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The mode of movement selection

Movement-related cortical potentials prior to freely selected and repetitive movements

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Abstract In two previous studies, the readiness potential (RP) has been reported to be influenced by the mode of movement selection. Freely selected movements were found to have a higher RP amplitude than fixed repetitive movements. This was attributed to the higher demands on planning for the performance of freely selected movements. However, movements in the free mode are distinct from movements in the fixed mode in more than one respect. For example, they are also associated with a higher degree of alteration of the side and/or the finger of movement execution and hence serial "novelty" across blocks of trials. The aim of our study was to establish whether the greater novelty of movements in the free mode could also contribute to the enhanced RP amplitude of movements in the free mode of movement selection by comparing free versus fixed movements performed in long and short sequences that differ in terms of serial novelty. The RP was recorded in 31 healthy young subjects with electrodes placed over Fz, C3, Cz, C4 and Pz. Two types of movement were studied: randomly chosen button presses with right or left index or middle finger (free mode), and repetitive pressing of a predetermined button (fixed mode). We found that: (1) in confirmation of previous studies, the amplitude of the RP was higher for freely selected than free movements; (2) the effect of the mode of movement selection was present over central electrodes but was most pronounced for parietal electrode Pz, with movements in the free mode showing the earliest and greatest increase in negativity at this site; (3) this parietally enhanced negativity in free compared with the fixed mode was absent after the subjects had performed a block of long movement sequences, suggesting that serial novelty of movements also contributed to the effect of mode on the RP amplitude; (4) both the latency and the magnitude of the lateralized readiness potential (LRP) were altered by the mode of movement selection. Movements in the free mode showed an earlier onset of the LRP, which had a higher peak than the LRP prior to movements in the fixed mode. This effect was mainly due to an increased amplitude of the RP over the electrode contralateral to the side of movement prior to freely selected movements. These findings are discussed in relation to previous RP and positron emission tomography studies.

Key words Event-related potentials · Readiness potential · Primary motor cortex · Supplementary motor area · Mode of movement selection · Human

Introduction

Voluntary self-paced movements are preceded by the Bereitschaftspotential or readiness potential (RP), a slow cortical potential, first reported by Kornhuber and Deecke (1965), beginning approximately 1,5 s before movement onset. Previous research has demonstrated the RP to have its maximal amplitude at the vertex and above the primary motor cortex (MI) contralateral to the side of movement. Two main epochs of the RP have been distinguished, an earlier symmetrical component followed by a later asymmetric component from about 500 ms before movement onset. The two components of the RP may reflect differential activity of the supplementary motor area (SMA) and the MI. Whereas the early symmetric part of the RP appears to result mainly from activity of the SMA, the later, contralaterally pronounced component seems increasingly related to – mainly contralateral – MI activation (Deecke 1987; Deecke and Kornhuber 1978; Lang et al. 1989, 1991; Shibasaki et al. 1993).

A positron emission tomography (PET) study (Deiber et al. 1991) reported that the mode of movement selection, i.e. whether a movement is made in a pre-determined or self-determined direction, is associated with

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an altered activity of the SMA. During a sequence of randomly performed movements, which had to be chosen out of a set of four possible movements – the so-called free mode of movement selection – the mean SMA activity was higher than during a sequence consisting of a single pre-determined movement that had to be performed repetitively – the so-called fixed mode of movement selection.

Subsequent RP studies (Praamstra et al. 1995; Touge et al. 1995) have reported an effect of the mode of movement selection on the RP amplitude. Freely selected movements were found to be associated with a higher RP amplitude than pre-determined repetitive movements in the fixed mode. One of the previous RP studies on the effect of the mode of movement selection found this effect to have its maximum near the central midline (Praamstra et al. 1995). Using a four-dipole model, the mode effect on the RP was found to be explained best by activity of the most mesial frontal dipole (Praamstra et al. 1996) and to be absent in patients with Parkinson's disease (Touge et al. 1995), who have impaired activation of the SMA (Jahanshahi et al. 1995; Playford et al. 1992). Accordingly, the enhanced central negativity prior to movements in the free mode was attributed to increased SMA activity, which was considered to reflect the higher demands of planning before the execution of freely selected random movements (Praamstra et al. 1995; Touge et al. 1995).

Movements in the free mode are different from repetitive movements in more than one respect. Freely selected movements require increased planning. In addition, they are accompanied by a higher rate of alteration or trial-by-trial "novelty" of the executed movement. For example, when selection is between the executing finger (index compared with middle) and the side of movement (left compared with right hand), freely selected movements are also distinct from repetitive movements with respect to the mean number of alterations of finger and hand and hence serial novelty of the movements in a sequence. This novelty feature describes whether or not an identical movement has been performed shortly before. A particular movement can be more frequently selected and performed during long than during short sequences. Therefore, the mean serial novelty of this movement is higher in a short than in a long sequence. If movement novelty is an important feature partly responsible for the effect of the mode of movement selection on the RP, we would expect even the mean amplitude of the RP for the repetitive fixed movements to be higher in the short than in the long sequences. In contrast to novelty, the planning aspect should be consistently higher for freely selected than for repetitive movements, regardless of the length of the sequence. Therefore, if serial novelty is an additional important feature contributing to the mode effect, we would expect sequence length (short compared with long) to create a differential influence on the effect of mode of movement selection on the amplitude of the RP, hence resulting in a significant interaction of sequence length and mode.

