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RESEARCH ARTICLE

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Movement-related potentials associated with self-paced, cued and imagined arm movements

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Abstract Self-paced movements, movement to a cue and imagined movement have all been reported to be preceded by a prolonged negativity on averaged electroencephalograph (EEG) recordings. Considerable evidence supports an important contribution from the supplementary motor area (SMA) to this potential and all three types of movement have been shown to be associated with SMA activation. This study was designed to compare the premovement component of these movement-related potentials (MRPs) in a group of subjects who performed each of these three types of movement. In addition, in view of the greater SMA activation in association with proximal arm movements, we studied movements at multiple joints in the right arm. All the potentials were largest at Cz. Self-paced movements were preceded by a negativity (mean onset 1.2 s prior to electromyographic activity) with two distinct phases – an early slow increase (early BP, Bereitschaftspotential) and a later, steeper phase (NS', negative slope). Proximal movements were associated with a larger peak amplitude (mean peak amplitude for shoulder 11.6 μV, finger movement 9.0 μV at Cz, n=14) due to a bigger NS' phase. Movements to a regular cue, but not to a randomly timed cue, were also preceded by a long duration negativity, but the NS' phase began earlier and was less distinct than for self-paced movements (mean peak amplitude for shoulder movement 9.1 μV, finger 8.2 μV at Cz, n=12). Imagining the movements to a regular cue was associated with a slow negativity, with no clear NS' phase (mean peak amplitude for shoulder movement 6.5 μV, finger 6.2 μV at Cz). Our results indicate that the MRPs prior to the three types of movement have distinct characteristics, most notably for the NS' phase. The MRP associated with movement to a regular cue may be analogous to the S2-related negativity of the contingent negative variation (CNV). We discuss the findings in the light of current evidence from functional imaging as to the cortical areas activated in similar movements.

Keywords Bereitschaftspotential · Movement related potentials · Motor control · Contingent negative variation

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Introduction

Averaged electroencephalograph (EEG) reveals activity, termed "movement-related potentials" (MRP), beginning prior to the onset of voluntary movement. Deecke et al. (1969) in an early study, had subjects flex their right index finger repeatedly at irregular intervals, and reported a slow negative potential (the RP or readiness potential) beginning on average 850 ms prior to the onset of movement and maximal at the vertex. Classically, these potentials have been recorded prior to the onset of "self-paced" movements, in the absence of any external timing cue. Three consistent components of the MRP have since been described: an early gentle slope, commonly termed the Bereitschaftspotential (BP), a subsequent steeper slope, prior to the onset of electromyograph (EMG) activity, commonly called the negative slope (NS'), and a third peak, directly related to the EMG activity, the motor potential (MP) (Shibasaki et al. 1980). Initially the potentials were thought to be generated by volume conduction from the motor cortices, but the vertex potential was soon suggested to arise mainly from the underlying supplementary motor area (SMA; Deecke and Kornhuber 1978). During the NS' phase, the MRP becomes asymmetrical, supporting a contribution from the contralateral motor cortex (Shibasaki et al. 1980; Boschert and Deecke 1986). Independently, a slow potential had been described earlier in association with movement to a warned cue – the contingent negative variation (CNV; Walter et al. 1964). This potential, specifically the component related to the second "imperative" cue (S2), resembles the MRP preceding self-paced

movements. Some authors have regarded the S2-related component as equivalent to the MRP prior to self-paced movements (e.g. Rohrbaugh et al. 1976). More recently, the presence of a slow negative potential, also loosely termed an MRP, has been reported prior to the imagination of movement (Beisteiner et al. 1995; Cunnington et al. 1996). Of necessity, the movements are imagined to a cue, but the cue-related cerebral activity can be subtracted from the overall activity, leaving a slow negative component, which, like the BP, is maximal over the vertex.

Functional imaging is an alternative noninvasive method, with high anatomical resolution, for assessing cerebral activation in association with voluntary movements. Self-timed, cued and imagined movements have all been investigated using these techniques. Activation of the SMA has been demonstrated in association with complex finger sequences (Roland et al. 1980), with simple, externally-timed limb movements (e.g. Colebatch et al. 1991; Jahanshahi et al. 1995), and with the imagination of movements (Stephan et al. 1995; Cunnington et al. 2001). Important parallels have been shown between the level of SMA activation measured by functional imaging and the size of MRPs under similar conditions. For example, MRPs are larger when the timing of movement is determined by the subject (Jahanshahi et al. 1995) and when subjects are required to decide the direction of a forthcoming movement, compared with those occurring when making a single movement repetitively (Touge et al. 1995). Analogous studies using functional imaging have shown greater activation in frontal regions, including the SMA, with paradigms requiring movement selection and with self-paced movements (Deiber et al. 1991; Jahanshahi et al. 1995). Jenkins et al. (2000), in particular, compared their findings on positron emission tomography (PET) with MRPs and argued for a very close correspondence between the level of SMA activity recorded with functional imaging and the size of the MRP. Motor cortex activity is substantially less for imagined than for actual movements (Porro et al. 1996; Roth et al. 1996; Cunnington et al. 2001). Thus the MRP with imagined movement has been assumed to receive little or no contribution from the motor cortex (Cunnington et al. 1996).

The present study was designed to explore further the relationship between the premovement MRPs in relation to self-paced, externally-cued and imagined movements. We also wished to determine whether the MRP, or its components, reflected previously demonstrated patterns of SMA activation with these three different "modes" of movement. The initial part of the study compared a series of movements about different joints of the right arm in view of the greater activation of the SMA reported for proximal movements (Colebatch et al. 1991; Matelli et al. 1993). In light of the differences we found, the remainder of the study was performed using both a distal (index finger abduction) and a proximal (shoulder abduction) movement. Our ability to detect characteristic features of the MRPs preceding different types of movement was enhanced by using the same subjects for all tasks, and our confidence in these differences was strengthened by using at least two different movements for each task.

