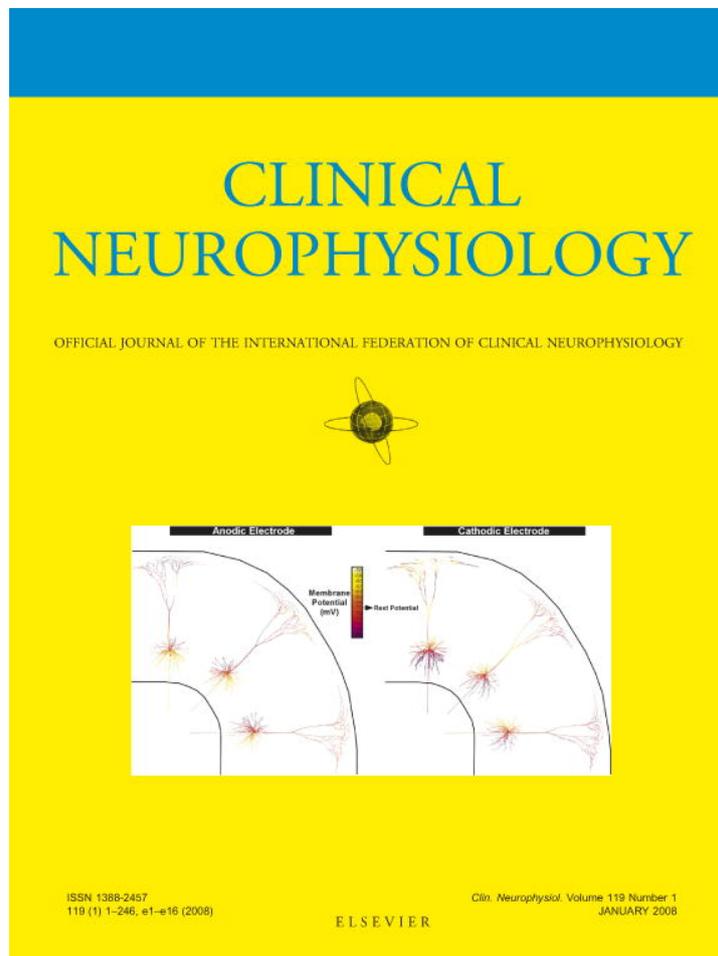


Provided for non-commercial research and education use.
Not for reproduction, distribution or commercial use.



This article was published in an Elsevier journal. The attached copy is furnished to the author for non-commercial research and education use, including for instruction at the author's institution, sharing with colleagues and providing to institution administration.

Other uses, including reproduction and distribution, or selling or licensing copies, or posting to personal, institutional or third party websites are prohibited.

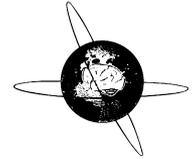
In most cases authors are permitted to post their version of the article (e.g. in Word or Tex form) to their personal website or institutional repository. Authors requiring further information regarding Elsevier's archiving and manuscript policies are encouraged to visit:

<http://www.elsevier.com/copyright>



ELSEVIER

Clinical Neurophysiology 119 (2008) 88–99



www.elsevier.com/locate/clinph

On the time-course and frequency selectivity of the EEG for different modes of response selection: Evidence from speech production and keyboard pressing

Pascale Tremblay^{a,b,*}, Douglas M. Shiller^{a,b}, Vincent L. Gracco^{a,b,c}

^a McGill University, Faculty of Medicine, School of Communication Sciences and Disorders, Montreal, Canada

^b Centre for Research on Language, Mind and Brain, McGill University, Montreal, Canada

^c Haskins Laboratories, New Haven, CT, USA

Accepted 16 September 2007

Available online 19 November 2007

Abstract

Objective: To compare brain activity in the alpha and beta bands in relation to different modes of response selection, and to assess the domain generality of the response selection mechanism using verbal and non-verbal tasks.

Methods: We examined alpha and beta event-related desynchronization (ERD) to analyze brain reactivity during the selection of verbal (word production) and non-verbal motor actions (keyboard pressing) under two different response modes: externally selected and self-selected.

Results: An alpha and beta ERD was observed for both the verbal and non-verbal tasks in both the externally and the self-selected modes. For both tasks, the beta ERD started earlier and was longer in the self-selected mode than in the externally selected mode. The overall pattern of results between the verbal and non-verbal motor behaviors was similar.

Conclusions: The pattern of alpha and beta ERD is affected by the mode of response selection suggesting that the activity in both frequency bands contributes to the process of selecting actions. We suggest that activity in the alpha band may reflect attentional processes while activity in the beta band may be more closely related to the execution and selection process.

Significance: These results suggest that a domain general process contributes to the planning of speech and other motor actions. This finding has potential clinical implications, for the use of diverse motor tasks to treat disorders of motor planning.

© 2007 International Federation of Clinical Neurophysiology. Published by Elsevier Ireland Ltd. All rights reserved.

Keywords: Response selection; Speech production; Externally specified movements; Self-selected movements; Voluntary actions; Event-related desynchronization (ERD)

1. Introduction

The process of selecting contextually appropriate voluntary behaviors is crucial for successful interpersonal interactions. From a physiological perspective, little is known

about the neural mechanisms underlying the organization of action and the complex interplay between action selection and action execution. Even simple motor actions require the integration of a large number of neuronal populations working in a coordinated fashion yet how these distributed processes are integrated over time remains poorly understood.

It has been hypothesized that there exists two canonical modes of action selection: externally specified and self-selected (or intention-based) (e.g. Goldberg, 1985; Godschalk et al., 1985; Mushiaki et al., 1991; Jahanshahi and Frith, 1998). An externally specified action is defined as a

* Corresponding author. Address: McGill University, Faculty of Medicine, School of Communication Sciences and Disorders, 1266 Pine Avenue West, Montreal, Que., Canada H3G 1A8 and Centre for Research on Language, Mind and Brain, 3640 de la Montagne, Montreal QC H3G 2A8. Tel.: +1 514 398 6998; fax: +1 514 398 8123.

E-mail address: pascale.tremblay@mail.mcgill.ca (P. Tremblay).

voluntary action that is directly elicited by an environmental stimulus and reflects a direct mapping between an arbitrary stimuli and an appropriate motor response. Externally specified actions require no decision about which action to perform. The relationship of the stimulus (stimulus-response compatibility) to the response, and the simplicity of the response (single- vs. multiple-choice) influence the reaction time (e.g. Lau et al., 2004; Woo and Lee, 2006; Schumacher and D'Esposito, 2002). Self-selected actions, in general, are those that are not elicited directly by environmental stimuli (Frith, 1991). When a response is self-selected, it requires a conscious decision about which response to perform to attain a given result. Importantly, to qualify as "self-selected" the response must be selected from among a number of equally appropriate responses (Frith et al., 1991). As a corollary of Fitts Law (Fitts, 1954; Fitts and Peterson, 1964), it has been found that as the number of possible responses increases, accuracy decreases (e.g. Woo and Lee, 2006; Tremblay and Gracco, 2006) and/or reaction time increases (e.g., Hick, 1952; Luce, 1986; Lau et al., 2004; Carbonnell et al., 2004).

It is not clear to what extent these two modes of response selection (externally specified and self-selected) differ with respect to their neural correlates. It has been suggested that externally and self-specified actions rely on two distinct cortical areas (e.g. Goldberg, 1985): the lateral premotor area (PMA) and the supplementary motor area (SMA), both located in subfields of Brodmann's area 6. Consistent with this hypothesis, recent evidence has suggested a role for the pre-SMA in the selection of motor responses (e.g. *finger movements*: Deiber et al., 1996; Hyder et al., 1997; Sakai et al., 2000; Lau et al., 2004, 2006; Cunningham et al., 2006; *speech*: Alario et al., 2006; Tremblay and Gracco, 2006). For the PMA, a recent study by Schumacher and D'Esposito (2002) demonstrated that neural activity related to response selection was modulated in relation to changes in stimulus-response compatibility. Uncertainty concerning the action to perform (two competing stimuli) also increases activity in PMA (Sakai et al., 2000). While these results suggest a role for the PMA in externally specified actions, a number of other studies have failed to demonstrate strong involvement of the PMA in externally specified actions compared to self-selected actions (e.g. Deiber et al., 1996; Weeks et al., 2001; Lau et al., 2004; Tremblay and Gracco, 2006). Additionally, there is accumulating evidence for a role of prefrontal areas in response selection. It appears that the prefrontal cortex is more strongly involved in self-selected tasks than externally selected ones for speech (Helps et al., 1997; Crosson et al., 2001; Alario et al., 2006) as well as finger movements (Deiber et al., 1996; Hyder et al., 1997; Desmond et al., 1998). Overall, it appears that multiple cortical areas in the frontal and prefrontal regions are involved in response selection.