The aim of our study was to establish whether the novelty feature of freely selected random movements contributes to the increased negativity of the RP in the free mode of movement selection in addition to increased planning. More specifically, the aims of our study were: (1) To determine whether the effect of the mode of movement selection on the RP can be replicated using a different selection of random and repetitive movements; (2) to determine whether, besides "planning", the other feature of freely selected movements, that is, serial novelty, also contributes to the effect of mode of movement selection on the RP by comparing freely selected and repetitive movements performed as part of short and long sequences.

Materials and methods

Subjects

Thirty-one subjects (15 men) aged 20–30 years (mean 24.2 years, SD 2.7 years) participated in the study. All were right-handed (Oldfield 1971) and had no history of psychiatric or neurological disease.

Design

Subjects made self-paced flexion movements with the index or middle finger of their left or right hand by pressing one out of four response buttons. There were two conditions, free or fixed: In the free mode, subjects had to press down buttons randomly, with the instruction to avoid repetitive sequences of more than two button presses. In the fixed mode, subjects had to press down a particular predetermined button repetitively across trials in a block.

There were two types of block. In a long block, subjects had to perform a series of 70 button presses eight different times, four of which were in the free mode and four of which were in the fixed mode. In a short block, they had to perform a series of eight button presses 56 times, half of which were in the free mode and half of which were in the fixed mode. Thus, the main difference between the two blocks was that during the long blocks subjects could develop a motor or attentional set when making movements of the same type, but in the short blocks the sequence was interrupted after a short time (eight button presses) and subjects switched to a different type of movement. Each subject performed one long and one short block, giving a total of 1008 button presses per session. Half the subjects started with the long block and the other half started with the short block. These orders were referred to as "start long" or "start short" and "continued long" or "continued short".

Performance of a free- and a fixed-mode condition alternated across the session. In both the long and the short blocks there were four types of series in the fixed mode, with movements performed using the right middle finger, right index finger, left middle finger or left index finger.

Procedure

Subjects were comfortably seated with their arms supported by padded armrests. At the end of the left and right armrests, two buttons were displayed horizontally at a distance so that they could be reached comfortably by the subjects with the appropriate fingers. The inter-button distance on each side was 2.5 cm. Before starting the task and during its execution, subjects had to fixate on a point straight ahead in order to minimize eye movements. At the end of each sequence (8 or 70 movements for short or long blocks, respectively) subjects were instructed via the intercom about the type of movement (free compared with fixed mode) and, in the latter case, the finger (left or right index or middle finger) they should proceed with in the next block. Subjects were required to make brisk flexion movements irregularly but no earlier than 5.0 s after the previous movement. They were instructed neither to count nor to maintain any other rhythmic activity during the entire session. The mean inter-movement interval of the subjects was about 8.0–9.0 s, with just a few movements not included in further analysis because of inter-movement intervals that were too short.

The total duration for the completion of the tasks was about 3 h. In between the blocks, subjects were allowed to have a break. They had four breaks of approximately 10 min in the course of testing.

Recording of RPs

Electroencephalographic (EEG) activity was recorded unipolarly using Ag/AgCl electrodes from the sites Fz, C3, Cz, C4 and Pz (electrode position according to the international 10–20 system; Chatrian et al. 1985), referenced to linked mastoids. In addition, horizontal and vertical electro-oculogram (EOG; electrode positions, above and below the left eye and adjacent to the outer canthus of each eye) and electromyogram (EMG) from left and right musculus flexor digitorum superficialis were recorded. Electrodes were attached on the carefully cleaned skin by collodion, and their impedance was kept below 3 kΩ.

Electrical activity was recorded using a PC-supported, 64-channel DC amplifier system (Lindinger 1990; Lindinger et al. 1990) with the following settings:

1. EEG, DC mode, HF cut-off 150 Hz, time constant 999 s
2. EOG, DC mode, HF cut-off 41 Hz, time constant 999 s
3. EMG, AC mode, frequency band 0.1–300 Hz, time constant 0.03 s

EEG, EOG and the EMG hull curve were digitized on-line at a rate of 250 Hz and stored for subsequent analysis. The EEG was corrected for minor eye blink artefacts using an automatic blink correction. All trials with artefacts remaining after this procedure were rejected from further analysis. For each trial, the EEG was averaged in reference to movement onset.

The period used for statistical analysis started 1000 ms prior to movement onset and lasted till 500 ms after movement onset, with a baseline calculated from 2250 to 1750 ms before movement onset. In what follows, the term RP is used for all parts of the potential.

Data analysis

Means were calculated for each block, e.g. short block with repetitive left index finger movements. For each block, the mean amplitude was calculated for three time intervals or epochs. Each of the three epochs lasted 500 ms. The earlier pre-movement epoch started 1000 ms before movement and was followed by a later pre-movement epoch starting 500 ms before movement onset. There was an additional post-movement epoch lasting from movement onset to 500 ms after.