Materials and methods

Subjects

Fourteen volunteers aged 23 to 56 years (mean age 34.9) took part in the study. None had a history of neurological illness. All subjects gave informed consent for the study, which had been approved by the Ethics Committees of the South Eastern Area Health Service and the University of New South Wales.

All seven males were right-handed according to the Edinburgh handedness inventory (Oldfield 1971). Two of the seven females were left-handed and they were included because handedness appears to have little effect on the MRPs associated with simple movements (Brunia et al. 1985).

Experimental tasks

In the first set of experiments ("self-paced" movements) the 14 subjects were instructed to make four different movements with the right arm: abduction of the index finger, flexion of all fingers, elbow flexion and shoulder abduction, at intervals of at least 3 s. The muscles used to trigger EEG collection were the first dorsal interosseous (FDI), flexor carpi ulnaris, biceps brachii and deltoid, respectively. The order of movement was randomised and each movement performed in a separate block. Subjects were told if they moved too frequently and were instructed to count neither the number of movements nor the time between them. Auditory feedback of EMG was provided and the subjects were told if the movements were excessively long, the desired EMG duration being approximately 250 ms. During data collection the subjects were asked to fixate on a red dot and to avoid blinking or moving their eyes.

In a subsequent recording session, finger and shoulder abduction (one distal and one proximal movement) were performed using additional different "modes" of movement. Subjects were instructed to perform finger abduction in response to a tone occurring at a fixed interval of 3 s and to move as soon as they heard the tone ("cued movements"). In the next task they were instructed to imagine abducting the finger, using kinaesthetic imagery, in response to the same tone ("imagined movements"). The subjects then repeated the tasks with shoulder abduction as the required movement. The response to the fixed interval tone alone was recorded at the end of the session. All 14 subjects were told the desired way of imagining the movement (i.e. kinaesthetic rather than visual) at least 24 h prior to the study so that they could practise. Two of the original 14 subjects were not studied as they reported that they were unable to imagine the movements.

Seven subjects were subsequently studied performing finger and shoulder abduction to a random interval tone ("randomly cued movements"). The tone was set to occur at time intervals of between 3 and 5 s, the exact interval being randomly selected by a computer. The order of the two movements was randomised between subjects. The response to the tone alone was also recorded.

A further subgroup of seven subjects repeated self-paced shoulder abduction plus actual and imagined finger and shoulder abduction to a fixed interval tone with the addition of an extra electrode, C1 (midway between C3 and Cz). Surface EMG activity was recorded from paraspinal muscles of the neck, thorax and lumbar region during this test to assess postural muscle activity.

Recording technique

Adhesive silver-silver chloride electrodes were affixed over the muscles of interest bilaterally in a tendon-belly arrangement with 4–6 cm between electrodes. EMG was amplified, filtered with a low cut-off of 32 Hz and a high cut-off of 1.6 kHz, and rectified. For self-paced movements, a custom-built level detector was used to generate trigger pulses from the rectified EMG. EEG recordings were made through 9 mm silver-silver chloride electrodes applied to the scalp at Cz, Fz, Pz, C3' (1 cm anterior to C3, over the hand motor area; Papa et al. 1991) and C4' (1 cm anterior to C4), and referred to linked electrodes over the mastoids. Electrode impedances were always kept below 5 kΩ. The EEG signals were amplified and filtered with a time constant of 5 s and a high frequency cut-off of either 100 Hz or 300 Hz (D150 amplifiers; Digitimer Co., Welwyn Garden City, UK). Sampling was at either 160 Hz or 200 Hz. Electrooculograms were recorded with the same filter settings as that of the EEG to detect any artefact due to eye movement. All signals were collected by a personal computer using an analogue/digital converter and associated software (1401Plus and SigAvg v. 6.33; Cambridge Electronic Design, Cambridge, UK). Signals were collected for a period of 2 s prior to EMG onset and 0.5 s after the trigger point for self-paced movements and 1.5 s prior to and following the auditory cue in the cued tasks. Movements that started less than 3 s after the previous movement were rejected, as were movements occurring prior to the tone in cued recordings and movements contaminated by eye movements or blinks. Movements with any bilateral EMG activity were rejected during the recording and excluded from analysis. For imagined movements, any recordings with evidence of EMG activity were excluded from analysis. Each trial was stored on hard disc for off-line analysis. The tone (1 kHz, 50 ms duration) used for the cued movement was generated by an ST10 Sensor (Medelec, Surrey, UK) and played through loudspeakers placed approximately 2 m from the subject.

Data analysis

For the self-paced movements, the stored traces were manually shifted either slightly earlier or later in relation to the trigger point in order to ensure that the trigger coincided with the onset of EMG in the muscle of interest (Barrett et al. 1985). To keep the number of points constant, in adjusting the trigger point, the software moved some of the points from the beginning to the end of the recording, or vice versa ("time-rotation"). Any remaining trials contaminated by electrooculogram artefact or with bilateral EMG activity were rejected. A total of 64 acceptable trials from each muscle were averaged for each subject.

The recordings obtained in response to the tone alone at fixed intervals, i.e. auditory-evoked potentials (AEP), were averaged but not time-rotated. The averaged response to the tone alone was subtracted from each of the cued movement and imagined "movement" traces for each subject, to exclude any auditory-evoked potential from the final waveform. Cued movements were then "time-rotated" and averaged as for self-initiated movements. Sixty four trials were averaged for each paradigm for each subject. Self-paced and cued movements were aligned to EMG onset whereas imagined movements were aligned to the auditory cue (there being no EMG). The latency criteria for imagined movements were determined using the expected timing of EMG onset following the tone. The latter was determined from the average interval between the tone and EMG onset for the corresponding cued movements for each subject.

