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A new method to determine temporal variability in the period of pre-movement electroencephalographic activity

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ABSTRACT

The readiness potential (RP), a slow electroencephalographic (EEG) pre-movement potential, was used in earlier studies to determine the onset and order of neural processes preceding voluntary movement. Latencies in these studies were always calculated from the averaged RP, whereas onset times of individual trials remained inaccessible. The aim of this study was to use a different, statistical approach to examine how variable the onset of single-trial RPs within subjects is. We recorded RPs in 15 right-handed healthy subjects while they made self-paced repetitive unilateral button presses with their dominant right hand. Skewness, a measure of distribution asymmetry, was analysed in sets of single-trial RPs to discriminate between fixed onset and variable onset models. Results show that skewness has values around zero across all electrodes and pre-movement intervals without any significant deviation. This result obtained for the original data was replicated using modelled data with fixed onset times, whereas alternative models with variable onset times (i.e., including trials with exceptionally early onset) showed significant deviations of skewness from zero. In conclusion, for simple repetitive movements with the dominant hand these results confirm a fixed onset model of the RP with similar onset times of pre-movement cortical activation across trials. The methodology might be also applicable for other paradigms to test basic assumptions of mental chronometry.

The readiness potential (RP) is a widespread EEG potential that precedes voluntary movements and is caused by neural processes involved preparing and executing the commands to move. Because the potential is small in relation to the ongoing background EEG activity, several movements are made, and the potential averaged with respect to the onset of each. The shape of the averaged RP is a ramp-like increase of negativity. As a consequence of the averaging procedure, onset and time course of the single-trial RPs are not clear from examination of the averaged waveform (Fig. 1).

Several physical and psychological factors such as force, context and speed of movement, habituation, alternation, attention and fatigue influence the time course and amplitude of the averaged RP (Benecke et al., 1985; Birbaumer et al., 1990; Dirnberger et al., 2002, 2004; Freude et al., 1995; Rösler et al., 1997). Because of the low signal-to-noise ratio, it is difficult to determine in single-trial data where precisely a clear increase of negativity above the level of background noise sets in. Previous research therefore implicitly assumed that if external factors are controlled, all single-trial RPs of one individual have about the same time course; the computation of averaged waveforms and the concept of 'onset times' for the averaged RP is meaningful only in this context (e.g., Deecke et al., 1969). The contrasting concept of variable onset times would have important implications for studies utilising averaged potentials to discriminate successive periods of unconscious and conscious preparation (Libet et al., 1983): Voluntary acts that appear identical to observers from outside and perhaps even ourselves would differ with respect to the period of unconscious preparation (Bolbecker et al., 2002; Trevena and Miller, 2002).

The aim of this study was to use a new, statistical approach to examine how variable the onset of single-trial RPs within subjects is. Subjects were tested in a RP paradigm on a simple repetitive button press task. Skewness, a measure of distribution asymmetry, was analysed in sets of single-trial RPs to discriminate between fixed onset and variable onset models. In case of variable onset times we predicted that skewness would have negative values in early intervals which would gradually increase to neutral and then positive values in later pre-movement intervals. Alternatively, if onset times of all single-trial RPs are similar, skewness would have small values around zero for the entire pre-movement period. The sensitivity of the applied methodology was tested with modelled data.

1. Methods

1.1. Participants

Fifteen subjects (8 females) aged 21 to 30 years (mean 25±SD 3 years) participated in the study. All subjects were right-handed

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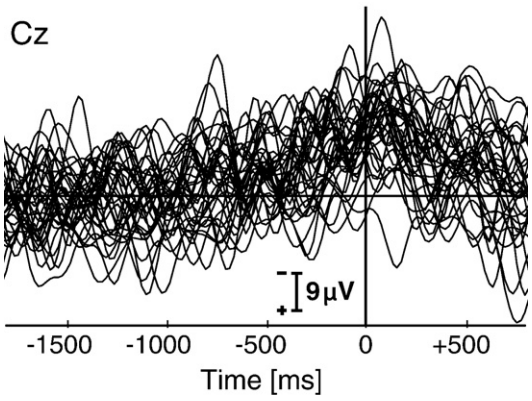

Fig. 1. Single-trial RPs from one subject making repetitive button presses with his right index finger. Waveforms of n=56 single trials recorded from electrode Cz are superimposed to illustrate the variability across trials. Because of the low signal-to-noise ratio, it is difficult to decide in single-trial data where precisely a clear increase of negativity above the level of background noise sets in. The zero mark on the time axis indicates movement onset.

(Oldfield, 1971) and had no history of psychiatric or neurological disease. Written informed consent was obtained from each subject in accordance with the guidelines approved by the Medical University of Vienna.

