Movement-related changes in cortical excitability:

A steady-state SEP approach

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Abstract

This study explored the use of steady-state somatosensory evoked potentials (ssSEPs) as a continuous probe on the excitability of the somatosensory cortex during the foreperiod and the response time of a cued choice reaction time task. ssSEPs were elicited by electrical median nerve stimulation at the left and right wrist, using a stimulation frequency of 22.2 Hz. Scalp-recorded ssSEPs were analyzed by means of dipole source analysis to achieve optimal separation of left and right hemisphere ssSEPs. The time course of ssSEP modulation at the source level was extracted by means of a wavelet transform. In addition to the extraction of ssSEPs, the analysis included the derivation of lateralized attention and movement-related potentials, i.e. the attention-directing anterior negativity (ADAN) and the lateralized readiness potential (LRP). The results revealed a time course of ssSEP modulation remarkably similar to the time course of ADAN and LRP. The time course was characterized by a reduction of ssSEP amplitude at latencies just following the peak latency of the ADAN (~ 400 ms) and the peak latency of the LRP (~1200 ms). This reduction was greater for contralateral than for ipsilateral movements. The study demonstrates that ssSEP methodology represents a feasible approach to the measurement of movement-related changes in cortical excitability, which may be used to resolve ambiguities in the interpretation of lateralized event-related brain potentials.

1. Introduction

Analyses of amplitude modulations of sensory-evoked EEG responses are a long-established approach in the study of selective attention mechanisms (see Mangun and Hillyard, 1995 for review). In the field of visual selective attention, Müller and co-workers (Müller et al., 1998) have made a strong case for the study of such amplitude modulations by means of steady-state visual-evoked potentials (ssVEPs). Since ssVEPs are elicited by sustained trains of repetitive stimuli, they provide a continuous measure of the modulation of sensory function by attentional processes (Müller et al., 1998). In the domain of sensorimotor function, amplitude modulations of somatosensory-evoked potentials (SEPs) have been used to probe the state of the sensorimotor system during the preparation and execution of movement (Böcker et al., 1993; Cheron and Borenstein, 1987; Cohen and Starr, 1987; Jones et al., 1989; Shimazu et al., 1999). Here, the use of a continuous measure, rather than intermittent probes by means of transient evoked responses, would potentially have a similar advantage as the use of ssVEPs in visual selective attention research. The present study used the ssSEP approach with the aim to explore its feasibility in a motor task and in order to address questions regarding the generation of lateralized movement-related brain potentials.

Preparation for a forthcoming movement is reflected in slow brain potentials, i.e. the readiness potential, the contingent negative variation (CNV), and the lateralized readiness potential (LRP). The LRP can be measured during the foreperiod between a cue and response stimulus and reflects the differential activity between the contralateral and ipsilateral hemisphere motor cortex (for review see Eimer and Coles, 2003). In the present study we measured the LRP following an arrow cue that instructed participants to

prepare a left or a right hand button press. The LRP thus provided an independent measure of the time course of movement preparation allowing a comparison with the information that we aimed to gain from simultaneously recorded ssSEPs.

While the LRP already provides a sensitive measure of movement preparatory processes, it has a major limitation inherent in the fact that it is a difference measure between the EEG activity recorded over the hemispheres contra and ipsilateral to the side of movement. Vidal et al. (2003) and Praamstra and Seiss (2005) have suggested, on the basis of current source density transformation of EEG data, that the LRP during movement preparation and execution involves contralateral activation and ipsilateral inhibition. The bi-hemispheric involvement in the preparation of a unimanual response underlines the limitations of the LRP and the potential value of complementing it with ssSEPs. The present study was especially interested in exploiting this approach to clarify the generation of the lateralized ADAN (anterior directing-attention negativity) component, which is derived in the same manner as the LRP and precedes the latter during the fore period between a cue and response stimulus. The ADAN is associated with the executive control of spatial attention (e.g. Hopf and Mangun, 2000; Eimer et al., 2002) and with the selection between response hands or response directions (Praamstra et al., 2005; Verleger et al., 2000; Gherri et al. 2007). As to the generation of the ADAN, it is commonly assumed that the selection of a location in space or side of a response involves activation of the contralateral frontal cortex, expressed in electrocortical activity of negative polarity. However, the ADAN can also be explained by ipsilateral activity of positive polarity serving the suppression of the non-selected response (Praamstra et al., 2005). The modulation of ssSEPs in the time window of the ADAN enables an evaluation

of these alternative explanations.