A customised program written using Matlab 5 (Mathworks Inc, Natick, Mass., USA) was used for the analysis. This program employed a new technique based upon regression analysis as an objective method to separate the early gentle slope, which we will term the "early BP" and the second steeper slope, the NS'. Linear regressions were fitted between two selected points (one at the onset of the MRP, one at the peak of the NS'). The adequacy of a single linear fit was compared with that for two lines. For the latter condition, the software repeatedly fitted two lines to the data, systematically changing the point where the two lines met. The best division between the two fits was calculated as that giving the largest geometric mean of the two correlation coefficients. The time for optimum fitting of the two regressions we termed the "breakpoint". The correlation coefficient of the single line was compared with the geometric mean of the correlation coefficients for two lines to determine which had the better fit.

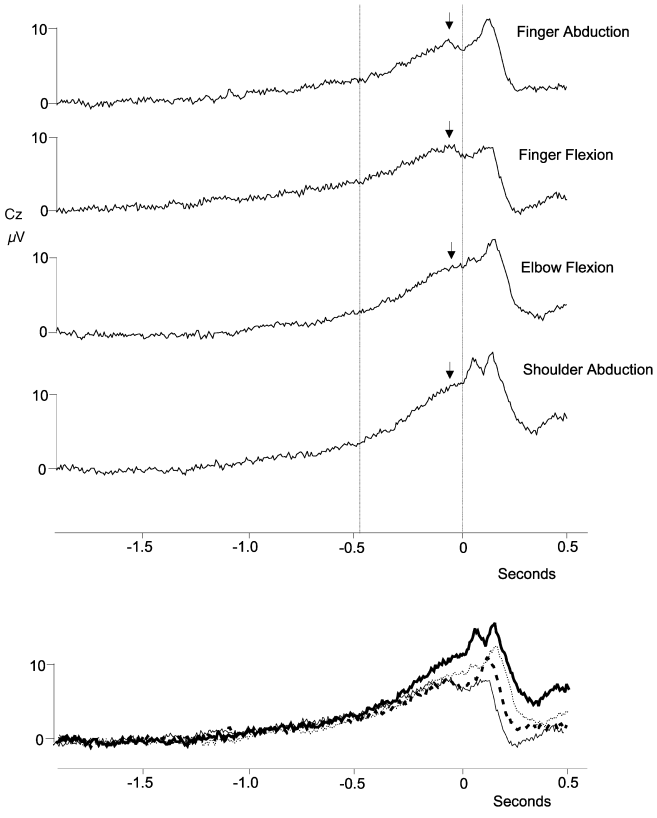

Fig. 1 Grand average (n=14) of the premovement potentials recorded prior to all four self-paced movements at Cz electrode site (superimposed below). The peak amplitude was greatest for shoulder abduction (*thick line*) and smallest for finger flexion (*thin line*). The initial component (early BP) was similar for all four movements. The NS' phase began approximately 475 ms (*left vertical dotted line*) prior to EMG onset (*right vertical dotted line* at 0 seconds). *Arrowhead* denotes the site of measurement of the peak amplitude. In the bottom traces, the *dashed line* represents finger abduction and the line between it and the solid line represents elbow flexion

The baseline was defined by averaging the activity between two cursors, typically separated by about 50 ms, prior to the onset of the MRP. The onset of the early BP was determined by visual examination as the point where the averaged EEG deviated from baseline. The "peak" amplitude was measured from the baseline to the peak of the potential occurring prior to EMG onset (Fig. 1).

Additional statistical analysis was performed using analysis of variance (ANOVA) with repeated measures. Post hoc analysis was performed using paired sample t-tests with Bonferroni corrections. Where sphericity could not be assumed, Greenhouse-Geisser corrections were employed. Analysis was performed separately for the 14 subjects performing self-paced movements and for the 12 subjects who participated in the investigation of the three modes of movement. Significance was accepted at the 0.05 level of probability. All statistics were performed using the SPSS 10 for Windows package (SPSS Corporation, Chicago, USA).

Table 1 Mean amplitude of the early BP phase and mean peak amplitude of the movement-related potential (MRP) for four different self-paced movements of the right arm (14 subjects, all values in μV)

MRP site	Finger abduction		Finger flexion		Elbow flexion		Shoulder abduction	
	Early BP	Peak	Early BP	Peak	Early BP	Peak	Early BP	Peak
C3'	1.6	5.5	2.0	6.5	1.8	5.0	1.5	6.3
Cz	**3.4**	**9.0**	**3.9**	**8.8**	**3.3**	**9.5**	**3.7**	**11.6**
C4'	1.9	4.0	1.8	4.8	1.8	4.4	2.2	5.4
Fz	1.8	3.2	1.6	2.6	1.6	3.9	1.9	4.1
Pz	2.2	5.0	1.6	4.1	1.5	4.6	1.9	5.6

Results

Self-paced movements

The premovement potentials for all four movements of the right arm (finger abduction, finger flexion, elbow flexion and shoulder abduction) were largest at Cz. The mean time of onset of the MRP (at Cz, using individual subject data) prior to EMG activity was 1.2 s (range 1.0–1.3 s). The onset latency did not differ significantly between the movements ($F_{3,39}$=1.629, P=0.198). The averaged potentials at Cz all showed two distinct gradients (Fig. 1) and were all better fitted with two lines than with a single line on regression analysis. The averaged potentials at Pz were also better fitted with two gradients for all movements except elbow flexion. For the grand average for finger abduction, the initial gradient (early BP component) at Cz was 3.4 μV/s (r=0.94) and the second gradient (NS') was 13.6 μV/s (r=0.98) whereas the best fit for a single line for the same potential gave an r-value of 0.94. The breakpoint between the two gradients was 413 ms prior to the onset of EMG. For finger flexion the gradients were 3.4 V/s (r=0.93) and 11.5 μV/s (r=0.98) with a breakpoint at 525 ms prior to EMG onset, whereas for elbow flexion the gradients were 4.0 μV/s (r=0.95) and 15.7 μV/s (r=0.98) with a breakpoint 456 ms prior to EMG onset. The r-value for a single line was 0.94 for both finger flexion and elbow flexion. For shoulder abduction, the initial gradient was 4.1 μV/s (r=0.96) and the second gradient was 18.3 μV/s (r=0.99), whereas the r-value for a single line fit was 0.93. The breakpoint for shoulder abduction was 500 ms prior to EMG onset. The second gradient was always greater than the first (average 3.9 times greater) and both gradients increased for the more proximal movements. In view of the findings for the breakpoints, 475 ms prior to EMG onset was chosen as the time separating the early and late premovement components of the MRP for our analysis of early BP and NS' amplitudes.