Despite their value in providing information about localization, brain-mapping studies provide limited information regarding the dynamic characteristics of underlying

neural processes. In contrast with fMRI and PET, magneto- and electro-encephalography (MEG and EEG) are methods that are well suited to the examination of the time-course and frequency selectivity of brain activity associated with different aspects of motor preparation, such as response selection. It is generally accepted that time-varying, frequency specific changes in the ongoing EEG signal reflect cognitive and motor activity across large neuronal populations. Dirnberger et al. (1998) examined differences in the Readiness Potential (RP), a measure of slow wave changes across a wide frequency range, in two types of movements: self-selected and fixed (learned) sequences of finger flexions. Self-selected movement sequences were accompanied by a RP of greater amplitude compared with the externally selected movement sequences. This effect was particularly enhanced over the central parietal site. Using a comparable experimental paradigm, Waszak et al. (2005) also demonstrated that self-selected responses are accompanied by a pre-movement RP signal of greater intensity compared with externally specified responses. Using a more complex quantification method, Thut et al. (2000) examined the spatial and temporal configuration of the event-related EEG response occurring prior to the initiation of self-selected and externally specified (choice reaction-time) finger movements. Only a modest difference in EEG patterns was observed between externally and self-selected responses. Lateral frontal sites (presumed to be PMA) were activated for a longer duration for externally specified responses compared with self-selected responses, while medial premotor sites (presumed to be SMA/pre-SMA) were activated for a longer duration for self-selected responses compared with externally specified responses. These results were taken as further evidence that the SMA and PMA are differently involved in externally specified and self-selected actions, respectively.

Another widely used approach to quantifying EEG and MEG signals is to measure frequency specific changes in ongoing oscillatory activity. Large neuronal pools produce high amplitude, low frequency signals (e.g. alpha band, around 10 Hz) while smaller neuronal pools produce smaller amplitude signals with higher frequency components (e.g. beta band, around 20 Hz and gamma band, around 30–40 Hz) (Pfurtscheller and Lopes da Silva, 1999). Activity within these bands and others reflects the functional state of the underlying neuronal population. Highly synchronous activity is reflected at the scalp by a band-specific increase in power (event-related synchronization or ERS) while desynchronized activity is reflected at the scalp by a band-specific decrease in power (event-related desynchronization or ERD) (e.g. Pfurtscheller and Aranibar, 1977). While ERS may reflect a state of cortical idling (e.g. Pfurtscheller et al., 1996), the lack of attention (e.g. Verstraeten and Cluydts, 2002) or an active inhibition of irrelevant information (e.g. Cooper et al., 2003), the ERD is often seen as reflecting a state of sensory or cognitive information processing or movement preparation (e.g. Pfurtsch-

eller, 1992). It has been shown, for example, that a decrease in power in the beta band occurs in relation to the planning and execution of actions, reflecting neuronal activity in primary motor areas (e.g. Sanes and Donoghue, 1993; Jackson et al., 2002; Szurhaj et al., 2003), the SMA (e.g. Ohara et al., 2000), and the PMA (Lebedev and Wise, 2000). Suppression of this rhythmic oscillatory activity (ERD) has been demonstrated in relation to finger movements (e.g. Salenius et al., 1997; Ohara et al., 2000; Pfurtscheller et al., 2003) and speech production (e.g. Salmelin et al., 1995; Salmelin et al., 2000; Salmelin and Sams, 2002). Beta ERD starts before the onset of movement, continues throughout movement execution, and then quickly subsides. It has also been shown that the beta ERD is sensitive to parameters of the response selection process (Kaiser et al., 2001).

In sum, the neuroimaging literature suggests that there are differences in the neural substrate for different modes of response selection (externally specified vs. self-selected). However, it is not known with certainty whether the two modes of response selection differ in terms of the dynamics of neural processing, or whether there are frequency specific changes associated with the selection and execution of actions. Kaiser et al. (2001) suggested that the beta rhythm is reactive to differences in how motor responses are selected. However, it is unclear whether other frequency bands are also sensitive to response mode differences, nor is it clear whether different behaviors affect the patterns of brain activity associated with externally specified and self-selected movements. Most MEG studies (and all EEG studies) have examined the response selection process with tasks involving finger movements (finger tapping, finger opposition, button pressing). In order to examine the generality of the processes we compared response modes in two different motor systems: movements of a finger for pressing keys on a keyboard and movements of the lips and jaw for producing a short word. If alpha and beta ERD reflects the neural processing that underlies the selection of responses, then we would expect to see differences in both ERD measures between externally specified and self-selected movements. Moreover, if the underlying oscillatory process is domain general then one should observe comparable ERD patterns for both the speech and non-speech tasks.

2. Methods

2.1. Experiment 1: speech

2.1.1. Participants

Six healthy right-handed English speakers (2 males) participated in the study (26 ± 4.91 years). All participants were strongly right handed as measured by the Edinburgh Handedness Inventory. All participants had normal or corrected to normal vision and no history of neurological disorder. All participants gave their informed consent.

2.1.2. Study procedure

The experiment consisted of three tasks: reading a word (EXT), generating a word (INT) and producing an oral non-speech mouth movement (*lip protrusion*). The oral non-speech movement task was not analyzed for this article. All tasks were visually cued and presented in random order. For the EXT task, participants were instructed to say the word “pie” aloud as quickly as possible when the word was presented visually on a computer screen. For the INT task, participants were instructed to generate, as quickly as possible, a one-syllable word starting with “p” when visually cued by the sequence “p**” (matching “pie” in terms of number of characters). Unlike the EXT task, the INT task required a decision of what response to produce.

During the experiment, participants were seated in a comfortable armchair facing a computer screen in a dimly lit room. The experiment started with a practice session during which familiarity with testing materials was ensured. The practice session consisted of a short version of the experiment during which participants produced a single word or an oral gesture (lip protrusion) in response to a visual stimulus, with verbal feedback provided about their performance. Additionally, in order to minimize the possibility of EEG artifacts associated with speech production, participants were instructed to speak using a low voice intensity level and to minimize head movement during speaking. Participants were also trained to refrain from blinking as much as possible, during experimental trials.

For all tasks, the visual stimuli were matched for length and display properties (white letters in Courier font). Stimuli were presented for 250 ms on the center of a black screen. A total of 60 trials were obtained in each of the conditions. The inter-trial interval was 10 s. In between trials, participants were presented with a fixation point on the computer screen and asked to maintain their gaze on that location. Presentation software (Neurobehavioral Solutions) running on a laptop computer was used for experimental control and stimulus delivery. The experimental design is illustrated in Fig. 1a–c.

2.1.3. EEG and EMG acquisition

EEG was recorded from 64 pin-type active Ag–AgCl electrodes mounted in a headcap (arranged according to the extended 10–20 system) and connected to an Active-Two AD-box (Biosemi, Amsterdam). The use of active electrodes eliminates 60 Hz interference pickup by the electrode wires, even when the electrode impedance is high (MettingVanRijn, Peper & Grimbergen, unpublished technical note). Scalp EEG was digitized at 1024 Hz with online digital band pass filtering (0.05 to 100 Hz). Two electrodes were placed above and below the right eye. Two flat electrodes were used to record muscle activity related to the production of speech. These electrodes were placed above the upper lip and below the lower lip, over the orbicularis muscle.