One previous study examined the modulation of SEPs during the foreperiod of a forewarned reaction time task, but this did not involve an evaluation of the effects of response choice (Böcker et al., 1993). Closer to the goals of the present study, Eimer et al. (2005) used transient SEPs to tactile stimuli delivered during the foreperiod of a cued choice response task. Stimuli were delivered randomly to either the cued or the non-cued hand at two possible delays, producing different SEP amplitudes depending on stimulation at the cued or non-cued side. In the present ssSEP study, by contrast, repetitive stimuli were applied during the entire foreperiod (Figure 1). In addition, the stimulation was applied to both hands simultaneously under the assumption that generation of ssSEPs in the contralateral primary somatosensory cortex would enable the selective recovery of each hemisphere's ssSEP modulation by an analysis at the source level using dipole source modeling.

---------- Insert Figure 1 about here ----------

2. Results

Reaction times

The reaction times (mean ± SD) were 180 ± 49 ms and 177 ± 48 ms for the left and the right hand, respectively, in the presence of electrical stimulation. For the trials where there was no electrical stimulation, the reaction times were 188 ± 53 ms and 186 ± 50 ms for the left and the right hand, respectively. A 2 x 2 ANOVA with the factors Electrical stimulation (present vs. absent) and Response hand (left vs. right hand) revealed that the participants responded faster in the presence compared to the absence of electrical stimulation ($F(1,7)=6.3$, $p=0.04$). There was no difference between response hands ($F<1$)

nor an interaction between the two factors ($F<1$). The faster reaction times in the stimulation condition may be due to altered sensation in the hand, produced by the stimulation, leading to a lack of modulation in the motor response, i.e. a much stronger force than needed. In addition, the peripheral stimulation itself may have contributed to a brisker movement of the index finger pressing the response button.

---------- Insert Figure 2 about here ----------

Lateralized potentials

The directional information provided by left or right pointing arrows induced transient laterized activity over the frontocentral scalp area. The earliest lateralization corresponds to the ADAN component peaking around 400 ms after the directional cue (Figure 2). The ADAN amplitude in the time window from 350-450 ms after the cue was -0.5 ± 0.4 μV and -0.4 ± 0.4 μV with and without electrical stimulation, respectively. The amplitude difference was not significant ($t<1$). The ADAN component was followed by a slowly developing lateralized component, the lateralized readiness potential (LRP) (Figure 2). The LRP amplitude during the last 200 ms before the imperative stimulus was -0.6 ± 0.6 μV and -0.4 ± 0.5 μV with and without electrical stimulation, respectively. Again, this amplitude difference was not significant ($t(7)=1.13$, $p=0.30$).

---------- Insert Figure 3 about here ----------

Dipole source localisation

SsSEPs had maximal amplitudes, with opposite polarity, over frontal and parietal areas (see Figure 3). Applying dipole source analysis, they could be satisfactorily modeled by two symmetrical single dipole sources. This was the case in all participants, with source locations always close to the central sulcus (Figure 4). The goodness of fit of individual

subjects' dipole source models in explaining the high S/N ratio short segments of ssSEPs was 93.6 ± 3.0 %. The Talairach-Tournoux coordinates of the source locations correspond to a location in the primary sensory cortex. For the left (right) hemisphere source they were x = -(+)36.0 ± 4.3, y = -17.0 ± 6.2 and z = 49.5 ± 2.8. The azimuth and the polar angle defining source orientations were $\theta = 85.7 \pm 32.1^{o}$, $\varphi = 69.6 \pm 25.4^{o}$ and $\theta = -82.5 \pm 22.2^{o}$, $\varphi = -64.4 \pm 22.7^{o}$ for the left and the right hemisphere source, respectively.