Peak amplitude

The peak amplitude was greatest for shoulder abduction for all electrodes for both the averaged and the individual subject data. For each of the four movements, the peak amplitude was greatest at Cz and the amplitude at C3' was greater than at C4' (Table 1). This difference in amplitude between C3' and C4' was significant ($F_{1,13}$=6.39, P=0.025). The peak of the premovement potential at Cz occurred at a mean of 58 ms prior to the onset of EMG. There was no significant difference in the timing of the peak of the MRP between the four movements ($F_{3,39}$=0.108, P=0.930). ANOVA with repeated measures for the peak amplitude of each subject's data, using site of movement and site of electrode as factors, revealed a main effect of electrode ($F_{4,52}$=19.946, P<0.001). Site of movement just failed to reach significance ($F_{3,39}$=2.622, P=0.064) and there was no significant interaction between site of movement and electrode ($F_{12,156}$=2.15, P=0.170). Pairwise comparisons demonstrated that Cz amplitudes were significantly larger than amplitudes at all the other electrodes (P<0.001). ANOVA performed on the Cz data showed a significant effect of site of movement ($F_{3,39}$=3.673, P=0.002) with significant differences between finger flexion and shoulder abduction (P=0.001) and between finger abduction and shoulder abduction (P=0.01) (Figs. 1 and 2). ANOVA with repeated measures for Pz also showed a significant effect of site of movement ($F_{3,39}$=2.951, P=0.044). Analysis of data for the other electrodes showed no effect of site of movement (C3' $F_{3,39}$=2.294, P=0.093; C4' $F_{3,39}$=0.466, P=0.707; Fz $F_{3,39}$=2.717, P=0.058).

Early BP amplitude

Despite the (small) increase in the initial gradient with more proximal movement, the mean amplitude of the early BP component of the MRP showed no clear tendency to increase as the movement performed became more proximal (Table 1). ANOVA with repeated measures, using electrode and site of movement as factors, showed no effect of site of movement ($F_{3,39}$=0.665, P=0.579) but a significant effect of electrode ($F_{4,52}$=13.700, P<0.001). The latter was a reflection of the larger amplitude at Cz. There was no interaction between site of movement and electrode. Analysis of the Cz data alone also showed no effect for site of movement for the early BP amplitude ($F_{3,39}$=0.290, P=0.832). Mean C3' values were not larger than those for C4'.

NS' amplitude

As would be expected given the result for the early BP amplitude, the NS' amplitude displayed the same trend to increase as the movement became more proximal as was

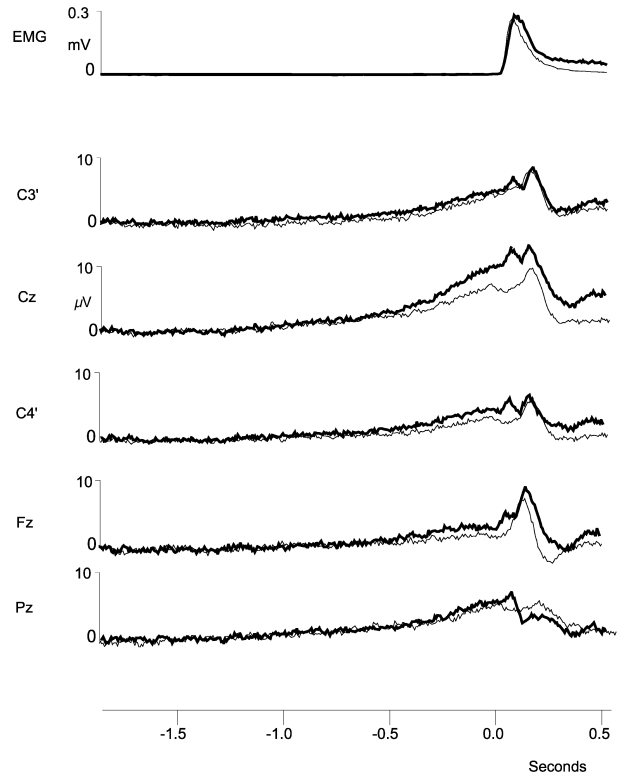

Fig. 2 Grand average (n=14) of EMG and of the premovement potential at various electrode sites for self-paced finger abduction (*thin line*) and shoulder abduction (*thick line*). There was little difference in the early BP component of the potential at any of the electrodes. There was a greater NS' component and peak amplitude for the proximal movement, particularly at Cz where the movement-related potential for the shoulder movement diverged from that for the finger movement approximately 500 ms prior to the onset of EMG