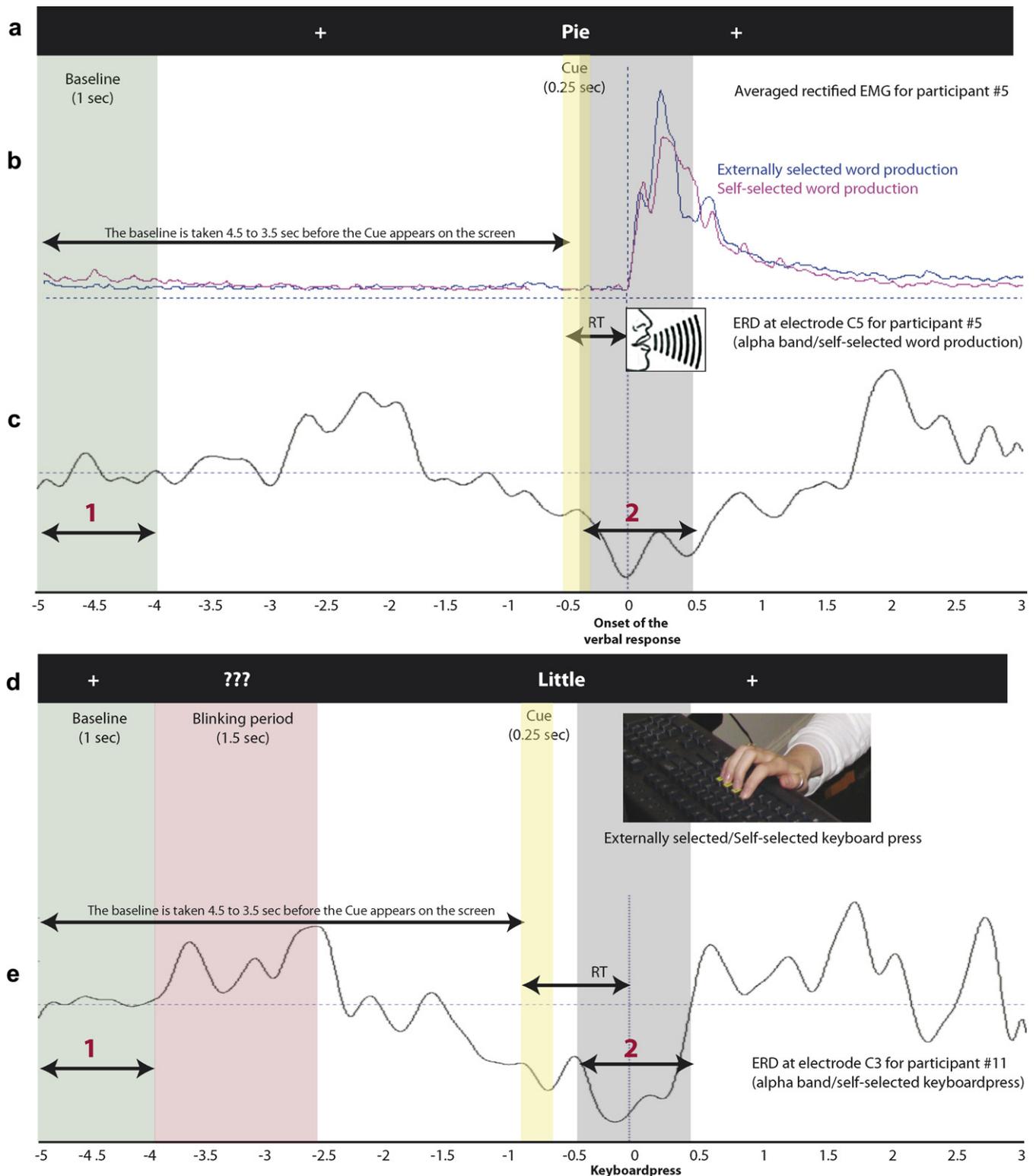


Fig. 1. Task paradigm and intervals used for the analysis of the EEG data for studies #1 and #2. The top panel illustrates the task design for the speech study, while the bottom panel illustrates the task design for the keyboard press study. The 1 s intervals in gray (4.5 to 3.5 s prior to the presentation of the visual cue) and green gray (0.5 s before to 0.5 s after the onset of the response) were used to determine subject's reactive frequency ranges in the alpha and beta bands (power spectral analysis). The green interval (identified as 1) was used as the pre-movement time-window and the interval in gray (identified as 2) was used as the movement time-window. (a) Illustrates the timing of the presentation of the visual cues in the speech study. (b) Illustrates the timing of the lip EMG activity, averaged across trials and rectified, for one representative subject. The vertical line represents time 0 corresponding to the onset of the lip muscle EMG activity. (c) Illustrates the time-course of the alpha band ERD at electrode C5 for one representative subject, for the speech study. The Green interval was used as the baseline interval for the calculation of the ERD. (d) Illustrates the timing of the presentation of the visual cues in the keyboard press study. (e) Illustrates the time-course of the alpha band ERD at electrode C3 for one representative subject, for the keyboard press study.

2.2. Experiment 2: non-speech

2.2.1. Participants

A total of 19 healthy English-speaking participants (9 females) participated in the study (mean age, 22.7 ± 2.27 years; mean number of school years completed = 13.58 ± 2.51). All participants were strongly right handed, as measured by the Edinburgh Handedness Inventory. All participants had normal or corrected to normal vision and no history of neurological disorder. All participants gave their informed consent. Only 6 participants (3 females) were included in the present analysis in order to match the sample size in Experiment #1.

2.2.2. Study procedure

The study consisted of three experimental conditions including (1) an externally specified task (EXT), (2) a self-selected keyboard press task (4 choices) (INT), and (3) a self-initiated and self-selected keyboard press task. This last task was not analyzed for this article. In the EXT task, participants were presented with the name of one finger (index, middle, little or ring) on the computer screen and instructed to press the appropriate key as quickly as possible. The visual cue disappeared as soon as the keyboard was pressed. This task required no decision of which response to make. For INT task, participants were presented with the word “finger” and were required to choose a finger and press the corresponding button on the keyboard. Participants were instructed to randomize the choice of the finger. As in Experiment #1, both tasks were externally paced; only the mode of selection varied.

During the experiment, participants were seated in a comfortable armchair facing a computer screen in a dimly lit room. Participants placed their right hand on a keyboard. Four keyboard keys were labelled in the following manner: I (for index), M (for middle), R (for ring) and L (for little). Participants were instructed to place their fingers over the appropriate keys without pressing. The experiment started with a practice session to ensure familiarity with testing material and to verify that the subject understood the tasks. The experiment was divided into twelve short blocks. Each task was performed four times in four separate blocks of 35 trials, for a total of 140 repetitions of each. Half way through the experiment, participants were given a 10-min break. The inter-trial interval was varied randomly between 3 and 6 s. Before a trial started, three stars (***) appeared on the computer screen for 1.5 s and participants were free to blink during this period. For the remainder of the trial, participants were asked to refrain from blinking.

Presentation software (Neurobehavioral Solutions) running on a laptop computer was used for experimental control and stimulus delivery. All stimuli were presented using pale blue letters on a black screen.

The experimental design is illustrated in Fig. 1d and e.

2.2.3. EEG acquisition

EEG was recorded from 64 pin-type active Ag–AgCl electrodes mounted in a headcap (arranged according to the extended 10–20 system) and connected to an Active-Two AD-box (Biosemi, Amsterdam). EEG data was sampled at 1024 Hz with online digital filtering (0.05 to 100 Hz). Two ocular channels were recorded, one above and one below the right eye.

2.3. Data processing and analysis

The EEG recordings were analyzed offline using EMSE (Source Signal Imaging, San Diego, CA, USA). A digital high pass filter (1 Hz cutoff) was first applied to all channels, as well as a notch filter (60 Hz). A variant of spatial PCA-projection (implemented in EMSE) that controls for the principal topographies of ongoing EEG activity was used to remove blinks from the EEG signal. The resulting time-series were further examined for artifacts related to muscle activity. All trials containing muscle artifacts – identified by abnormally large, within-trial changes in amplitude – were removed from the analysis. A common average reference was applied to the remaining channels.

For each subject, two separate 1-s power-spectra (taken prior to and during the response) were calculated to determine their specific reactive frequencies in the alpha and beta bands (Pfurtscheller and Lopes da Silva, 1999). The reactive frequency ranges for electrode C3 (for the keyboard press experiment) and C5 (for the speech experiment) were determined by comparing the two spectra and identifying the frequency ranges showing a decrease in power during the response interval compared with the pre-movement interval. Following the identification of the reactive frequency, the data for each subject were band pass filtered (peak frequency ± 2 Hz) and converted to power. Subject-specific mean reactive frequencies in the alpha range were for Experiment #1: 9.5; 12; 9; 10.5; 10; and 11 Hz, with a mean of 10.33 ± 0.89 Hz. For Experiment #2: 10; 9; 11; 9; 10 and 11 Hz, with a mean of 10 ± 1.08 Hz. Subject-specific mean reactive frequencies in the beta range were, for Experiment #1: 19; 22; 17; 28; 17; and 20.5 Hz, with a mean of 20.85 ± 4.12 Hz. For Experiment #2: 17.5; 20.5; 23; 16.5; 20 and 19.5 Hz, with a mean of 19.5 ± 2.33 Hz.