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Source waveform analysis

The next analysis step of ssSEPs was to reduce the 128 channel scalp ssSEP averages to two dipole source waveforms, separately for each condition and subject. Thus, the dipole source waveforms represent the time course of ssSEPs recorded over the left and right sensory cortex during the entire trial epoch. To quantify the ssSEP amplitude modulation over time, the signal envelope (Figure 5) was extracted using a continuous wavelet transformation (CWT). Figure 6 shows the envelopes of the ssSEP source waveforms contra and ipsilateral to left and right hand movement conditions. The time course of the ssSEP modulation was remarkably similar to the time course of ADAN and LRP, in the sense that increased lateralized activity of negative polarity in ADAN and LRP was accompanied by decreased ssSEP amplitudes. The amplitude of the envelopes was analysed in three different time windows defined on the basis of the grand average data, i.e. 375-575 ms, overlapping with the ADAN component, 800-1000 ms, coinciding with the foreperiod LRP, and 1250-1450 ms, immediately following the overt response.

The modulation of the ssSEPs source waveforms during the 375-575 ms interval was assessed by a means of a 2 x 2 ANOVA with factors Hemisphere (left/right) and Response side (contralateral/ipsilateral). There was no significant main effect of hemisphere ($F(1,7)=1.8$, $p=0.226$). By contrast, a main effect of Response side ($F(1,7)=6.1$, $p=0.043$) was due to ssSEPs being reduced in amplitude when the contralateral hand was cued, compared to when the ipsilateral hand was cued. As can be seen in Figure 7A, this ipsilateral-contralateral difference was very small for the left hemisphere ssSEPs. Post-hoc t-tests confirmed that only the modulation of the right hemisphere source reached significance ($t(7) < 1$ and $t(7)=4.2$, $p=0.004$).

The ssSEP source waveforms were analyzed in the same way in the time window from 800 to 1000 ms, i.e. the last 200 ms of the preparatory period, where no significant modulation was found. By contrast, the ssSEP source waveforms were strongly modulated in amplitude during and after movement (i.e. the button press following the imperative cue). An ANOVA applied to the amplitude values in this time window did not show a significant effect of Hemisphere ($F(1,7)=1.5$, $p=0.254$), but there was again a main effect of Response side ($F(1,7)=14.3$, $p=0.007$). This effect resulted from a greater ssSEP amplitude reduction following contralateral compared to ipsilateral movements. As in the case of the early time window, the asymmetry was more pronounced for the right hemisphere ssSEPs (Figure 7B), although it reached significance for both left and right hemisphere ssSEPs ($t(7)=2.7$, $p=0.03$, and $t(7)=3.4$, $p=0.012$, respectively).

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3. Discussion

The present study used steady-state SEPs to provide a continuous measure of somatosensory cortex excitability during the selection, preparation, and execution of a unimanual response. The use of ssSEPs to probe cortical excitability aimed to provide information complementing the information derived from movement-related potentials. Results revealed an amplitude modulation of ssSEPs whose time course closely resembled the time course of lateralized movement-related potentials. We will first discuss the results in relation to movement-related potentials and then address some methodological issues.

At approximately the latency of the ADAN component (~ 400 ms after cue onset), the amplitude of ssSEPs was modulated as a function of which hand was cued by the cue signal. ADAN type lateralized potentials following a directional cue were extensively investigated by Eimer (1993, 1995) and, at the time, interpreted as automatic response activation, i.e. as LRP. However, the ADAN derives its name as attention-related component from its association with the executive control of spatial attention (e.g. Hopf and Mangun, 2000; Eimer et al., 2002). More recently, it is recognised that the ADAN not only reflects the control of spatial attention, but is also elicited when a directional cue guides the selection of a manual response, suggesting a role in response selection (Mathews et al., 2006; Praamstra et al., 2005; Verleger et al., 2000). Source characterization of the ADAN (Mathews et al., 2006; Praamstra et al., 2005) provides evidence for a generation of the ADAN in the dorsal premotor cortex, an area with attention and movement-related functions (Wise et al., 1997; Boussaoud, 2001; Simon et al., 2002). Importantly, as a lateralized component reflecting the voltage difference

between homologous electrodes over left and right hemisphere, it is ambiguous whether the ADAN reflects negative polarity activity over the contralateral hemisphere or positive polarity activity over the ipsilateral hemisphere (Praamstra et al., 2005). The current data, with a depression of ssSEP amplitude in the ADAN time window, which was stronger when the contralateral hand was cued, suggest that the ADAN results from an activation of the hemisphere contralateral to the side of a manual response.