A repeated-measures analysis of variance (ANOVA) was carried out for each epoch separately, with Mode of movement selection (free compared with fixed), Length of block (long compared with short), Side of movement (left compared with right), Finger (index compared with middle finger) and Electrode (Fz, C3, Cz, C4, Pz) as the within-subject factors, and Order (whether a subject started with the long or with the short block) as the between-groups factor. Where appropriate, Geisser-Greenhouse corrected, univariate F-values are reported. Interactions with the factor Electrode were re-calculated with normalized data (McCarthy and Wood 1985). For each subject and group separately, this procedure sets the normalized value of the electrode site with the highest amplitude of the RP to 1, and the normalized value of the electrode site with the lowest amplitude of the RP to zero. All intermediate amplitudes of the RP are set to a value between 1 and zero according to their relative negativity. For interactions with the factor Electrode, F-values derived from this second analysis are always reported. Only significant main or interaction effects are reported.

To investigate any lateralized effects of the mode of movement selection over the electrodes C3 and C4, the lateralized readiness potential was calculated using the following formula (Coles 1989; De Jong et al. 1988): LRP = $(C3{-}C4)_{\text{left hand}}-(C3{-}C4)_{\text{right hand}}$.

First, the voltage difference between these homologous electrodes was computed separately for each mode of movement selection and movements to the left and to the right. In the second step, for each mode of movement selection separately, the value for right-hand movements was substracted from the corresponding value for left-hand movements. For the resulting score, the bigger the LRP, the greater the degree of lateralization is.

Results

Figure 1 shows the grand mean RP across all subjects for movements with the right index finger in the free mode and in the fixed mode separately. For both conditions, the mean negativity slowly increases from about 1750 ms prior to movement onset, with a steeper rise (Barrett et al. 1986) during the last 500 ms before movement onset. After movement onset, the potential rapidly returns to near baseline. The term RP is used here for all parts of the potential.

The general shape of the potential is the same for both the free- and the fixed-mode condition. However, an enhanced negativity can be seen for movements in the free mode compared with movements in the fixed mode, mainly at the contralateral electrode C3, the central electrode Cz and the parietal electrode Pz. This "Mode" effect, that is differences in amplitude between free and fixed modes, starts very early for the contralateral and parietal electrode. The mean muscle activity is equal for both types of mode of movement selection, as indicated by equal EMG signals.

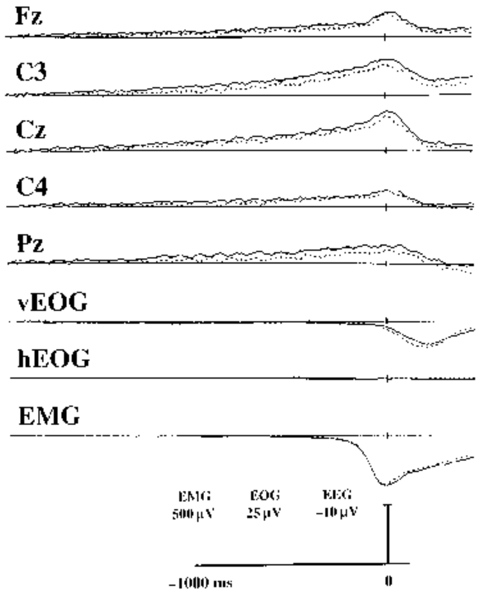

Fig. 1 Grand mean of the readiness potential preceding fixed repetitive (*broken line*) and freely selected (*solid line*) movements with the right index finger. The *vertical mark on the time axis* indicates movement onset (*hEOG* horizontal electro-oculogramm, *vEOG* vertical electro-oculogramm, *EMG* electromyogram, right forearm flexors)

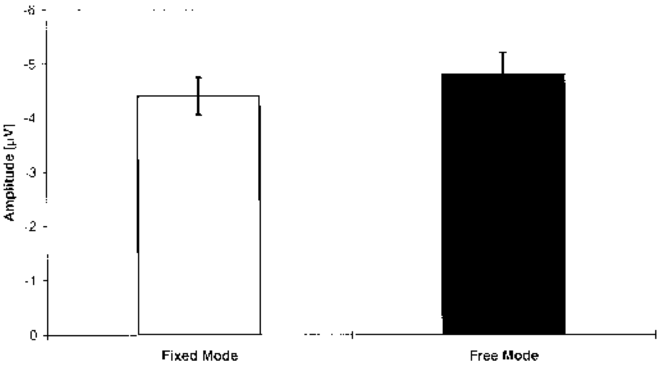

Fig. 2 The main effect of the mode of movement selection. The mean amplitude of the readiness potential in the epoch from 500 ms before movement onset to movement onset across all electrodes, showing higher amplitude for movements in the free mode (*black bar*) than for movements in the fixed mode (*white bar*). *Error bars* indicate standard error. Significant difference, $P < 0.05$