Power samples were averaged across all trials and the resulting time series were converted to percent change relative to a 1 s baseline taken 4.5 to 3.5 s before the onset of response, according to the formula: $(A - R)/R \times 100$, where A represents movement-related activity and R represents activity during the pre-movement (resting) period (Pfurtscheller and Lopes da Silva, 1999).

Data analysis was confined to the activity measured at the medial central electrodes (FCz, Cz and CPz), which presumably cover the pre-SMA and SMA proper, as well as the lateral central electrodes (left: C3 and C5; right: C4 and C6), which cover the PMA as well as the primary motor area (M1). From the percent-change time-series,

the magnitude and time-to-peak of the ERD peak (maximal decrease in power) was measured for each electrode, frequency band and response mode. In addition, the onset of ERD with respect to response onset (defined as the point where amplitude reached 10% of the maximal ERD value) and the ERD duration were computed.

Statistical analysis in the form of a mixed-model ANOVA was conducted on 4 dependent variables: ERD peak amplitude, ERD onset time, ERD duration and time-to-peak for ERD. The within subject variables were response MODE (external, self-selected) and frequency BAND (alpha, beta), and the between-subject variables were TASK (keyboard press, speech) and REGION (left, right, medial).

The two lip EMG channels in Experiment 1 were digitally band passed filtered offline (20–200 Hz), rectified, and then low pass filtered (10 Hz). For each response, the EMG onset was determined manually. The onset of the EMG was defined as the point where the amplitude of the averaged signal reached 10% of the peak EMG amplitude. In order to minimize bias, this procedure was carried out blind to the experimental condition.

The speech reaction time (RT) was defined as the interval between the stimulus onset and EMG onset. For the non-speech task, reaction time was defined as the interval between the stimulus onset and the keyboard press. A paired sample *t*-test was used to compare RTs for the different conditions (EXT vs. INT) within each TASK (speech, non-speech).

3. Results

3.1. Behavioral results

3.1.1. Reaction time

For both tasks, the reaction time for EXT were shorter than the reaction time for INT. For speech, the reaction time for the EXT was 11 ms faster than for the self-selected task (301 ± 75.08 and 312 ± 75.42 ms, $p = 0.169$). For the non-speech tasks, the reaction time was 89 ms faster for EXT than for INT (436 ± 95.26 and 525 ± 157.33 ms, $p = 0.129$).

3.1.2. Accuracy

For the EXT tasks, participants produced the correct response on 100% of the speech and 99.8% of the non-speech trials. Participants made no mistakes on the INT trials.

3.2. EEG results

3.2.1. Overall ERD pattern

For each task, there was a clear pre-movement alpha and beta ERD. The time-course (relative to the onset of the response) of activity in the alpha and beta bands is presented for the speech task in Fig. 2, and for the non-speech task in Fig. 3. As shown in the figures, the onset of the

speech and non-speech response was preceded by an alpha and beta ERD, with onset time averaging 145 ms prior to response in the alpha band, and 382 ms prior to the response in the beta band for the EXT condition. Similarly, for the INT condition the ERD onset preceded the behavioral response by 279 ms in the alpha band, and 464 ms in the beta band. Regardless of the condition or mode of response, the duration of the alpha ERD was longer than the duration of the beta band ERD. Despite some timing differences, the overall ERD pattern was similar for the speech and the non-speech tasks.

3.2.2. Response mode

All of the four variables that were examined (ERD amplitude, onset, duration and time-to-peak) were influenced by the response MODE. For the ERD onset, an omnibus ANOVA revealed a significant main effect of MODE ($F(1,78) = 5679$, $p = 0.007$). The ERD onset occurred 116 ms closer to the onset of the response in EXT than in INT (averages -261 and -377 ms, respectively). Given the relatively large RT difference between the speech and the non-speech tasks, we conducted two separate mixed-model ANOVAs, one for each TASK. For speech, the mixed-model ANOVA revealed no significant main effect of MODE. For the non-speech task, the mixed-model ANOVA revealed a significant main effect of MODE ($F(1,39) = 13,960$, $p = 0.001$), and a significant MODE by BAND interaction ($F(1,39) = 5806$, $p = 0.020$). In both bands, the ERD started earlier (closer to response onset) in EXT than in INT.

The ERD duration was also significantly affected by MODE ($F(1,78) = 25,032$, $p = 0.000$). Overall, the duration of the ERD was 270 ms longer for INT compared with EXT, averaging 1.463 and 1.191 s, respectively. This pattern of ERD duration was similar regardless of the task performed (speech, non-speech). The ERD duration results are illustrated in Fig. 5. The ERD time-to-peak was also affected by MODE, as revealed by a mixed-model ANOVA ($F(1,78) = 29,526$, $p = 0.000$). Overall, the time-to-peak was 212 ms longer for INT compared with EXT, averaging 739 and 527 ms, respectively. While the effect of MODE did not reach significance for ERD amplitude, there was a tendency for the ERD amplitude to be influenced by the MODE, with INT being associated with a greater ERD compared with EXT.

To summarize, the INT task compared with the EXT task was associated with a longer ERD that started earlier, ended later, peaked later and tended to be of greater amplitude.

3.2.3. Band-specific contribution

A number of temporal differences were noted with regard to the two frequency bands. With regard to the ERD onset, an omnibus ANOVA revealed a significant main effect of frequency BAND as well as a significant BAND by REGION interaction. Overall, the beta ERD began earlier than the alpha ERD. For speech, the

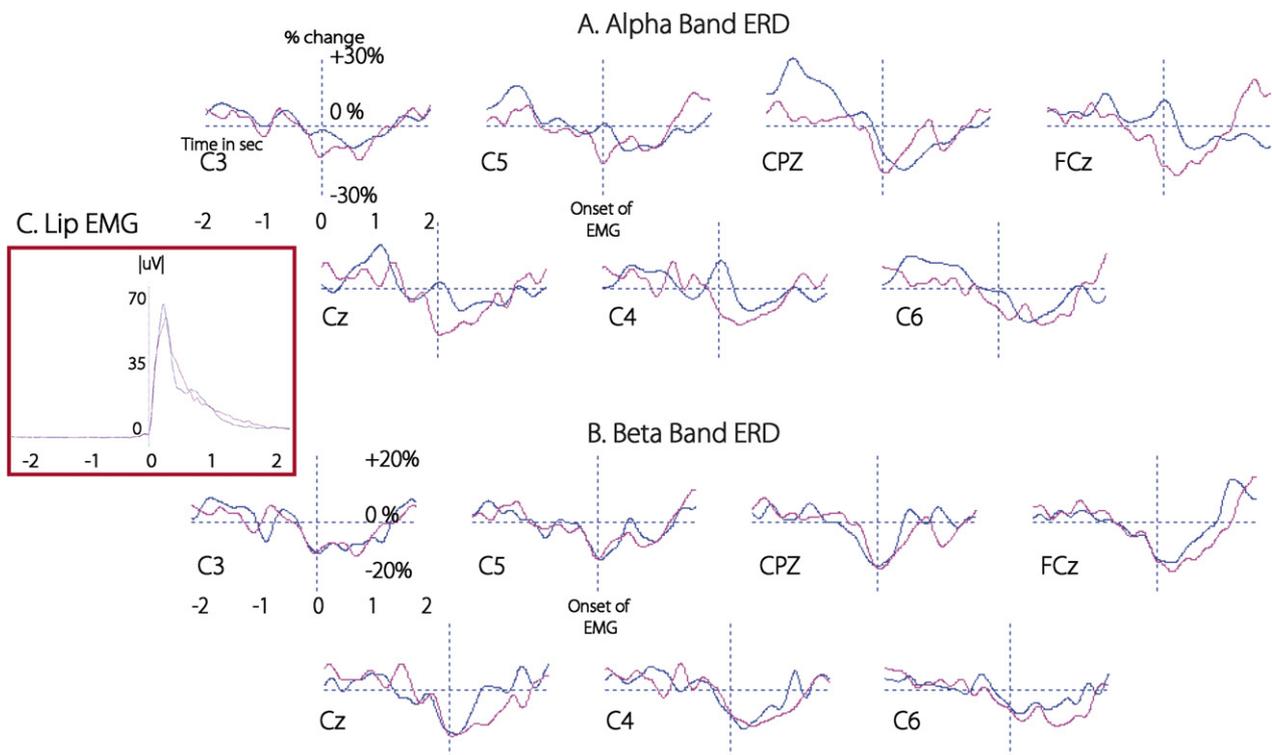


Fig. 2. Event-related changes in power for the speech task for the group expressed as a percent change from the baseline. The top panel displays the results for the alpha band. The bottom panel displays the results for the beta band. The blue line represents the externally cued task; the red line represents the self-selected task. The vertical line represents time 0 corresponding to the onset of the lip muscle EMG activity.