The ADAN is generally followed by a foreperiod LRP representing movement-preparatory activity, as it is in the present data (see Figure 2). One would predict that ssSEPs are reduced in amplitude over the hemisphere contralateral to the prepared response during this time window. Such a reduction was seen for the magnetoencephalographic somatosensory P30m as early as 1500 ms before a self-initiated movement (Wasaka et al., 2003). Although our ssSEP data do show an asymmetry, this effect did not reach significance, possibly due to insufficient power. During and following the motor response, by contrast, there was a robust modulation of ssSEP amplitude with a stronger attenuation after contralateral than after ipsilateral movements.

Previous studies on the modulation of somatosensory information during motor preparation have shown effects on transient evoked-potentials dependent on the latency of the component. Whereas during movement execution all components are reduced in amplitude (Böcker et al., 1993), during movement preparation late somatosensory potentials P90 and N140 are enhanced (Böcker et al., 1993; Eimer et al., 2005; Kida et al., 2004), while short and middle latency somatosensory potentials N30 and P50 are decreased in amplitude (Böcker et al., 1993; Kida et al., 2004). The amplitude reduction

of the N30 and P50 components is commonly discussed in terms of gating, whereas the enhancement of late components has been associated with attentional mechanisms (Böcker et al., 1993; Eimer et al., 2005). In the present investigation, we used a stimulation frequency of 22.2 Hz, corresponding to an interstimulus interval of 45 ms, which makes it likely that the elicited ssSEPs correspond to short or mid latency transient SEP components. Indeed, such an equivalence has also been proposed earlier (Snyder, 1992). From this perspective, the suppression of ssSEPs during movement preparation and execution is in agreement with previous work using transient SEPs.

Whereas attenuation of SEPs during movement may arise at peripheral as well as central levels ("centripetal gating"; Jones et al., 1989), pre-movement SEP suppression occurs prior to movement and the arrival of peripheral feedback, thus suggesting a central "centrifugal" mechanism (Cohen and Starr, 1987, Shimazu et al., 1999, Wasaka et al., 2003). Voss et al. (2006) used transcranial magnetic stimulation to investigate the characteristics of the efferent motor signal causing sensory attenuation. The authors demonstrated that this efferent signal must originate upstream from the primary motor cortex. This result fits well with the ssSEP attenuation in the time window of the ADAN, supporting an interpretation of the ADAN as activity of the premotor cortex associated with the selection and/or covert activation of a motor response (Gherri et al., 2007; Mathews et al., 2006; Praamstra et al., 2005). It should be noted, however, that there is continuing debate about precentral contributions to the generation of SEPs (Huang et al., 2000; Waberski et al., 1999; Wasaka et al., 2003). Hence, it cannot be ruled out that instead of being mediated by an efferent signal to the somatosensory cortex, the attenuation of SEPs occurs through a more direct mechanism within the motor cortex. For

instance, the characteristic event-related desynchronization of beta activity preceding voluntary movements could play a role in the attenuation of (ss)SEPs, given that phase-locking of beta activity contributes to the generation of the N30 SEP component (Cheron et al., 2007).