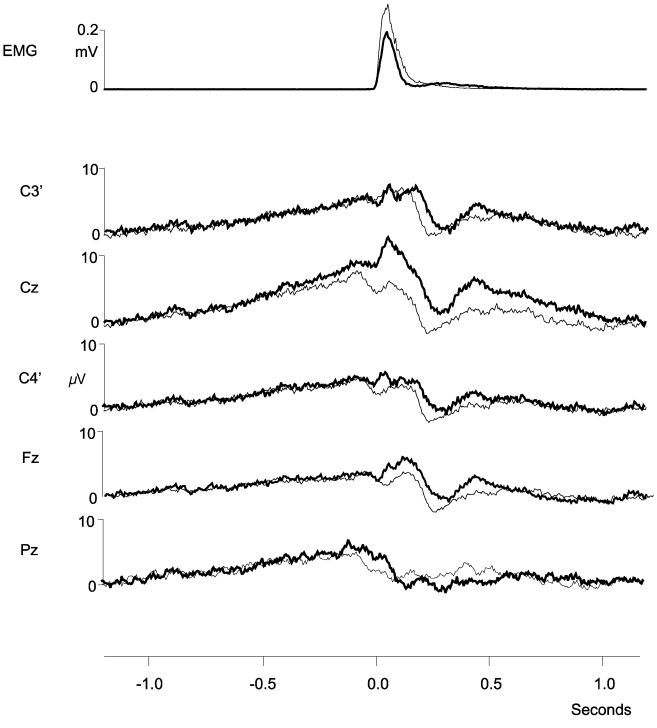

Fig. 3 Grand average (n=12) of EMG and of the movement-related potential at various electrode sites for regularly cued finger abduction (*thin line*) and shoulder abduction (*thick line*). There was little difference between the two traces at most electrodes; however, at Cz, the potential for shoulder abduction had a greater amplitude. The NS' phase is less obvious than for self-paced movement (Fig. 2)

observed with the peak amplitude. ANOVA with repeated measures, using site of movement and electrode as factors, revealed a significant effect of both site of movement ($F_{3,39}$=2.839, P=0.05) and electrode ($F_{4,52}$=16.839, P<0.001) with no interaction between these two factors ($F_{12,156}$=1.842, P=0.103). Pairwise comparisons showed significantly larger values at Cz than at all other electrodes (P≤0.015), and a trend towards significance between finger and shoulder abduction (P=0.061). ANOVA performed on the Cz data alone showed a significant effect of site of movement ($F_{3,39}$=3.945, P=0.015). Post hoc analysis showed significant differences between finger and shoulder abduction (P=0.048) and between finger flexion and shoulder abduction (P=0.037).

Cued movements

Regular cue

A distinct MRP was present prior to regularly cued movements at both the index finger and shoulder (Fig. 3). The onset latencies for the grand averages were 1.2 s and 1.1 s prior to the EMG onset for the finger and shoulder movements respectively. The peak amplitude of the MRP was largest at Cz and was 8.2 μV for cued finger abduction and 9.1 μV for cued shoulder abduction (grand average). Peak C3' amplitudes were on average almost 1 μV larger than for C4' (Table 2). This difference tended

Table 2 Mean peak amplitudes (μV) of the movement-related potential (MRP) for the three modes of movement performed with the index finger and at the shoulder (12 subjects)

	Finger abduction			Shoulder abduction		
	Imagined	Cued	Self-paced	Imagined	Cued	Self-paced
C3'	3.4	5.6	5.8	3.6	5.3	6.2
Cz	**6.2**	**8.2**	**9.5**	**6.5**	**9.1**	**12.0**
C4'	3.0	4.6	4.7	3.2	4.4	5.3
Fz	3.5	5.1	3.5	4.0	4.1	4.6
Pz	3.2	3.9	5.2	3.3	4.9	5.7

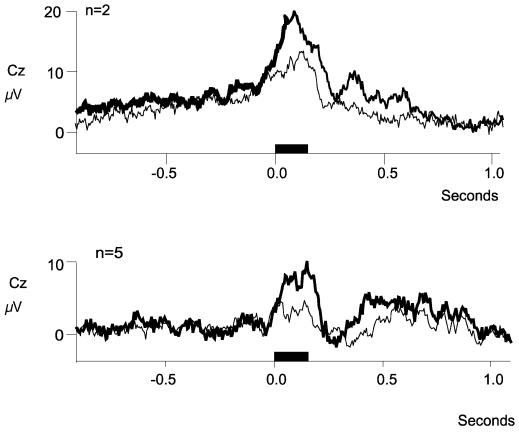

Fig. 4 Two subjects who reported they were able to anticipate the random tone showed a small movement-related potential (MRP) prior to both finger abduction (*thin line*) and shoulder abduction (*thick line*) (upper traces). The other five subjects, who did not report being able to anticipate the tone (lower traces), showed no MRP prior to movements cued by a tone occurring at random intervals for either the finger or shoulder movement. The *solid rectangle* represents the average onset and duration of EMG activity. The tone occurred approximately 90 ms prior to EMG onset. All recordings at Cz

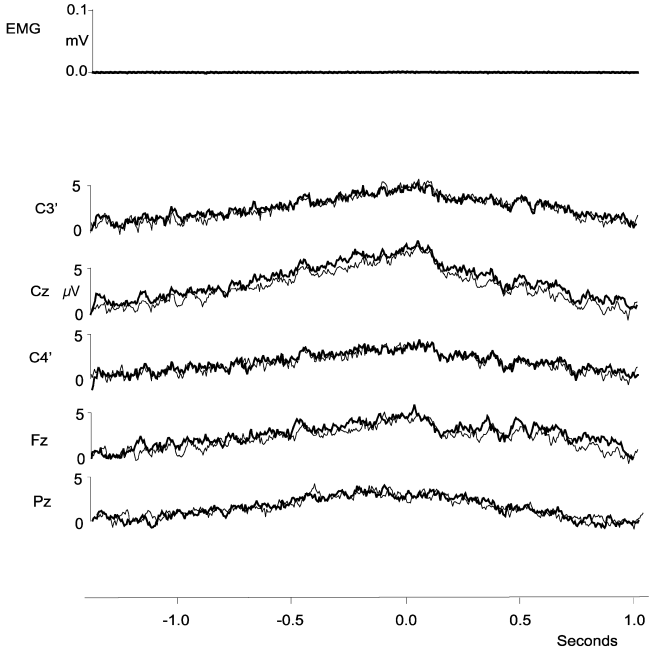

Fig. 5 Grand average (n=12) of EMG and of the movement-related potential at various electrode sites for imagined finger abduction (*thin line*) and shoulder abduction (*thick line*). The potential has the same gradient throughout its initial course. There was little difference between the potentials for the two imagined movements at any of the electrodes