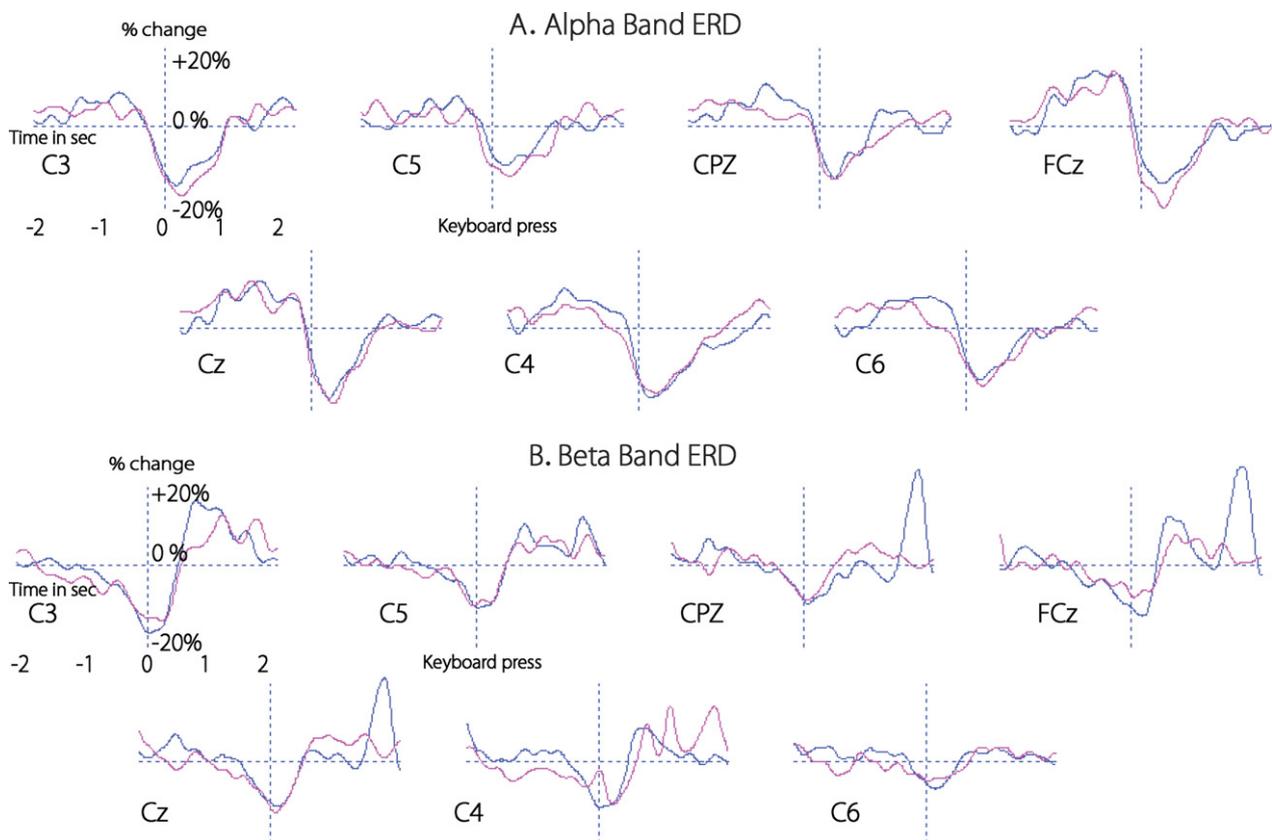


Fig. 3. Event-related changes in power for the keyboard pressing task for the group expressed as a percent change from the baseline. The top panel displays changes in the results for the alpha band. The bottom panel displays the results for the beta band. The blue line represents the externally cued task; the red line represents the self-selected task. The vertical line represents time 0 corresponding to the onset of the keyboard press.

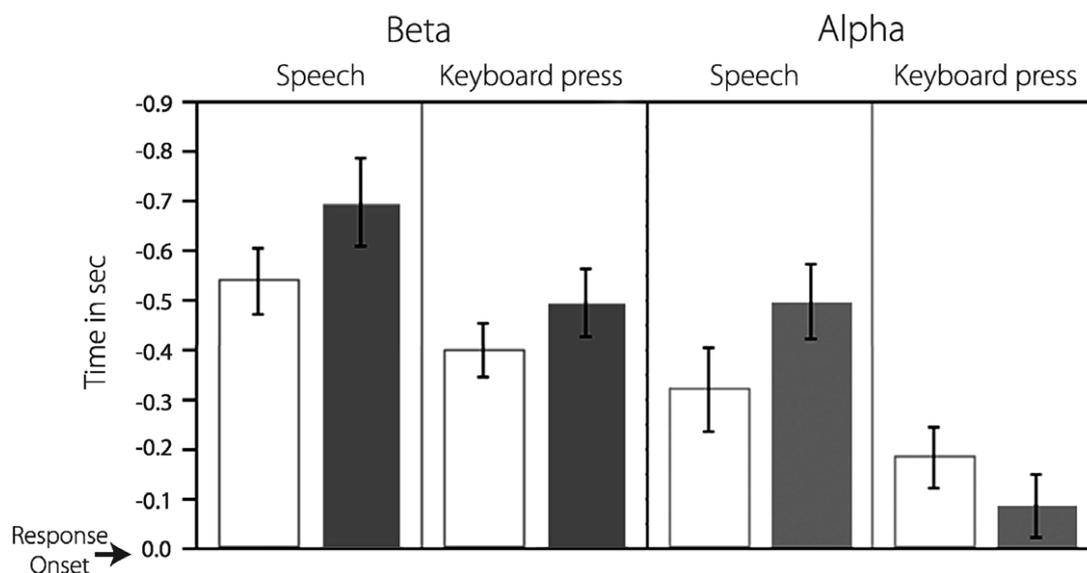


Fig. 4. Mean (\pm SE) onset time (in seconds from the onset of the motor response) for the speech task and for the keyboard press task, for the group, for the externally cued responses (white bars) and self-selected ones (gray bars), within each frequency band: alpha (top two panels) and beta (bottom panels). The data represent the average onset times from all electrodes. Longer bar represents earlier onset ERDs.

mixed-model ANOVA revealed a significant main effect of frequency BAND ($F(1,39) = 27,241, p = 0.000$), with the beta ERD onset occurring 311 ms earlier than the alpha ERD (average -319 and -8 ms with respect to response onset, respectively). The onset of beta ERD began with the onset of the stimulus while the onset of alpha ERD began at or close to response onset. The ANOVA also revealed a significant 2-way interaction between frequency BAND and REGION ($F(2,39) = 5728, p = 0.007$) indicating earlier beta ERD onset at the medial electrodes compared with the lateral electrodes. For the non-speech task, the mixed-model ANOVA also revealed a significant main effect of frequency BAND ($F(1,39) = 7341, p = 0.010$), with the beta ERD onset starting earlier than the alpha ERD (average -513 and -358 ms with respect to response onset, respectively). Similar to the speech

results, the onset of the beta ERD was more closely related to the onset of the stimulus while the onset of alpha ERD began closer to response onset. For the non-speech task, the BAND by REGION interaction did not reach significance. There was, however, as was observed for speech, a trend for the difference in the onset of the alpha and beta band ERD to be more pronounced at the medial electrodes. The ERD onset results are illustrated in Fig. 4.

With regard to the duration of the ERD, there was a very strong band effect ($F(1,78) = 21,110, p = 0.000$). The alpha ERD, overall, was longer than the beta ERD. There was also evidence of earlier ERD timing noted at the medial compared to the lateral electrodes.

