Movement Rate Effect on Activation and Functional Coupling of Motor Cortical Areas

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Toma, Keiichiro, Tatsuya Mima, Takahiro Matsuoka, Christian Gerloff, Tatsuhito Ohnishi, Benjamin Koshy, Frank Andres, and Mark Hallett. Movement rate effect on activation and functional coupling of motor cortical areas. J Neurophysiol 88: 3377–3385, 2002; 10.1152/jn.00281.2002. We investigated changes in the activation and functional coupling of bilateral primary sensorimotor (SM1) and supplementary motor (SMA) areas with different movement rates in eight normal volunteers. An auditory-cued repetitive right-thumb movement was performed at rates of 0.5, 0.75, 1, 2, 3, and 4 Hz. As a control condition, subjects listened to pacing tones with no movements. Electroencephalogram (EEG) was recorded from 28 scalp electrodes and electromyogram was obtained from the hand muscles. The event-related changes in EEG band-power (ERpow: activation of each area) and correlation (ERcor: functional coupling between each pair of cortical areas) were computed every 32 ms. Modulations of ERpow and ERcor were inspected in alpha (8–12 Hz) and beta (16–20 Hz) bands. Motor cortical activation and coupling was greater for faster movements. With increasing movement rate, the timing relationship between movement and tone switched from synchronization (for 0.5–1 Hz) to decoupling (for 3–4 Hz). Results suggested that for slow repetitive movements (0.5–1 Hz), each individual movement is separately controlled, and EEG activation and coupling of the motor cortical areas were immediately followed by transient deactivation and decoupling, having clear temporal modulation locked to each movement. In contrast, for fast repetitive movements (3–4 Hz), it appears that the rhythm is controlled and the motor cortices showed sustained EEG activation and continuous coupling.

INTRODUCTION

During externally guided movements, each movement is timed with a separate external cue. For slow rhythmic movements, the timing of each individual movement is controlled with regard to each external cue because there is enough time to prepare for each movement. By contrast, it seems difficult to execute fast rhythmic movements precisely in response to rapidly presented external cues. In such a rapid-movement task, rhythm or trains of movements seems more important than individual movement. Mayville et al. (1999) examined the timing relationship between external cues and movements at different movement rates and found that the relationship changes at the movement rate of about 2 Hz. Subjects who were requested to execute movements in the syncopated (anti-phase) manner could no longer keep such a syncopated relationship with tones and switched to a synchronization mode. The findings suggest that there is a critical movement rate for executing individual repetitive movements. Positron emission tomography (PET) and functional magnetic resonance imaging (fMRI) studies have shown that movement rate affects magnitudes of activation at the primary (M1) and supplementary (SMA) motor areas. Regional cerebral blood flow (rCBF) in PET (Blinkenberg et al. 1996) or blood oxygenation level-dependent (BOLD) signal in fMRI (Jäncke et al. 1998; Rao et al. 1996; Schlaug et al. 1996) was greater for the faster movement in the M1. Sadato et al. (1996) found a stepwise increase in rCBF between 1- and 2-Hz movements but did not observe a significant change from 0.25 to 1 Hz as well as from 2 to 4 Hz. Jäncke et al. (1998) also showed a dip of M1 activation at the movement rate of 1.5 Hz in fMRI. Although there is controversy concerning linear or stepwise activation of M1, the findings of these studies (Jäncke et al. 1998; Sadato et al. 1996) suggest possible different neuronal mechanisms between slow and fast rhythmic movements. With regard to SMA activation, previous neuroimaging studies showed inconsistent findings: positive (Schlaug et al. 1996), negative (Sadato et al. 1996), or uniform activation (Blinkenberg et al. 1996) with increasing movement rates. Neuroimaging studies have poor temporal resolution, and the number of trials included in the same scan time is more for faster movement, confounding interpretation of the movement rate effect on motor cortical activation; activation of motor cortical areas does not represent a change in neural activity caused by a single movement. In addition, PET and fMRI studies yield little information on the functional coupling between the M1 and SMA, only providing information of activation of each area.