Turning to methodological aspects, our study shows that it is feasible to analyse ssSEPs at the source level and extract meaningful time course information and meaningful asymmetries in the modulation of ssSEPs. With few exceptions (Giabbiconi et al., 2007) steady state evoked response studies have relied on analyses of steady state response amplitude at selected electrodes. Especially with the dipolar field distribution of SEPs, it is a distinct advantage to include all electrodes and achieve a data reduction not through selection of electrodes but by means of a source analysis, as performed here. Such an approach is facilitated by prior knowledge of early and steady-state somatosensory evoked responses being generated primarily in the primary sensory cortex (Allison et al., 1989; Pollok et al. 2002; Nangini et al., 2006) and by the predominantly contralateral projection of somatosensory pathways. In spite of this anatomical background, it is possible that asymmetries were diluted by our approach. This is because even with unilateral stimulation, evoked responses can be measured over the ipsilateral hemisphere, as a result of volume conduction. It is therefore important to point out that the here applied approach can be improved by choosing different stimulation frequencies for left and right hand, analogous to previous ssVEP investigations by Müller and co-workers (Müller et al., 1998). Such a modification would eliminate ‘crosstalk’ in the modeling of ssSEPs originating in left and right hemisphere sensory cortex. A further practical point concerns the choice of stimulation modality. While the present study used

electrical median nerve stimulation, it is currently more common to elicit ssSEPs with vibrotactile stimulation. Tactile stimulation is also used for eliciting transient SEPs (e.g. Eimer et al., 2005) and is better tolerated as well as less intrusive and has therefore obvious advantages over electrical stimulation in the context of behavioural experiments.

4. Experimental Procedure

Participants

Six males and 2 females (age 30 ± 8 yrs), seven of whom were right-handed, took part in the experiment. All had normal or corrected-to-normal vision. None of them had a history of hand injuries, psychiatric or neurological disorders. All the participants provided their informed consent after full explanation of the study.

Task and apparatus

The experiment consisted of a cued choice-response task, divided in 8 blocks of approximately 5 minutes each, preceded by a practice block of the same duration. Each block consisted of 80 trials. The trial structure is presented in Figure 1. Throughout each block four brackets delineating a square fixation area were displayed at the centre of a computer screen, along with two square boxes to the left and to the right of the centre. Trials started with the display of a directional cue (right or left pointing arrows) in the fixation area for a duration of 100 ms, informing the subjects to prepare a right or left hand response. Following a cue-target interval of 1000 ms, two identical response stimuli appeared in the square boxes for 100 ms. In 90% of the trials the stimuli consisted of 5 horizontal bars, which prompted the participants to respond (as swiftly and accurately as

possible) with the prepared hand. In the remaining 10% of the trials the bars were oriented vertically, instructing the participants to withhold the prepared response. Left and right pointing cues were of equal probability. The time interval between two successive directional cues was 4000 ms.

Electrical median nerve stimuli for eliciting ssSEPs were applied on alternate trials by a constant current stimulator (Digitimer model DS7A). Stimulation was always bilateral and applied at the wrist using disposable Ag/AgCl electrodes (TECA Accessories, 900X156). The electrical stimulation consisted of trains of square wave pulses (0.5 ms duration each) at a frequency of 22.2 Hz. Stimulation started 500 ms before the cue presentation for a duration of 2500 ms. The intensity of the electrical stimuli was approximately 60% of the motor threshold. The motor threshold was determined separately for each participant by unilaterally applying discrete electrical square wave pulses (0.5 ms duration each) at the median nerve at the inside of the wrist. The lowest value which produced a twitch of the thumb (observed by the experimenter) was taken as the motor threshold. This procedure was run separately for each hand.

The experiment was run in a quiet, normally illuminated room. The participants were seated comfortably in an armchair with the forearms placed on the armrests of the chair. The response keys were attached to the armrests, over which the participants placed the middle fingers of each hand. Responses were made by pressing the response key using the middle finger of the left or right hand.

The stimuli were presented in white against a grey background on a 17 inch monitor at a resolution of 800 x 600. The viewing distance was 100 cm. The bracket enclosed fixation area measured 0.75^{o} x 0.75^{o} of visual angle, whilst the boxes

surrounding the imperative stimuli measured 1^o x 1^o of visual angle. The vertical distance between the positions of cue and imperative stimuli was 1^o of visual angle (centre to centre), whilst the horizontal distance was 2.5^o (centre to centre) of visual angle.