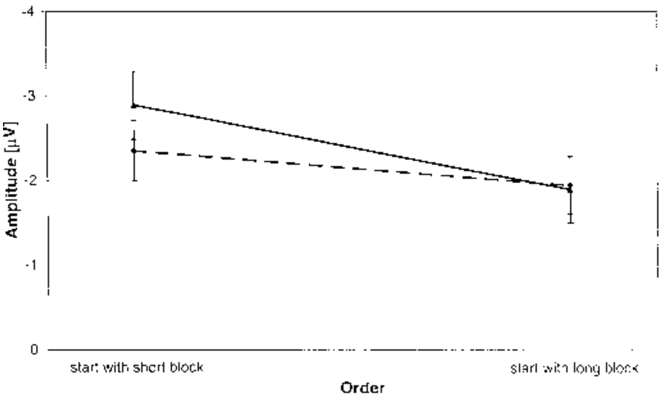

Fig. 3 Schematic representation of the interaction of the factors Mode × Order across all electrodes in the epoch from 1000 ms to 500 ms before movement onset. Movements in the free mode (*solid line*) are associated with an increased amplitude of the readiness potential compared with movements in the fixed mode (*broken line*) in the subgroup of subjects who started with the short block. *Error bars* indicate SE

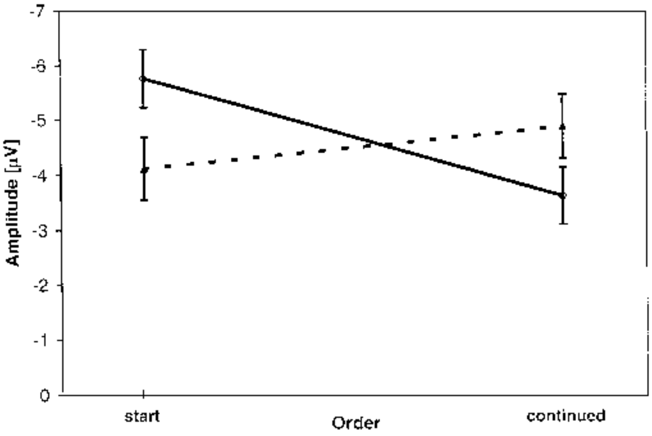

Fig. 4 Interaction of the factors Length of block × Order in the epoch from 500 ms before movement onset to movement onset across all electrodes. *Order*, whether subjects started or continued with long (*dotted line*) or short (*solid line*) block. The amplitude of the readiness potential for movements in the start short block is significantly higher than for movements in the continued short block ($P < 0.01$). *Error bars* indicate SE

The main effect of Mode was significant for the epoch –500 ms to 0 ms ($F_{1,29} = 4.42$; $P < 0.05$). As shown in Fig. 2, this indicated that the freely selected movements are associated with a higher RP amplitude than movements in the fixed mode. This significant Mode effect was obtained despite the fact that the mean muscle activity was equal for the two modes of movement selection, as indicated by equal EMG signals in Fig. 1.

The main effect of Electrode, which was significant for all epochs ($F_{4,116} = 15.75$, 28.41, 9.14, respectively; all $P < 0.01$), resulted from the RP amplitude having its highest peak at the central electrode Cz. Main effects of Length of block, Side of movement, Finger and Order were not significant.

A significant two-way interaction Mode × Order was found for the earliest epoch from –1000 ms to –500 ms ($F_{1,29} = 4.67$; $P < 0.05$; Fig. 3). Post hoc analysis showed that subjects who started with the short block had significantly higher amplitude of the RP in the free than in the fixed mode ($F_{1,14} = 7.75$; $P < 0.05$). No such significant difference was found for those subjects who started with the long block.

From –500 ms to 0 ms, we found a significant interaction of Length of block × Order ($F_{1,29} = 5.52$; $P < 0.05$) (Fig. 4). Post hoc analysis showed that this interaction is due to the fact that the mean RP amplitude was highest for the short blocks when performed first, whereas it was lowest for the short blocks performed in continuation of long blocks (unpaired *t*-test: $t_{1,29} = 2.92$; $P < 0.01$). Both the long blocks, whether performed first or in continuation of short blocks, showed an intermediate amplitude.

The interaction Electrode × Side of movement was also significant through all three epochs ($F_{4,116} = 21.97$, 80.28, 44.09, respectively; all $P < 0.01$), which was associated with a higher RP amplitude contralaterally to the Side of movement.

A significant three-way interaction Mode × Side of movement × Electrode was found for all three epochs from –1000 ms to +500 ms ($F_{4,116} = 4.37$, 6.97, 3.92, respectively; all $P < 0.01$). This was explained by a distinct effect of the Mode of movement selection on the lateral electrodes C3 and C4 (Fig. 5).

For both sides of movement execution, an increased negativity over the contralateral electrode site (C3 for right-sided and C4 for left-sided movements) was found for movements in the free mode of movement selection compared with movements in the fixed mode. This Mode effect was significant for movements with the right hand (paired *t*-test, $t_{1,30} = 3.14$, 3.48, 2.58, respectively; $P < 0.01$ for the two pre-movement epochs, $P < 0.05$ for the post-movement epoch). For movements in the free mode, there was also a non-significant tendency for a diminished ipsilateral amplitude of the RP.