1.2. Experimental design and procedure

Subjects had to perform a series of 70 self-paced button presses with their right index finger. Each button press triggered an electrical signal. The onset of this signal was defined as movement onset. Subjects were comfortably seated with their arms supported by padded armrests. At the end of the right armrest a button was displayed at a distance so that it could be reached comfortably with the index finger. Subjects were instructed always to rest their finger on the button. The force required to press down the button was about 4 N. Before starting the task, and during its execution, subjects had to fixate on a point straight ahead in order to minimise eye movements. Subjects were required to make brisk flexion movements irregularly but no earlier than 5 s after the previous movement. The average inter-movement interval of the subjects was about 8 s.

1.3. Recording of RPs

Electroencephalographic (EEG) activity was recorded using Ag/AgCl electrodes from the sites Fz, C3, Cz, C4 and Pz (Chatrian et al., 1985), referenced to linked mastoids. In addition, horizontal and vertical electrooculogram (EOG) and electromyogram (EMG) from left and right musculus flexor digitorum superficialis were recorded. Electrodes were attached on the cleaned skin by collodion. Their impedance was kept below 5 kΩ. Electrical activity was recorded with a PC-supported DC amplifier (Lindinger et al., 1990).

EEG and EOG were recorded in DC mode, frequency band DC to 100 Hz (EEG) and DC to 41 Hz (EOG), respectively. EMG was recorded in AC mode. The analogue EMG was band pass filtered 0.1 to 300 Hz and the filtered signal then rectified (Lindinger et al., 1990). EEG, EOG and the envelope of the rectified EMG were digitised on-line at a rate of 250 Hz. Trials with gross artefacts, bilateral EMG activity or EMG activity earlier than 300 ms before movement onset were rejected manually after trial-by-trial visual inspection.

For each trial, the EEG was analysed in reference to movement onset. The period used for statistical analysis started 1000 ms prior to movement onset and lasted till 200 ms after movement onset, with a baseline lasting from 2250 to 1750 ms before movement onset. We focussed on a 1000 ms pre-movement period because most sub-components of the RP begin in this interval (Deecke et al., 1969) and animal studies also suggest variability of onset times in the same interval (e.g., Tanji et al., 1987). The short post-movement interval was included to increase the power of the statistical analysis.

1.4. Methodological background

There are hints from studies in humans and animals that the onset of pre-movement neural activity is not constant. Cell recordings of self-initiated movements in monkeys suggest that onset times of cortical single neuron activities differ from trial to trial. In some of these studies, the ramp-shaped increase of negativity appears steeper in trials where the onset of negativity occurs later (Tanji et al., 1987). If many trials with such a time course are averaged, the result would look similar to the averaged RP (Fig. 2, middle column). It is therefore conceivable that single-trial RPs have a continuous increase of negativity with variable onset. An alternative time course of single-trial RPs is a step function with variable onset. The proportion of trials for which pre-movement negativity has already increased to peak amplitude would be the higher the closer we come to movement onset. If the growth of this proportion is about linear, the resulting average would again have ramp shape as the averaged RP (Fig. 2, right column). In line with the step function hypothesis are observations made by Kukleta and Lamache (2001), who described 'steep negative slope[s] followed by plateau' at varying intervals in the single-trial EEG activity preceding voluntary movements. Finally, single-trial RPs may have about the same onset times and time course as the averaged RP (Fig. 2, left column). This is in fact what most previous research implicitly assumed.

The three alternatives outlined above can be distinguished by standard statistical tests applied to sets of single-trial data. Skewness is a measure of distribution asymmetry in a random variable. Positive skewness indicates that higher (more positive) values of a variable are more frequent than expected in a symmetric distribution (tail extending out towards more positive values), whereas negative skewness indicates that smaller (more negative) values are more frequent (Press et al., 2002).

1.5. Skewness as an indirect measure of onset time variability

Skewness can be calculated for sets of single-trial EEG data in short time intervals before movement onset. If onset times and time course of single-trial RPs are rather constant, then values of the RP amplitude should have a Gaussian distribution and skewness will have values close to zero across intervals (Fig. 2, bottom of left column). In contrast, for a ramp-shaped increase of single-trial negativity with variable onset times, skewness will initially have negative values (Fig. 2, bottom of middle column). This is because there are only a few trials with early RP negativity ('negative tail'), whereas most trials remain at more positive values. For later intervals RP negativity will have set in for a higher proportion of trials. Skewness will therefore slowly increase to neutral and then positive values the closer we come to movement onset. Changes of skewness over time would be similar in case of a step function with variable onset times (Fig. 2, bottom of right column). The time course of skewness from negative to positive values is the same for all functions where a small proportion of trials has early negativity whereas for the majority of trials pre-movement negativity sets in later (Press et al., 2002). For all three models, skewness in the post-movement intervals will further develop from the values held at movement onset and finally return to neutral values when activity time-locked to movement onset has terminated. Effects might be attenuated in later intervals because of increased overall variability in the time course of RP amplitudes associated with accumulating asynchrony in the onset of various motor preparatory processes.