towards significance (finger abduction $F_{1,11}$=3.531, P=0.087; shoulder abduction $F_{1,11}$=3.496, P=0.088). Regression analysis of Cz data showed a better fit with a single line than with two lines for both cued finger abduction (gradient 6.9 μV/s, r=0.98) and cued shoulder abduction (gradient 8.2 μV/s, r=0.96), indicating that the gradients were more uniform than for self-initiated movements. Using the point where the slope diverged from that for imagined movement (see below), the gradients for cued finger abduction were 3.7 μV/s (r=0.69) and 8.6 μV/s (r=0.94) and for cued shoulder abduction 4.7/s μV (r=0.88) and 11 μV/s (r=0.97), i.e. the second gradient was 2.3 times the first gradient for both movements.

Random cue

Five of the seven subjects showed no MRP prior to their movements cued by the random tone (Fig. 4). The other two reported that they felt that they could predict the timing of the random tone and were also the only subjects to move before the tone. A MRP was evident prior to the onset of the movement for these two subjects (mean peak amplitude at Cz was 5.5 μV for finger abduction and 7.5 μV for shoulder abduction).

Imagined movements

An MRP was present prior to imagined finger and shoulder abduction cued by the tone occurring at a fixed interval with the largest amplitude at Cz (Fig. 5). The averaged potential began 0.94 s prior to the cue for imagined finger abduction and 0.91 s prior to the cue for imagined shoulder abduction. After adjustment for the cue-EMG interval observed with regularly cued movements, these onset latencies became 1.03 s and 1.00 s respectively. Regression of the averaged potential for all five electrodes gave r-values for a single line that were always higher than the geometric mean for two. For imagined finger abduction, the gradient of the MRP was 5.6 μV/s (r=0.95) and the peak amplitude was 6.2 μV. For imagined shoulder abduction the gradient was 5.8 μV/s (r=0.95) and the peak amplitude was 6.5 μV (all measurements at Cz on grand average). The amplitude of the early component of the MRP, measured using 475 ms prior to the expected EMG onset as the breakpoint, was 2.4 μV for imagined finger abduction and 3.5 μV for imagined shoulder abduction. Using the same breakpoint, the gradients of the early and late components of the MRP for imagined finger abduction were 5.0 μV/s and 5.9 μV/s and for imagined shoulder abduction were 4.1 μV/s and 6.1 μV/s respectively. Amplitudes at C3' and C4' were not significantly different (finger abduction $F_{1,11}$=0.093, P=0.767; shoulder abduction $F_{1,11}$=0.012, P=0.916) (Table 2). On ANOVA, there was no effect of site of movement for the peak amplitude ($F_{1,11}$=2.397, P=0.150) or gradient ($F_{1,11}$=0.739, P=0.408) of the MRP prior to imagined movements.

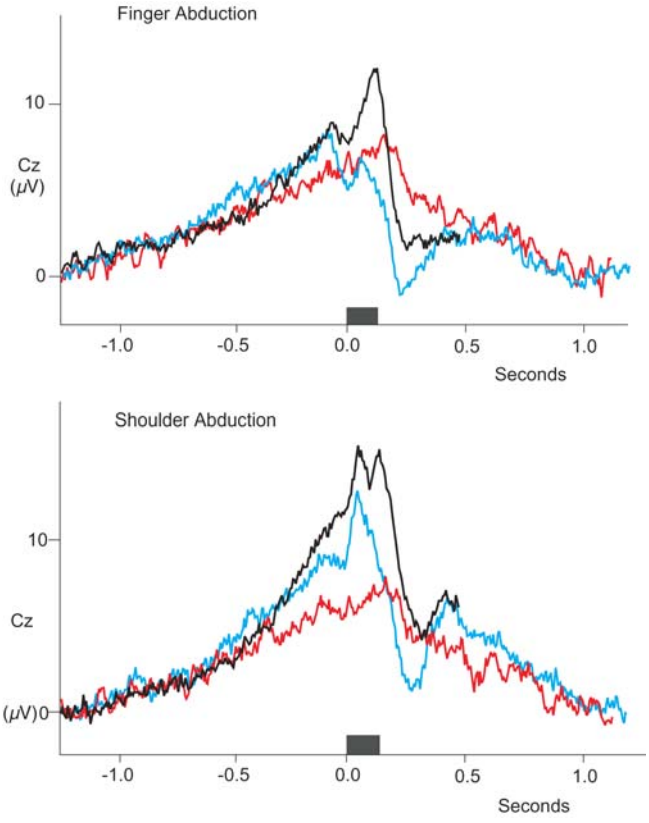

Fig. 6 Averaged traces for movement-related potential (MRP, at Cz) of the 12 subjects who performed finger abduction and shoulder abduction for all three movement paradigms. The MRP for self-paced movements was largest for both the finger and shoulder movements (*black line*), followed by cued movements to a tone at a fixed interval (*blue line*) and imagined movements (*red line*) to a tone at a fixed interval. The initial component of the potential was similar for all three movements. The MRP for self-paced movements showed a marked increase in slope (NS' phase) prior to EMG onset (at 0 seconds). The MRP for cued movements diverged earlier from the imagined MRP but had a smaller increase in slope. The traces for self-paced and cued movements were aligned to EMG onset. For imagined movements the timing of EMG onset was estimated using the delay between the tone and EMG onset for the cued movements

Comparison of modes of movement

The grand averages for the 12 subjects who performed all three tasks were directly compared (Fig. 6). For both the finger and the shoulder movements, the three MRPs were similar in their initial phases and then diverged. For both finger and shoulder movements, the potential preceding the imagined movement was smallest, that for the self-paced the largest and that for the regularly cued movement intermediate. The potential for the regularly cued movement diverged from that of the imagined movement approximately 600 ms prior to the onset of EMG. The potential for self-paced movement deviated from that of imagined movement approximately 470 ms prior to EMG onset.