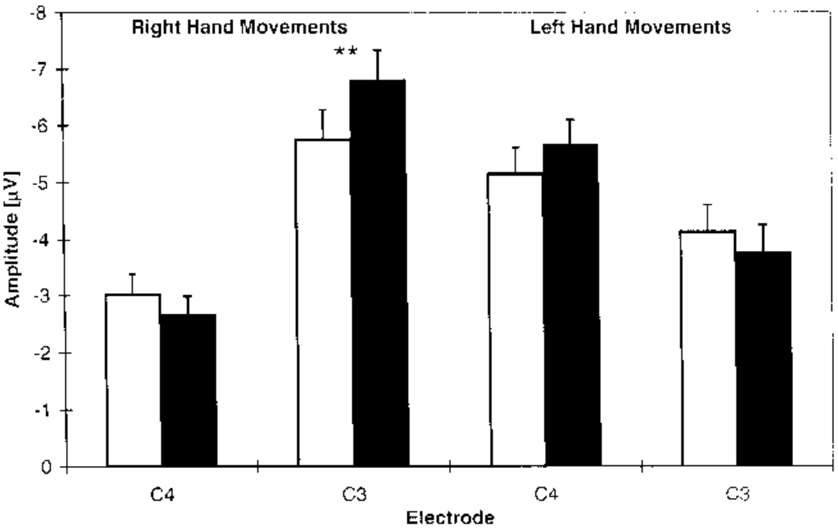

Fig. 5 Mean amplitude of the readiness potential for left- and right-hand movements in the freely selected (*black bars*) and fixed repetitive (*white bars*) movements at the lateral electrodes C3 and C4 for the epoch from 500 ms before movement onset to movement onset. This shows increased contralateral negativity during free mode movements. *Error bars* indicate SE ($^{**}P < 0.01$)

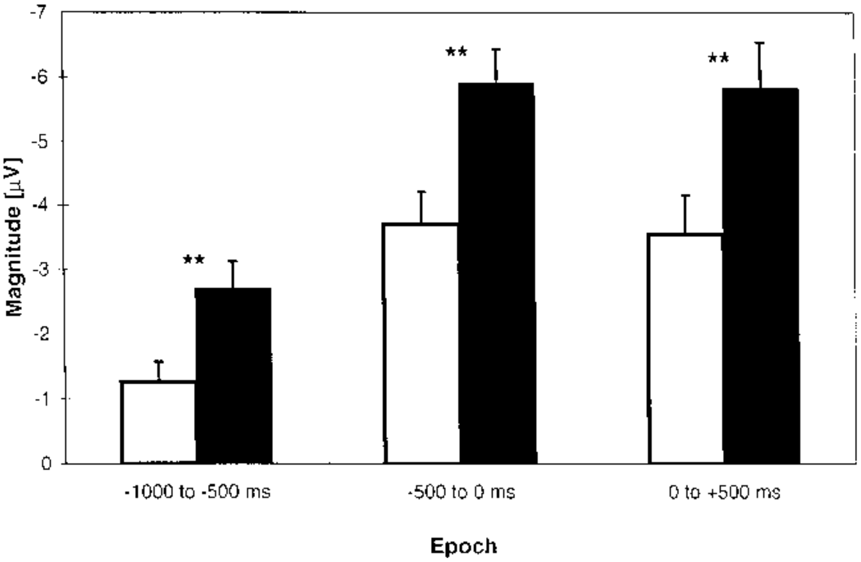

Fig. 6 Lateralized readiness potential (LRP) of freely selected (*black bars*) and fixed repetitive (*white bars*) movements for each of the three epochs. This shows that movements in the free mode are associated with higher LRP during all three epochs than movements in the fixed mode. *Error bars* indicate SE ($^{**}P < 0.01$)

The LRP showed an earlier onset and significantly enhanced magnitude across all three epochs from –1000 ms to +500 ms (paired *t*-test: $t_{1,30}$ = 3.56, 5.57, 6.03, respectively; all $P < 0.01$; Fig. 6).

For the first two epochs from –1000 ms to 0 ms, a significant three-way interaction Mode × Finger × Side of movement was found ($F_{1,29}$ = 4.83, 6.47, respectively; all $P < 0.05$; Fig. 7), which resulted from free mode movements with the left middle finger showing highest RP amplitude, fixed mode movements with the right index finger showing the lowest, and all other movements showing intermediate amplitudes of the RP. Only the differences between the lowest and highest amplitudes of the RP were significant (paired *t*-tests, $t_{1,30}$ = 2.34, 3.01, respectively; $P < 0.05$, $P < 0.01$, respectively for the two epochs).