EEG data acquisition

EEG was recorded continuously with Ag/AgCl electrodes from 128 scalp electrodes relative to an (off-line) averaged mastoid reference. The electrodes were placed according to the 10-5 extension of the International 10-20 electrode system (American Electroencephalographic Society, 1994; Oostenveld and Praamstra, 2001) using a carefully positioned nylon cap. Vertical eye movements and blinks were monitored using two electrodes positioned under the left and right eye, while horizontal movements were monitored using the nearest to the eyes cap electrodes (FFT9h/FFT10h). EEG signals were amplified by a BioSemi ActiveTwo amplifier and sampled at 1024 Hz.

Data analysis

EEG data processing was performed off-line using BrainVision Analyzer software (Brain Products GmbH). The continuous data were segmented in epochs from 700 ms before to 2300 ms after cue onset. Individual trials containing eye movement artefacts were rejected before averaging. No-go trials and trials containing incorrect responses were also removed before averaging. Averages were constructed for each subject and condition separately. Following averaging, the data were processed to derive lateralized event-related brain potentials (ADAN and LRP) and to extract ssSEPs.

Lateralized potentials

The LRP was calculated separately for each condition, by initially computing the voltage difference between homologous electrodes contralateral and ipsilateral to the side of movement. Subsequently, the difference waveforms were averaged to obtain movement-related lateralized ERP components. LRP amplitude was quantified from pooled electrode pairs (C1/2, C3/4, FC1/2, FC3/4 and FCC3h/4h) in a time window between 800 and 1000 ms after the directional cue. The LRP was preceded by the attention-related ADAN (anterior directing-attention negativity) component, which was quantified from the same selection of electrodes as the mean amplitude between 350 and 450 ms after the cue. The selection of the electrode sites was based on the grand average topographies. The amplitudes of the ADAN and the LRP were compared between conditions by means of t-tests.

Steady state SEPs

The analysis of ssSEPs consisted of the following three steps: (i) dipole source analysis of individual subject ssSEPs, (ii) transformation of scalp ssSEPs of entire trial duration into source waveforms, (iii) extraction of the envelope of the ssSEP source waveforms to analyse the amplitude modulation.

(i) In order to optimise the ssSEP S/N ratio for source analysis, the raw data of each subject were segmented in epochs comprising the responses to 4 consecutive median nerve stimulations (length 181.6 ms per segment). These epochs were averaged across conditions for each subject separately and band-passed filtered (Butterworth zero phase-shift filters 48 dB/octave) between 20.2 Hz and 24.2 Hz (i.e. stimulation frequency ± 2

Hz). The resulting data sets (one set per subject) were subsequently modelled with Brain Electromagnetic Source Analysis (BESA 5.1.6, MEGIS software GmbH). Two symmetrical single dipole sources, one in each hemisphere, located close to the central sulcus, adequately explained the data in all participants. The source analysis used a four-shell ellipsoidal volume conductor head model (head radius 85 mm; brain conductivity 0.33 mho/m; scalp thickness 7 mm and conductivity 0.33 mho/m; bone thickness 7 mm and conductivity 0.0042 mho/m; cerebrospinal fluid thickness 1 mm and conductivity 1 mho/m). Source location was specified in Talairach-Tournoux coordinates and the orientation in theta and phi angles, which correspond to the azimuth and the polar angle, respectively.

(ii) In the next analysis step, the two-dipole ssSEP source models derived for each subject separately were applied to data corresponding to the entire trial duration (i.e. from 700 ms before to 2300 ms after the directional cue), separately for left and right hand conditions. The resulting dipole source waveforms per subject and condition were stored for further processing.