To summarize the band-specific differences in the time domain, the beta ERD was associated more closely with the timing of the stimulus while the alpha ERD was asso-

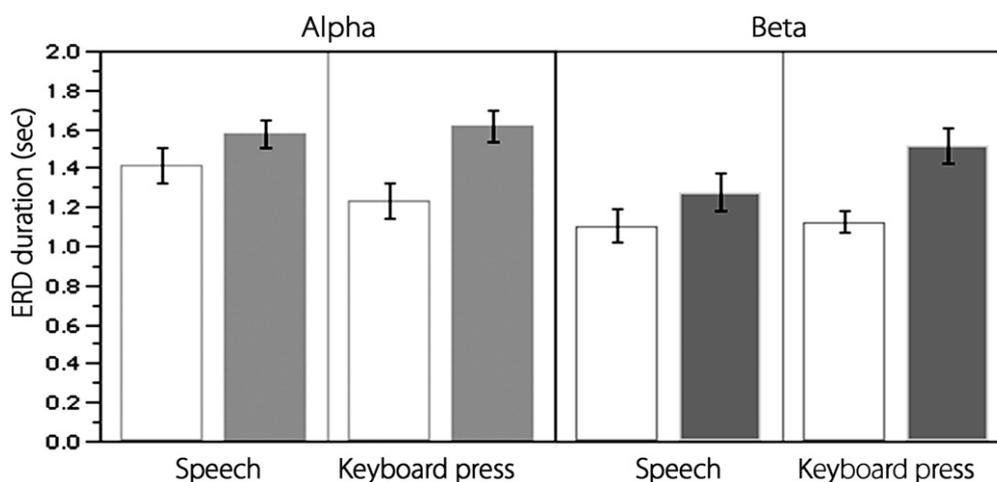


Fig. 5. Mean (\pm SE) ERD duration (in seconds from ERD onset) for the speech task and for the keyboard press task, for the group, in seconds, for the externally cued responses (white bars) and for the self-selected ones (gray bars), for the alpha band (left panel) and beta band (right panel) The data represent the average duration obtained from all the electrodes.

ciated more closely with the timing of the response. The beta ERD was of shorter duration than the alpha ERD.

3.2.4. *Speech vs. non-speech*

Overall, the ERD patterns for the speech and the non-speech tasks were similar: alpha and beta ERD preceded the response, and many characteristics of the ERD were similarly influenced by the response MODE and the frequency BAND. One difference that was observed between the tasks was that, regardless of the band, the ERD began later for the non-speech task than for the speech task.

4. Discussion

The main goal of the present study was to examine the characteristics of brain rhythmic activity in subject-specific alpha and beta frequency bands in relation to the mode of response selection (externally specified vs. self-selected) and the kind of motor task. It has been suggested that these two different response selection modes rely on two distinct cortical areas (e.g. Goldberg, 1985) involving the supplementary motor area (SMA) and the lateral premotor area (PMA). A number of empirical observations using a variety of techniques have provided general support for this dichotomy (e.g. Deiber et al., 1996; Hyder et al., 1997; Sakai et al., 2000; Lau et al., 2004, 2006). In the present study, we were interested in the contribution of different frequency bands (alpha and beta) and in the neural specificity of the processes underlying these different response conditions. Since the selection of a learned motor response is, arguably, a domain-general mechanism, we decided to examine two different kinds of simple motor behaviors, namely speaking and pressing buttons on a keyboard, in order to shed light on the commonalities in the neural process for selecting motor responses across effectors systems. Despite their apparent differences, speaking and keyboard pressing share some important features. Both kinds of actions are well learned and hence executed quasi automatically and with ease. Both are also used on a daily basis and thus are highly familiar. Moreover, both behaviors require fine motor control and, as such, the set of effectors underlying the execution of both kinds of behavior occupy large regions of the primary motor cortex in humans.

Overall, the results suggest that the brain activity patterns were similar for the speech and the keyboard pressing tasks and that there are band specific contributions to response selection. These findings provide new information about the contributions of different frequency bands to cognitive and motor processes and the manner in which well-learned motor actions are reflected in neuronal oscillatory behavior.

4.1. *Behavioral results*

Overall the reaction time (RT) for the non-speech task was longer than that for the speech task, a result that cannot be solely accounted for by the difference in the mea-

surement used (EMG vs. keyboard press). It appears that generating simple verbal responses, with the greater number of muscles required, is an easier task than pressing a key on a keyboard. This finding is not surprising, for speaking is indeed a well-practiced, highly familiar motor behavior and, despite its complexity, both cognitive and motor, it is accomplished quickly and with ease.

4.2. *Response mode*

The onset time and the duration of the ERD, as well as the ERD time-to-peak were modulated by the mode of response selection. Regardless of task and band, the ERD occurred earlier (closer to response onset) and was approximately 270 ms shorter, overall, for EXT than for INT, in line with Kaiser et al. (2001), and consistent with the more direct relationship between the visual stimulus and the response in EXT, and the resulting faster RTs. We observed also that the activity at the medial electrodes (covering the pre-SMA and SMA) tended to be more influenced by the response mode, particularly in the beta band, than activity at the lateral electrodes. Moreover, the beta ERD at the medial electrodes tended to begin earlier compared to the lateral electrodes. Such timing pattern (SMA/pre-SMA preceding M1) has been demonstrated with fMRI (e.g. Lee et al., 1999) and EEG (e.g. Carbonnell et al., 2004). Together, these results suggest that the activity recorded at the medial electrodes originated from the both SMA and pre-SMA, consistent with studies showing that medial wall motor areas are involved in the process of internally selecting responses (*for speech*: Alario et al., 2006; Crosson et al., 2001; Tremblay and Gracco, 2006; *for finger movements*: Deiber et al., 1996; Hyder et al., 1997; Sakai et al., 2000; Lau et al., 2004; Lau et al., 2006). In these studies, activity in the pre-SMA was greater for internally selected responses compared with externally specified responses. In line with these findings, the beta ERD recorded at the medial electrodes showed a longer and larger ERD for the self-selected task than for the externally specified task and there was also a tendency for the amplitude of the beta ERD to be greater for self-selected compared with externally specified responses. The connectivity pattern of the pre-SMA makes it an ideal candidate for contributing to the response selection process through its extensive connections with the prefrontal cortex and with frontal motor regions (e.g. Luppino et al., 1993; Bates and Goldman-Rakic, 1993; Lu et al., 1994; Rizzolatti et al., 1998).

Overall, our findings suggest that the beta ERD is involved in response selection and that the activity recorded over the medial electrodes reflects the contribution of both SMA and pre-SMA.

4.3. *Band-specific contributions*

Although both the alpha and the beta band ERD were influenced by the mode of movement selection, in the pres-

ent study, we observed that this difference was more pronounced in the beta band. Moreover, we found that the alpha band ERD was more closely related to the onset of the response, and lasted longer, than the beta band ERD. One possible interpretation is that an early alpha band ERD was masked by evoked alpha band activity present at the occipital electrodes. This alpha activity would be included in the common averaged reference that was used in this study and could have masked an alpha band ERD at the central recording sites. If that was the case, however, one might expect that it would have resulted in a large amplitude ERS across the central electrodes, which was not the case. The pre-movement ERS was maximal at the medial electrodes. Moreover, it has been shown previously that an alpha ERD occurs at the onset of a movement, and not prior to it (Alegre et al., 2003). Another possible interpretation of these results is that, in contrast to the beta ERD, the alpha band ERD is tied to motor execution as opposed to motor planning. However, given that the actual motor responses did not vary between the tasks, this interpretation does not seem plausible. An alternative explanation is that the alpha ERD reflects a self-monitoring or attentional process that oversees the execution of motor responses. Consistent with this interpretation, it has been suggested that the alpha ERD reflects general information processing or attentional demands (e.g. Alegre et al., 2003) and task difficulty is known to influence alpha ERD (e.g. Boiten et al., 1992; Babiloni et al., 2004). More attention or increased monitoring may accompany the execution of self-selected responses, compared to externally selected ones. Further studies, more specifically designed to examine the contribution of the alpha band activity to motor planning and execution, will be necessary in order to better understand the contribution of the alpha ERD to response selection.