Another three-way interaction, Mode × Side of movement × Length of block, was significant for all three epochs from –1000 ms to +500 ms ($F_{1,29}$ = 4.44, 5.97, 6.91, respectively; all $P < 0.05$). This resulted from freely selected movements to the left in the short blocks showing a significantly higher RP amplitude than repetitive right-side movements in the long blocks in the time window from –1000 ms to 0 ms (paired *t*-test: $t_{1,30}$ = 2.07, 2.64, respectively; all $P < 0.05$), and from –500 ms to +500 ms, freely selected movements to the left in the short blocks show significantly higher amplitude than fixed movements to the left in the short blocks in a time window from –500 ms to +500 ms (paired *t*-test, $t_{1,30}$ = 2.05, 2.10, respectively; all $P < 0.05$), with all other movements showing intermediate RP amplitudes not significantly different from any other.

A significant four-way interaction Mode × Elektrode × Length of block × Oder was present for all three epochs from -1000 ms to +500 ms ($F_{4,116}$ = 3.54, 4.24, 2.81, respectively; all $P < 0.01$). For the two epochs from –1000 ms to 0 ms, the Electrode component of the four-way interaction related to an enhanced Mode effect at

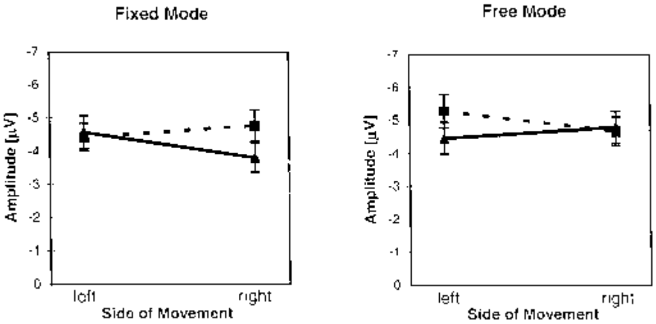

Fig. 7 Schematic representation of the interaction of the factors Mode of movement selection, Finger, Side of movement execution for the epoch from 500 ms before movement onset to movement onset. Index-finger (*solid lines*) and middle-finger (*dotted lines*) movements are shown for the right and left hands, for the free and fixed modes. Right index-finger movements in the fixed mode of movement selection show the lowest readiness potential amplitude, whereas left middle-finger movements in the free mode of movement selection show the highest readiness potential amplitude. *Error bars* indicate SE

Pz. This was indicated by the fact that the three-way interaction Mode × Length of block × Order was significant for the parietal electrode ($F_{1,29}$ = 10.04, 4.82, respectively; $P < 0.01$, $P < 0.05$, respectively) but for none of the central electrodes. Further post hoc analysis showed this three-way interaction to result from an enhanced amplitude of the RP during free-mode compared with fixed-mode movements at electrode Pz for both the long and the short block of those subjects starting with a short block (significant from –1000 ms to 0 ms; $F_{1,14}$ = 4.72, 7.71, respectively; all $P < 0.05$), and from an enhanced amplitude of the RP during free- compared with fixed mode movements for the long block of those subjects starting with a long block (significant from –1000 ms to –500 ms; $F_{1,15} = 4.31$; $P = 0.055$). Summing up the results of the post hoc analyses of the four-way interaction Mode × Electrode × Length of block × Order, this interaction could be shown to result from an increased amplitude of the RP for the free compared with the fixed mode at the parietal electrode for all blocks except the continued short block.

In summary, in relation to the three epochs, the main effect of Mode was only significant for the epoch prior to movement onset (–500 to 0 ms), whereas the interactions of Mode with the other variables of interest (Order, sequence Length, Electrode, Side of movement) were mainly present across all three epochs and therefore started earlier.

Discussion

To summarize the main results: (1) The mode of movement selection was found to have a main effect on the amplitude of the RP. Movements in the free mode are associated with a higher RP amplitude. (2) The amplitude of the RP was found to be particularly increased for freely selected movements performed with the left middle finger. (3) The increase in the amplitude of the RP started early over the parietal electrode Pz, an effect not found for the central electrodes. (4) The order of performance of long versus short block affects the amplitude of the RP. Short movement sequences are associated with the highest amplitude of the RP when performed before the long sequences, whereas short sequences show the lowest amplitude of the RP when performed in succession to a block of long movement sequences. (5) Movements in the free mode are accompanied by an enhanced amplitude of the RP contralaterally to the side of movement.

The onset and peak of muscle activity were equal for the two modes of movement selection, indicated by equal EMG signals. Thus, the results of the present study are not confounded by differences in the physical properties of movement execution between the two experimental conditions.

Freely selected movements are different from fixed repetitive movements in several respects. Their main difference is the need for self-selection when performing random movements. This means that the so-called “what to do” aspect or the precise nature of the to-be-executed movement is open before preparation for freely selected movements in contrast to the preparation for fixed repetitive movements. However, additional differences between the two modes of movement selection include a higher frequency of novel movements, that is, movements which have not been performed in the preceding trial in sequences of freely selected movements. Also, in order to monitor previous and to plan future movements, there is a higher demand for allocation of attention to the extrapersonal space in freely selected movements.