(iii) The dipole source waveforms consisted of oscillatory signals (at a frequency of 22.2 Hz), whose amplitude was modulated by the task requirements. To analyse the amplitude modulation, the envelope of the source waveform was approximated by means of a continuous wavelet transformation (CWT). The CWT is characterized by its high analysis speed and it offers the ability to study a signal at a specific frequency. The present study employed the CWT based on complex Morlet wavelets, which has proved to be a reliable and effective method for extracting transient information out of an oscillatory signal (Liu and Qiu, 2000; Sheen and Hung, 2004; Gao and Yan, 2006). The

parameters used were: frequency range 35-54 Hz, frequency linear steps 20, Morlet parameter c=5. The wavelet frequency band (scale) with centre frequency (i.e. 44 Hz) closest to the oscillation frequency of the rectified signal (i.e. 44.4 Hz) was extracted. The time course of the amplitude modulation of the above-mentioned frequency band sufficiently approximated the envelope of the oscillatory signal (Figure 5).

Statistical analyses of reaction times, lateralized potentials, and the modulation of ssSEPs were performed using repeated measures ANOVAs in SPSS, as further specified in the text.

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Legends

Figure 1

Schematic representation of a trial with repetitive median nerve stimulation (represented by the dotted line). Arrow cues pointed either to the left or the right with equal probability. The go-signal was given by the display of horizontal lines inside the boxes. Vertical lines appeared at 10% of the trials instructing the participants to withhold the prepared response.

Figure 2

Waveforms of the ADAN and LRP derived from grand average data from pooled fronto-central electrode sites (electrode pairs: C1/2, C3/4, FC1/2, FC3/4 and FCC3h/4h). The vertical lines denote cue and imperative stimulus onsets.

Figure 3

Sample ssSEPs as recorded from bilateral frontal and parietal electrodes. The scalp topography (20 ms window over a frontal negative peak) shows distinguishable frontal and parietal maxima in both hemispheres.

Figure 4

Dipole sources and source waveforms, illustrating their symmetrical location in the vicinity of the central sulcus (grand average data).

Figure 5

Sample ssSEP source waveforms with envelopes. The envelopes were extracted on the basis of the rectified signal using complex Morlet wavelets. The vertical lines at time 0 indicate cue onset and the vertical lines at time 1000 indicate the onset of the imperative signal.

Figure 6

Averaged source waveform envelopes of ssSEPs contra and ipsilateral to left and right hand cues. A clear reduction in amplitude around the latency of the ADAN and a more robust reduction following movement execution are evident for ssSEPs in the contralateral hemisphere. The grey rectangles indicate the time windows for analysis.

Figure 7

(A) Graph representing mean ssSEP source amplitudes for the time interval from 375-575 ms (i.e. time window of the ADAN component). (B) ssSEP source amplitudes for the time interval from 1250-1450 ms. The higher right hemisphere ssSEP amplitude, in both time windows, was caused by a single outlier and was not significant. The vertical error bars represent the standard error of mean.