4.4. Domain-general vs. domain-specific neural activity

One key question that we were asking in the present study was whether motor behaviors using a different set of effectors but arguably using a common response selection mechanism would exhibit similar patterns of neural activity. The general finding of similarities in EEG patterns between speech production and keyboard pressing suggests that the preparation of these different motor behaviors involves the use of overlapping, domain general neural mechanisms for the selection of motor responses. The extent to which the neural control of speech movements is task-specific and distinctively controlled from non-speech oral behaviors (such as swallowing, or isolated articulator movements) remains a matter of debate (e.g. Ziegler, 2003; Ballard et al., 2003). This issue has considerable clinical implications, in particular regarding the use of non-speech oral motor exercises (NS-OMEs) in the evaluation and treatment of speech disorders. The incorporation of NS-OMEs in the treatment of acquired and developmental speech disorders is a widespread and long-standing

practice among speech-language pathologists (Skahan et al., 2007). However, in a recent review of the literature, Weismer (2006) concluded that "...there is neither theoretical nor empirical support for a continued focus on oromotor, non-verbal tasks in our field, at least as a way to learn about speech motor control processes" (p. 342). This conclusion was based on the lack of clear empirical support for the idea that the speech motor planning makes use of underlying neural mechanisms that are shared with other motor tasks. The conclusion was also based on the considerable body of evidence demonstrating that the use of MS-OMEs in the treatment of speech disorders is therapeutically ineffective. The finding in the present study of similarities in EEG patterns between a speech and non-speech motor task stands in contrast with these previous findings, suggesting that at least some aspects of speech motor planning, such as response selection, may be controlled by domain-general, rather than task-specific, neural mechanisms. Further studies are required to explore in more detail the possibility that the sub-components of speech motor planning and execution may rely differentially on domain-general or domain-specific neural processes.

4.5. Speech-related artifact in the EEG signal

The recording of EEG signals during an orofacial movement task (such as speech production) is potentially problematic due to the electrical signals generated by a large number of contracting orofacial muscles (see, e.g. Morrell and Huntington, 1971; Brooker and Donald, 1980; Friedman and Thayer, 1991). Facial muscle activity has the potential to contaminate EEG signals in the alpha and beta bands; however, the degree of contamination depends crucially on the level of muscle contraction and the location of contracting muscles relative to the EEG array (Friedman and Thayer, 1991; Goncharova et al., 2003). Because signal strength decreases rapidly with distance, electrode sites at the periphery of the EEG electrode array are of particular concern due to their proximity to a number of facial muscles (e.g. temporalis and epicranium pars frontalis). While the present study examined activity only along a strip of centrally located electrodes (C3–C6), a number of steps were taken to minimize the contribution of facial muscle EMG to recorded EEG signals. Subjects were instructed to produce quiet, single syllable speech utterances involving low amplitude of lip, tongue and jaw movement, and consequently a reduced magnitude of speech-related muscle activity. In addition, subjects were instructed to minimize any extraneous movement during all tasks. Finally, following the application of steps to eliminate artifact in the EEG signal due to blinks and eye movement (see Section 2), all trials were inspected for any evidence of facial muscle-related artifact (e.g. bursts of high-frequency activity coinciding with the onset of speech, or higher than expected peak-to-peak amplitude within the trial). Trials showing any evidence of such EMG-based activity were excluded from further analysis.

There are a number of indicators that contamination of the EEG signal by facial muscle activity was negligible in the present study. One is the observed similarity in the latency and magnitude of ERD/ERS patterns between speech production and finger-movement, for which there was no risk of EMG contamination. Further evidence of minimal contamination comes from the failure, in the percent-change time-series (Fig. 1), to observe any movement-related increase in EEG signal amplitude at the onset of speech production. Recall that the calculation of ERD/ERS in speech involves band pass filtering the raw EEG signals (to isolate the alpha and beta bands), aligning individual trials on the basis of lip EMG onset, converting to power and then averaging. For repetitions of the same speech utterance, the magnitude of facial EMG signals would be expected to follow a consistent temporal pattern relative to onset. As with brain-related EEG signals, any muscle-related signals that were transduced by the EEG electrodes (and with significant energy in the alpha or beta band) would be amplified by the procedure of alignment and averaging, resulting in an increase in averaged EEG power during movement. In contrast, speech production was found to be associated with a decrease in EEG power (i.e. ERD) in the alpha and beta bands immediately preceding movement onset. Only after the movement had ended was an increase in power observed (i.e. ERS rebound).

5. Conclusion

In the present study, we used an ERD quantification method to compare frequency specific EEG reactivity for two canonical modes of response selection (externally and self-specified) within two different motor systems: orofacial (speech production) and finger (keyboard press). Differences in ERD patterns were observed between alpha and beta bands in relation to response selection and movement onset. Beta ERD patterns showed a closer relation to the process of response selection, with onset, duration and time to ERD peak showing an enhancement for internally specified responses relative to externally triggered responses. In contrast, alpha ERD patterns were found to be more closely related to response onset, perhaps reflecting attentional demands overseeing motor response execution. Importantly, ERD patterns for the speech and keyboard press tasks were found to be very similar across the frequency bands, suggesting that with respect to response selection, the two motor systems make use of common underlying neural mechanisms.

Acknowledgements

We thank Demetrios Voreades & Mark Pflieger (Source Signal Imaging, San Diego, US) for their invaluable help with signal processing and data analysis. We also thank

all the participants. These studies were funded by CIHR and NSERC.

References

- Alario FX, Chainay H, Lehericy S, Cohen L. The role of the supplementary motor area (SMA) in word production. *Brain Res* 2006;1076(1):129–43.
- Alegre M, Gurtubay IG, Labarga A, Iriarte J, Malanda A, Artieda J. Alpha and beta oscillatory changes during stimulus-induced movement paradigms: effect of stimulus predictability. *Neuroreport* 2003;14(3):381–5.
- Babiloni C, Miniussi C, Babiloni F, Carducci F, Cincotti F, Del Percio C, et al. Sub-second “temporal attention” modulates alpha rhythms. A high-resolution EEG study. *Brain Res Cogn Brain Res* 2004;19(3):259–68.
- Ballard KJ, Robin DA, Folkins JW. An integrative model of speech motor control: a response to Ziegler. *Aphasiology* 2003;17:37–48.
- Bates JF, Goldman-Rakic PS. Prefrontal connections of medial motor areas in the rhesus monkey. *J Comp Neurol* 1993;336(2):211–28.
- Boiten F, Sergeant J, Geuze R. Event-related desynchronization: the effects of energetic and computational demands. *Electroencephalogr Clin Neurophysiol* 1992;82(4):302–9.
- Brooker BH, Donald MW. Contribution of the speech musculature to apparent human EEG asymmetries prior to vocalization. *Brain Lang* 1980;9(2):226–45.
- Carbannel L, Hasbroucq T, Grapperon J, Vidal F. Response selection and motor areas: a behavioural and electrophysiological study. *Clin Neurophysiol* 2004;115(9):2164–74.
- Cooper NR, Croft RJ, Dominey SJ, Burgess AP, Gruzeliér JH. Paradox lost? Exploring the role of alpha oscillations during externally vs. internally directed attention and the implications for idling and inhibition hypotheses. *Int J Psychophysiol* 2003;47(1):65–74.
- Crosson B, Sadek JR, Maron L, Gökçay D, Mohr C, Auerbach EJ, et al. Relative shift in activity from medial to lateral frontal cortex during internally versus externally guided word generation. *J Cogn Neurosci* 2001;13(2):272–83.
- Cunnington R, Windischberger C, Robinson S, Moser E. The selection of intended actions and the observation of others' actions: a time-resolved fMRI study. *Neuroimage* 2006;29(4):1294–302.
- Deiber MP, Ibanez V, Sadato N, Hallett M. Cerebral structures participating in motor preparation in humans: a positron emission tomography study. *J Neurophysiol* 1996;75(1):233–47.
- Desmond JE, Gabrieli JD, Glover GH. Dissociation of frontal and cerebellar activity in a cognitive task: evidence for a distinction between selection and search. *Neuroimage* 1998;7:368–76.
- Dirnberger G, Fickel U, Lindinger G, Lang W, Jahanshahi M. The mode of movement selection. Movement-related cortical potentials prior to freely selected and repetitive movements. *Exp Brain Res* 1998;120(2):263–72.
- Fitts PM. The information capacity of the human motor system in controlling the amplitude of movement. *J Exp Psychol* 1954;47:381–91.
- Fitts PM, Peterson JR. Information capacity of discrete motor responses. *J Exp Psychol* 1964;67:103–12.
- Friedman BH, Thayer JF. Facial muscle activity and EEG recordings: redundancy analysis. *Electroencephalogr Clin Neurophysiol* 1991;79(5):358–60.
- Frith C. Positron emission tomography studies of frontal lobe function: Relevance to psychiatric disease. *Ciba Found Symp* 1991;163:181–9.
- Frith CD, Friston K, Liddle PF, Frackowiak RS. Willed action and the prefrontal cortex in man: a study with PET. *Proc Biol Sci* 1991;244(1311):241–6.
- Goncharova II, McFarland DJ, Vaughan TM, Wolpaw JR. EMG contamination of EEG: spectral and topographical characteristics. *Clin Neurophysiol* 2003;114(9):1580–93.
- Goldberg G. Supplementary motor area structure and function: review and hypothesis. *Behav Brain Sci* 1985;8:567–616.