The main effect of mode appears to be smaller in our results than in the previous RP studies (Praamstra et al. 1995; Touge et al. 1995). One possible explanation for this discrepancy might be that, in the study of Touge et al. (1995), EMG activity appears to be higher for freely selected than for fixed repetitive movements (Touge et al. 1995, their Fig. 3, p. 795). EMG activity is positively correlated with executed force (Aratow et al. 1993; Maier and Hepp-Reymond 1995; Jarvholm et al. 1991; Korner et al. 1984), which in turn is reported to be associated with a higher amplitude of the RP (Becker and Kristeva 1980; Freude and Ullsperger 1987; Hink et al. 1983; Kutas and Donchin 1974).

Furthermore, in light of the interaction of mode with sequence length and order in the present study, another factor contributing to the overall lower magnitude of the mode effect in this study compared with those of Praamstra et al. (1995) and Touge et al. (1995) may be the larger number of movements (total of 1008) in the present study.

Freely selected movements and SMA activity

The two previous studies of the effect of the mode of movement selection on the RP attribute the mode effect to an altered function of the SMA, because such a mode effect was less evident in patients with Parkinson's disease (Touge et al. 1995), whose SMA function is known to be impaired (Jahanshahi et al. 1995; Playford et al. 1992), and because the mode effect was most pronounced over the central electrode Cz, which is in the appropriate position to be influenced by a dipole in the SMA (Praamstra et al. 1995). A later dipole-source localization study gave further support to this view (Praamstra et al. 1996). In our results, similar to Praamstra et al. (1995), we found a main effect of Mode, that is, higher amplitude of the RP prior to freely selected movements than fixed repetitive movements for the latest pre-movement epoch.

Attributing this late pre-movement mode effect to SMA activity may seem incongruent with the "classic" two-component view of the RP, according to which the RP consists of consecutive components that reflect sequential activation of the SMA and MI. However, more recent evidence suggests that, in contrast to the classic two-component model of the RP proposing two consecutive intervals of *either* SMA *or* MI activity, there is pronounced activity of the SMA in voluntary movements also during a later stage immediately before movement onset.

Several studies with subdural or intracranial recordings in patients (Ikeda and Shibasaki 1992; Ikeda et al. 1995; Rektor et al. 1994) and animals (Tanji et al. 1987) found SMA activity starting early at a low level but then increasing and reaching peak activity around movement onset. Dipole-source localization studies have reported the SMA is the main source of the early RP, but also found, during the latest pre-movement epoch, enhanced activity of the SMA accompanied by the rise of activity in one or both MI (MacKinnon et al. 1996; Praamstra et al. 1996).

The postulated late SMA activity that is selectively influenced by the mode of movement selection might be distinct from the SMA activity during earlier pre-movement intervals. Consequently, we see the function of the SMA altered by the mode of movement selection more related to (late) movement preparation and movement execution than to planning. In addition, in our study the significant interactions of mode with sequence length and order suggests that the mode effect is more complex than appears at first sight and might reflect activation of other cortical regions such as the MI as well.

Mode of movement selection is altered by movement difficulty

The three-way interaction of the Mode of movement selection with the factors Finger (index compared with middle) and Side of movement execution (left compared with right) is in accordance with previous findings of higher RP amplitudes for middle-finger than for index-finger movements. This difference was explained by the middle-finger movements being, for anatomical reasons, more difficult and effortful than index-finger movements (Kitamura et al. 1993). In general, for right-handed subjects such as those of the present sample, reaction times for left-hand movements are slower than reaction times for right-hand movements. These previous findings are in agreement with our findings, as we found the movement that on an a priori basis appears to be the easiest, repetitive movements with the right index finger, to be associated with the lowest RP amplitude. In contrast, we found the movement that on an a priori basis appears to be the most difficult, randomly performed movements with the left middle finger, to be associated with the highest RP amplitude.

An enhanced mode effect over the parietal electrode may reflect attention to extrapersonal space

In the previous PET study by Deiber and collaborators (1991) on the effects of the mode of movement selection, the enhanced SMA activity during movements in the free mode of movement selection was found to be accompanied by a bilaterally increased parietal activity in Brodmann's areas 7 and 40. Increased parietal activity was also found in a PET study by Playford and collaborators (1992) for freely selected compared with cued repetitive movements. In these studies, the parietal activity was attributed to the need for subjects to allocate increased attention to extrapersonal space during a task demanding free selection of movements. Similar findings of enhanced activity in parietal areas were reported in a PET study by Bonda et al. (1995) for a task requiring mental rotation of hand photographs. Our finding of an increased RP amplitude over the parietal electrode in the free mode, which can be seen earlier than the centrally located increase in RP amplitude, may also be explained by the higher attentional demands associated with planning of the next finger movement in the freely selected sequences.