The peak amplitudes were always greater for shoulder abduction than for finger abduction, at Cz, for all three modes of movement (Table 2). ANOVA with repeated measures for the peak amplitude (n=12) using mode of movement (self-paced, cued or imagined), site of movement (finger or shoulder abduction) and electrode as factors, showed a significant effect of electrode ($F_{4,44}$=22.344, P<0.001) but marginal significance for mode of movement ($F_{2,22}$=3.270, P=0.089). There were significant interactions between mode of movement and electrode ($F_{8,88}$=2.693, P=0.011) and site of movement and electrode ($F_{4,44}$=3.864, P=0.009). Pairwise comparisons showed a significant difference between Cz and the other electrodes (P≤0.002). At Cz, using site and mode of movement as factors, there was a significant effect of site of movement ($F_{1,11}$=11.887, P=0.005) and a trend towards significance for mode of movement ($F_{2,22}$=3.795, P=0.068), with no interaction between these two factors. At C3' there was an effect of mode only ($F_{2,22}$=0.462, P=0.044), cued and self-paced movement having larger amplitudes than imagined movement. There was no effect for either factor at C4', Fz or Pz.

The averaged MRPs appeared to begin slightly earlier for self-paced movements than for the other two modes. Measurements of the individual subjects' data (n=12) gave a mean latency of onset prior to the onset of EMG activity for self-paced movements of 1.3 s for finger abduction and 1.2 s for shoulder abduction. For both cued finger abduction and cued shoulder abduction the mean onset latency was 1.0 s. After correcting for the time between the tone and EMG onset, the corresponding mean latency for both imagined movements was also 1.0 s. ANOVA with repeated measures, using mode of movement (self-paced, cued and imagined), site of movement (finger or shoulder) and electrode as factors, was performed on the individual onset latency data. There was a significant effect of mode of movement ($F_{2,22}$=17.506, P<0.001) for the onset latency of the MRP but not of site of movement ($F_{1,11}$=0.014, P=0.909). The effect of mode of movement was due to the difference between self-paced movement and the other two modes. There was a significant effect of electrode ($F_{4,44}$=19.435, P<0.001), which was due to an earlier onset at Cz (P≤0.003 on pairwise comparisons). There were no interactions between the three factors.

Additional recordings

The mean peak amplitude was always greater at Cz than C1 for the seven subjects in whom this was measured. The differences were larger for the three tasks involving shoulder movement (1.7–3.0 μV) than for the two tasks – cued and imagined movement – involving index finger movement (0.37–0.53 μV). Activation of paraspinal muscles occurred only when shoulder abduction was performed. No activation occurred prior to the onset of deltoid EMG and the profile of the paraspinal muscle EMG was similar to that of the deltoid.

Discussion

The premovement MRPs, while having broad similarities, also showed important differences, properties that must be explicable in terms of the cortical structures that generate them. The potentials were always maximal over the vertex. This site overlies Brodman's area 6 on the medial part of the superior frontal gyrus, an area which constitutes the SMA. Below the SMA lie the cingulate motor areas and recordings at Cz may potentially reflect activity within both areas. Likewise, the apparent contribution from the motor cortex may also include activity in the lateral premotor cortex as both show preparatory activity prior to movement (Riehle and Requin 1989). The SMA contains at least two functionally distinct areas – the more anterior pre-SMA and the more posterior SMA proper or caudal SMA. In monkeys, microstimulation of the more caudal part of the SMA evokes simple movements, whereas stimulation more rostrally evokes more complex movements (Matsuzaka et al. 1992). The two subdivisions also have distinct corticocortical connections (Luppino et al. 1993). Differences between the pre-SMA and SMA proper have been demonstrated using functional imaging in humans. Deiber et al. (1991) reported that when subjects were required to decide the direction in which to move there was greater activation in medial frontal cortex anterior to the Vac line (a line extending vertically above the anterior commissure; Tailarach and Tournoux 1988), i.e. in the pre-SMA. Time-resolved functional magnetic resonance imaging (fMRI) has confirmed that activity within the pre-SMA occurs prior to activity within more caudal parts of the SMA (Ball et al. 1999; Lee et al. 1999; Weilke et al. 2001). Activity in the SMA proper in turn precedes that in the motor cortex (Ohara et al. 2000; Wildgruber et al. 1997). Additional functional subdivision may be appropriate: the most caudal part of the SMA proper behaves like motor cortex and may act in parallel with the primary motor cortex (Stephan et al. 1995).

Imagined movement, defined as "the mental rehearsal of motor acts not accompanied by overt body movements", has been shown to have similar timing (Jeannerod and Decety 1995) and autonomic accompaniments (Decety et al. 1993) to those of actual movements. Early studies of regional cerebral blood flow (rCBF) showed robust activation of the SMA with imagined movements. This increase in rCBF was about 60% of the increase occurring in the same area when the movements were actually performed (Roland et al. 1980). Subsequent, more sensitive studies have shown that several cortical regions in addition to the SMA are also consistently activated during imagined movement. These regions include the parietal lobes, cingulate, lateral premotor and prefrontal areas (Decety et al. 1988; Stephan et al. 1995; Deiber et al. 1999; Gerardin et al. 2000). Activation within the motor cortex during imagined movements, if present, appears to be minor (Roland et al. 1980; Stephan et al. 1995; Gerardin et al. 2000). Cunnington et al. (1996, 1997) investigated the MRPs associated with imagined movement and concluded that these were likely to be generated by the SMA. Our observations are consistent with their interpretation. We found imagination-related MRPs that were symmetrical, largest at Cz, and had no definite NS' component, and which were similar for both the shoulder and the index finger tasks.