Figure 1

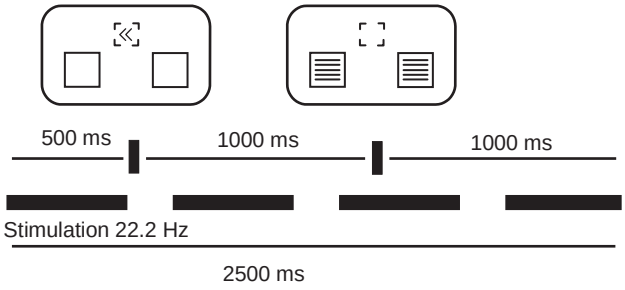


Figure 2

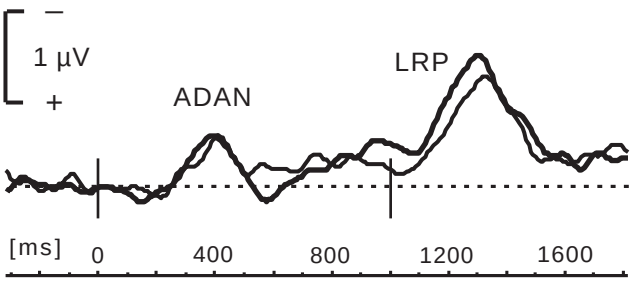
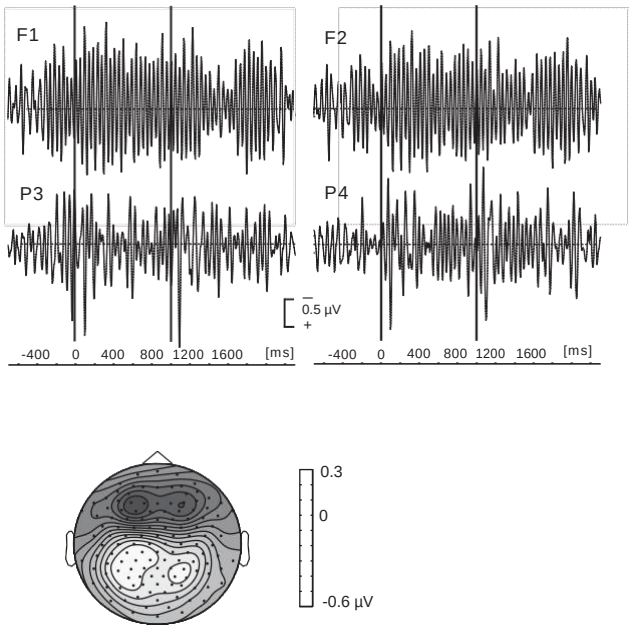


Figure 3


F1
F2
P3
P4
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+
-400 0 400 800 1200 1600 [ms]
-400 0 400 800 1200 1600 [ms]

0.3
0
-0.6 µV

Figure 4

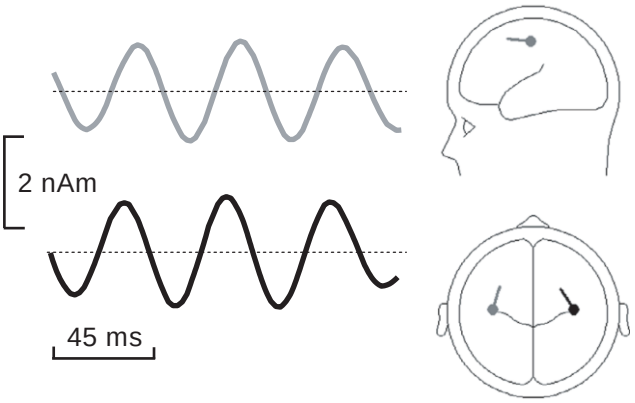


Figure 5

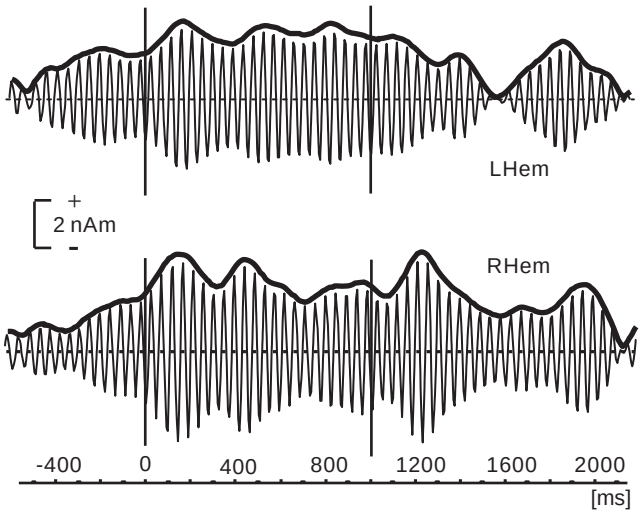
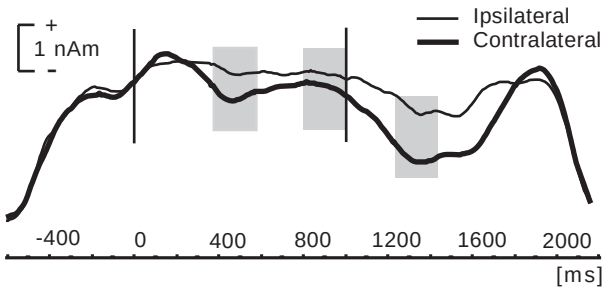


Figure 6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-
Ipsilateral
Contralateral
-400
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400
800
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Figure