The interaction of sequence length with order may indicate habituation effects

The two-way interaction of Length of block × Order, and the modulation of the enhanced mode effect at the parietal site by the two variables length of block and order, indicated by the significant four-way interaction Mode × Length of block × Order × Electrode, may constitute a habituation effect. In a RP time series analysis (Taylor 1978) carried out for movement sequences shorter than the long blocks of this study, it was found that after an initial rise over the first 20 movements, the amplitude of the RP at most electrodes decreases again. Although the measures of movement accuracy and response time in this study showed behavioural changes during the first half of the sequence, no such changes were found for the second half for which the decrease in the amplitude of the RP was reported. The finding of a decrease in the amplitude of the RP for the later part of the sequence could be explained by a habituation or motor learning effect that occurs with long movement sequences.

Our results indicate that the effect of sequence length (short compared with long) on the amplitude of the RP depends on order. When performed first rather than in continuation of a long sequence, the short sequences are associated with the highest RP amplitude, which presumably reflects the lowest degree of habituation of the RP. In contrast, when the opportunity for habituation was present, for example when performing short blocks after a long block, the amplitude of the RP was the lowest. These results suggest that, in addition to planning, serial novelty may also contribute to the mode effect on the RP.

Previous PET studies reported increased parietal activity in Brodmann's areas 7 and 40 for the learning of new movement sequences (Jenkins et al. 1994; Seitz and Roland 1992). As the movement sequences were learned and their execution became more automatic, the parietal activity decreased (Jenkins et al. 1994; Seitz and Roland 1992), which was considered to reflect the subject's partial withdrawal of attention from extrapersonal space when the task became automatic. Our finding of a four-way interaction, Electrode × Mode × Length of block × Order, was explained by a parietally enhanced amplitude of the RP for free relative to fixed mode movements for all blocks except the short block performed after a long block. In accordance with the earlier PET studies on motor learning, the absence of this parietally enhanced mode effect for the "continued short block" could reflect the subject's withdrawal of attention after having previously performed a long block prior to the short block.

Our findings suggest that, in future RP studies, to avoid habituation effects in a blocked design, the application of two or more shorter blocks is preferable to the inclusion of a single long block.

Activity of the contralateral primary motor cortex appears to be influenced by the mode of movement selection

The LRP is widely regarded to mirror the activity of the two MIs in preparation for a movement to be subsequently performed (Eimer 1995; Coles et al. 1995; Gratton et al. 1990). In our results, we found the amplitude of the LRP to be influenced by the mode of movement selection in the earliest pre-movement interval, –1000 ms to –500 ms before movement onset. This suggests that, if the change in the amplitude of the LRP does reflect altered MI activity, then the MI activity starts earlier than predicted by the traditional two-component model of the RP which postulates two consecutive intervals, respectively, without and with contribution of MI.

In a series of studies (Coles et al. 1995; Gehring et al. 1992; Gratton et al. 1990) it has been shown that providing the subject with advance information about the side of movement influences the LRP towards earlier lateralization, resulting in an earlier deviation of the LRP from baseline. In our study, subjects had to perform two types of movement. On the one hand, there were movements in the fixed mode of movement selection, for which maximum advance knowledge (always the same finger at the same side of the body) was provided before the sequence began. On the other hand, for movements in the free mode, just minimal external advance information was provided before the start of the sequence. Subjects were instructed to make the sequence random by avoiding more than two repetitions of a movement with the same hand and finger. For both modes of movement selection, no advance information was provided within the sequence *before* each trial.

Movements in the free mode had a higher magnitude of the LRP than movements in the fixed mode across all three epochs, and a greater degree of lateralization was reached even early in the course of the RP (–1000 ms to –500 ms) by movements in the free rather than in the fixed mode. The two modes of movement selection are not distinct at the level of the information provided *before* each trial. Nevertheless, the movements in the condition with a lack of pre-sequential advance information (that is free mode) show increased lateralization.

This effect of the mode of movement selection on lateralization of the RP could be explained by the different frequency of alteration of the side of movement execution. While executing a sequence of freely selected movements, subjects frequently had to prepare for a novel movement, which had not been performed on the immediately preceding trial. In contrast, during the continued execution of a single movement in the fixed mode, the same motor program is applied repetitively. To select and prepare a "new" movement on each trial could require some additional neuronal activity of the contralateral MI, not necessary for repetitive execution of a single movement. In relation to our finding of an enhanced RP amplitude contralaterally to the side of movement for movements in the free mode, it is difficult to determine to what degree a change in the executing finger as opposed to the side of the body can be associated with additional contralateral MI activity, due to a similar novelty effect following from the alteration of choice of finger.

If this interpretation of the MI activity is correct, the degree of randomization in a precued choice reaction task, for example, should influence the LRP. A lower degree of randomization, that is, a bias towards order, even when present without the subject being aware of it, should be associated with a later development and lower peak magnitude of the LRP. Consequently, a "badly randomized", precued choice reaction task should involve two opposite processes. On the one hand, the subject's advance knowledge of movement parameters should manifest itself in earlier preparation of the required movement even before the precue and an earlier rise of the LRP. On the other hand, on mean, a lesser degree of lateralization would be predicted as the hidden bias towards order across trials would produce some degree of repetition of movements with the same hand as in the immediately preceding trial. According to our reasoning, this repetition and lack of alteration and novelty would be associated with lower neuronal activity in MI and hence less lateralization. This proposition can be tested in future studies.

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