Premovement potentials are classically measured under "self-paced" conditions. Subjects are encouraged to move irregularly and to avoid internal cues such as counting. Under such conditions we recorded MRPs with two distinct phases, the early BP and later NS', for all four movements of the right arm. There was an approximately four-fold increase in gradient for the NS' component and the two distinct phases could be detected using our regression-based method. We used the same movement repetition rate (>3 s between movements) as Shibasaki et al. (1980), and our values for the onset of the NS' phase and for the initial and later gradients are almost identical to their observations. The values are likely to depend upon intermovement intervals as slower repetition rates are associated with a longer NS' phase (Dick et al. 1989; Papa et al. 1991). Whereas the early phase of the MRP was similar to that for imagined movement and for movement to a predictable cue, the potential began earlier prior to self-paced movements. When subjects are required to make decisions about the type or timing of movement, greater activation occurs in the pre-SMA and other prefrontal structures (Deiber et al. 1991, 1999; Jenkins et al. 2000). Current evidence, as discussed above, supports a rostral-to-caudal order of activation of the SMA. The earlier onset of the potential for self-paced movement is likely to be the result of greater pre-SMA activity under these conditions.

While a strong case has been made that the early BP component of the MRP is primarily generated by the SMA (see Jenkins et al. 2000), the origin of the NS' component is less certain. It was the NS' component prior to self-paced and regularly cued movements that showed clear differences between proximal and distal muscle groups but there was no significant difference in the potentials at Cz for imagination of the shoulder and finger movement. Assuming that the MRP with imagination is generated by the SMA, then a substantial contribution to the MRP during the NS' phase arises from the SMA. The NS' amplitude was greatest for self-paced movements made at the shoulder and was larger at C3' than at C4'. Given the somatotopic arrangement of the motor cortex, these findings support a contribution from the contralateral motor cortex to the NS' potential. The most caudal part of the SMA, an area that behaves like motor cortex (Stephan et al. 1995; Jenkins et al. 2000), may also contribute to the NS' potential because the SMA is more active when movement takes place than during its imagination (Roland et al. 1980; Decety et al. 1988; Stephan et al. 1995). Both the SMA and the motor cortex show greater levels of activation in association with proximal movements (Colebatch et al. 1991). Thus we propose that the NS' component of the MRP is generated by both SMA and motor cortex activity.

Cued movements were associated with two contrasting patterns of MRPs. When the cue was presented regularly and thus could be anticipated, there was a clear MRP. When the cue was made sufficiently irregular, no MRP was present prior to the stimulus. Making the cue sufficiently irregular was difficult, particularly for our relatively short repetition intervals. Papa et al. (1991), who used a 10 s mean repetition rate, reported that there was no recognisable BP/MRP prior to reaction-time movements in response to a variety of stimuli. When MRPs have been recorded during functional imaging it has been found that subjects have sometimes been anticipating even what appeared to be irregular stimuli (Jahanshahi et al. 1995). When observations are deliberately made with widely-varying intervals for the external stimuli, activation within the SMA is much reduced (Jenkins et al. 2000). Although these latter authors did not record the MRP under these conditions, our observations and those of Papa et al. (1991) indicate that it would have been much attenuated or absent, supporting the important role of the SMA in generating the MRP.

The averaged MRP (at Cz) for the predictable cue was different from that for self-paced movements of a similar rate. Whereas the marked increase in slope preceding the onset of self-paced movements could be detected using statistical methods, this was not the case for the regularly cued movements. However, when compared with imagined movements, regularly cued movements did appear to show two phases for both the finger and shoulder movements. The NS' phase for regularly cued movements demonstrated a smaller increase in slope but an earlier separation from the potential for imagined movements when compared with those for self-paced movements. The simplest explanation for these findings is that similar structures are responsible for the additional potential for the latter part of the MRPs for both predictably cued and self-initiated movement, but that earlier recruitment occurs when the stimulus can be anticipated. The earlier recruitment may partly explain the smaller increase in gradient for the NS' phase prior to regularly cued movements.

The relationship between the MRP recorded prior to self-paced movement and the CNV (contingent negative variation) has been a source of debate in the past. Two stimuli are used to record a CNV – an initial warning signal ("conditional stimulus", or S1) and a later "imperative stimulus" (S2) to which the subject must react (Walter et al. 1964). The CNV has an early component after S1, which may be positive or negative, and a late, negative component that precedes the second stimulus by approximately 1 s. The CNV is present without the second stimulus if the subjects are asked to react at the time they expect that the stimulus would have occurred (Walter et al. 1964). There is substantial support from functional imaging that SMA activation occurs both with movement to a regular cue (see Introduction) and for the CNV-type protocol (e.g. Lee et al. 1999). Given that the interval between S1 and S2 is usually of the order of 0.5–3 s and fixed, subjects can be regarded as reacting to an external cue with predictable timing. Thus the CNV paradigm appears analogous to our regularly (predictably) cued movement. Papa et al. (1991) recorded the MRP for a CNV paradigm on three subjects and reported that the NS' phase was "difficult to recognize" compared with the MRP for self-paced movement. We suggest therefore, that the potential preceding a stimulus to which a subject must react and whose timing can be anticipated by the subject, whether occurring in pairs or repetitively, is analogous to the S2-related component of the CNV. A small increase in gradient during the NS' phase appears to be characteristic.

By recording MRPs repeatedly in the same large group of subjects we have been able to discern the differences associated with different modes of movement. The fact that we had consistent differences for two distinct movements of the arm strengthens our observations. Our results, in conjunction with the results of functional imaging, support a major, but not exclusive, contribution from the SMA to the premovement MRP. Slow negative waves precede self-paced, regularly cued and imagined movements but features of the waveforms differ, reflecting differences in the cortical activity that produces them.

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