- Godschalk M, Lemon RN, Kuypers HG, van der Steen J. The involvement of monkey premotor cortex neurones in preparation of visually cued arm movements. *Behav Brain Res* 1985;18(2):143–57.
- Hick WE. On the rate of gain of information. *Q J Exp Psychol* 1952;4:11–26.
- Hyder F, Phelps EA, Wiggins CJ, Labar KS, Blamire AM, Shulman RG. Willed action: a functional MRI study of the human prefrontal cortex during a sensorimotor task. *Proc Natl Acad Sci USA* 1997;94(13):6989–94.
- Jackson A, Spinks RL, Freeman TC, Wolpert DM, Lemon RN. Rhythm generation in monkey motor cortex explored using pyramidal tract stimulation. *J Physiol* 2002;541(Pt 3):685–99.
- Jahansahi M, Frith CD. Willed action and its impairments. *Cogn Neuropsychol* 1998;15:483–533.
- Kaiser J, Birbaumer N, Lutzenberger W. Event-related beta desynchronization indicates timing of response selection in a delayed-response paradigm in humans. *Neurosci Lett* 2001;312(3):149–52.
- Lau HC, Rogers RD, Ramnani N, Passingham RE. Willed action and attention to the selection of action. *Neuroimage* 2004;21(4):1407–15.
- Lau H, Rogers RD, Passingham RE. Dissociating response selection and conflict in the medial frontal surface. *Neuroimage* 2006;29(2):446–51.
- Lebedev MA, Wise SP. Oscillations in the premotor cortex: single-unit activity from awake, behaving monkeys. *Exp Brain Res* 2000;130(2):195–215.
- Lee KM, Chang KH, Roh JK. Subregions within the supplementary motor area activated at different stages of movement preparation and execution. *Neuroimage* 1999;9(1):117–23.
- Lu MT, Preston JB, Strick PL. Interconnections between the prefrontal cortex and the premotor areas in the frontal lobe. *J Comp Neurol* 1994;341(3):375–92.
- Luce RD. Response times: their role in inferring elementary mental organization. New York: Oxford University Press; 1986.
- Luppino G, Matelli M, Camarda R, Rizzolatti G. Corticocortical connections of area F3 (SMA-proper) and area F6 (pre-SMA) in the macaque monkey. *J Comp Neurol* 1993;338(1):114–40.
- Morrell LK, Huntington DA. Electrocortical localization of language production. *Science* 1971;174(16):1359–61.
- Mushiaki H, Inase M, Tanji J. Neuronal activity in the primate premotor, supplementary, and precentral motor cortex during visually guided and internally determined sequential movements. *J Neurophysiol* 1971;66:705–18.
- Ohara S, Ikeda A, Kunieda T, Yazawa S, Baba K, Nagamine T, et al. Movement-related change of electrocorticographic activity in human supplementary motor area proper. *Brain* 2000;123(Pt 6):1203–15.
- Pfurtscheller G. Event-related synchronization (ERS): an electrophysiological correlate of cortical areas at rest. *Electroencephalogr Clin Neurophysiol* 1992;83(1):62–9.
- Pfurtscheller G, Lopes da Silva FH. Event-related EEG/MEG synchronization and desynchronization: basic principles. *Clin Neurophysiol* 1999;110(11):1842–57.
- Pfurtscheller G, Aranibar A. Event-related cortical desynchronization detected by power measurements of scalp EEG. *Electroencephalogr Clin Neurophysiol* 1977;42(6):817–26.
- Pfurtscheller G, Stancak Jr A, Neuper C. Event-related synchronization (ERS) in the alpha band – an electrophysiological correlate of cortical idling: a review. *Int J Psychophysiol* 1996;24(1–2):39–46.
- Pfurtscheller G, Graimann B, Huggins JE, Levine SP, Schuh LA. Spatiotemporal patterns of beta desynchronization and gamma synchronization in corticographic data during self-paced movement. *Clin Neurophysiol* 2003;114(7):1226–36.
- Phelps EA, Hyder F, Blamire AM, Shulman RG. FMRI of the prefrontal cortex during overt verbal fluency. *Neuroreport* 1997;8(2):561–5.
- Rizzolatti G, Luppino G, Matelli M. The organization of the cortical motor system: new concepts. *Electroencephalogr Clin Neurophysiol* 1998;106:283–96.
- Sakai K, Hikosaka O, Takino R, Miyauchi S, Nielsen M, Tamada T. What and when: parallel and convergent processing in motor control. *J Neurosci* 2000;20(7):2691–700.
- Salenius S, Schnitzler A, Salmelin R, Jousmaki V, Hari R. Modulation of human cortical rolandic rhythms during natural sensorimotor tasks. *Neuroimage* 1997;5(3):221–8.
- Salmelin R, Hamalainen M, Kajola M, Hari R. Functional segregation of movement-related rhythmic activity in the human brain. *Neuroimage* 1995;2(4):237–43.
- Salmelin R, Schnitzler A, Schmitz F, Freund HJ. Single word reading in developmental stutterers and fluent speakers. *Brain* 2000;123(Pt 6):1184–202.
- Salmelin R, Sams M. Motor cortex involvement during verbal versus non-verbal lip and tongue movements. *Hum Brain Mapp* 2002;16(2):81–91.
- Sanes JN, Donoghue JP. Oscillations in local field potentials of the primate motor cortex during voluntary movement. *Proc Natl Acad Sci USA* 1993;90(10):4470–4.
- Schumacher EH, D'Esposito M. Neural implementation of response selection in humans as revealed by localized effects of stimulus-response compatibility on brain activation. *Hum Brain Mapp* 2002;17(3):193–201.
- Skahan SM, Watson M, Lof GL. A nationwide survey of non-speech oral motor exercise use: implications for evidence-based practice. *Lang Speech Hear Serv Sch* 2007.
- Szurhaj W, Derambure P, Labyt E, Cassim F, Bourriez JL, Isnard J, et al. Basic mechanisms of central rhythms reactivity to preparation and execution of a voluntary movement: a stereoelectroencephalographic study. *Clin Neurophysiol* 2003;114(1):107–19.
- Thut G, Hauert C, Viviani P, Morand S, Spinelli L, Blanke O, et al. Internally triggered vs. externally cued movement selection: a study on the timing of brain activity. *Brain Res Cogn Brain Res* 2000;9(3):261–9.
- Tremblay P, Gracco VL. Contribution of the frontal lobe to externally and internally specified verbal responses: fMRI evidence. *Neuroimage* 2006;33(3):947–57.
- Verstraeten E, Cluydts R. Attentional switching-related human EEG alpha oscillations. *Neuroreport* 2002;13(5):681–4.
- Waszak F, Wascher E, Keller P, Koch I, Aschersleben G, Rosenbaum DA, et al. Intention-based and stimulus-based mechanisms in action selection. *Exp Brain Res* 2005;162(3):346–56.
- Weeks RA, Honda M, Catalan MJ, Hallett M. Comparison of auditory, somatosensory, and visually instructed and internally generated finger movements: a PET study. *Neuroimage* 2001;14(1 Pt 1):219–30.
- Weismer G. Philosophy of research in motor speech disorders. *Clin Linguist Phonet* 2006;20:315–49.
- Woo SH, Lee KM. Effect of the number of response alternatives on brain activity in response selection. *Hum Brain Mapp* 2006.
- Ziegler W. Speech motor control is task-specific. Evidence from dysarthria and apraxia of speech. *Aphasiology* 2003;17:3–36.