A change in electroencephalographic (EEG) oscillations during motor preparation and execution (Chatrian et al. 1959; Nagamine et al. 1996; Toro et al. 1994) enable us to observe involvement of motor cortical neurons associated with a single movement with millisecond resolution, thus being more appropriate for analyzing fast repetitive-movement tasks. An event-related change in EEG band-power (ERpow) represents the regional activation of motor cortical areas; event-related EEG correlation (ERcor) is a technique to examine their interre-
regional functional coupling. To understand the effect of movement rate on both activation and functional coupling of motor cortical areas comprehensively, we compared ERpow and ERcor in alpha and beta bands for different movement rates ranging from 0.5 to 4 Hz.

**M E T H O D S**

**Subjects**

Eight right-handed volunteers (4 males, 4 females) participated in the study. Mean age was $48 \pm 12$ (SD) yr, and none had suffered from neurological or psychiatric disorders. The protocol was approved by the National Institute of Neurological Disorders and Stroke Institutional Review Board; subjects gave their written informed consent after the study was fully explained.

**Behavioral paradigm**

**MOVEMENT TASK.** Each subject was seated in a comfortable chair in a quiet electrically shielded room and performed repetitive abduction of the right thumb at six different movement rates, 0.5, 0.75, 1, 2, 3, and 4 Hz, paced by a tone. The subject was simply requested to keep pace with the tones. Hands were masked from the subject to prevent visual feedback. Each session was recorded until number of movements exceeded 250.

**TONE (CONTROL) TASK.** As a control task, subjects listened to the tones with no movement at the same rates as the movement tasks, i.e., 0.5, 0.75, 1, 2, 3, and 4 Hz. The order of the six types of movement tasks and those of the control tasks was randomized.

**Data acquisition**

EEG was recorded with linked-ears reference from 28 scalp electrodes that were arrayed in an extended international 10–20 system of electrode placement and mounted on an elastic cap (Electro-cap International, Eaton, OH). In this configuration, electrodes were situated closely around bilateral primary sensorimotor (SM1) and medial frontal (MFC) areas (Fig. 1). Electromyogram (EMG) was obtained from the right and left abductor pollicis brevis and biceps brachii muscles. Electrode impedance was kept below 5 kΩ. EEG was band-pass filtered at 1–50 Hz and EMG signals at 5–100 Hz. Both EEG and EMG were digitized at the sampling rate of 250 Hz (Neuroscan, Neurosoft, Herndon, VA).

**Behavioral data analysis**

To examine a change in muscle force with increasing movement rate, a peak amplitude (EMG amplitude) of the averaged EMG was measured for each subject in the six movement tasks. Task difficulty for different rates was assessed by the coefficient of variation (CV) of inter-tapping interval (ITI), i.e., SD of ITI divided by the mean of ITI. Task difficulty was also evaluated by the discrepancy, i.e., mean tapping interval divided by the interval of the target rate. To explore patterns of sensorimotor integration, timing of taps was measured with regard to tone onset for different rates. The number of analyzed taps was 2,000 (250 taps per 1 subject) for each rate. Timing was expressed as a cycle from $-0.75$ to 0.25; movement that occurred at $-0.75$ to $-0.25$ cycle ($-270$ to $-90^\circ$) was defined as syncopated movement relative to tone and that at $-0.25$ to 0.25 ($-90$ to $90^\circ$) as synchronized movement. Mean phase shift from tone to movement for eight subjects was calculated for the six rate tasks.

**EEG data analysis**

To visually identify the precise onset of EMG discharge, EMG signals were rectified. EEG was segmented into epochs from $-2,560$ to 2,048 ms for the 0.5-, 0.75-, and 1-Hz movement and tone tasks and epochs from $-640$ to 512 ms for the 2-, 3-, and 4-Hz movement and tone tasks. Segmentation was done with regard to EMG onset for movement tasks and tone onset for control tone tasks. A criterion for automatic artifact rejection was 200 μV for EEGs. Then the epochs with minor artifacts were visually checked and removed from the analysis; $72 \pm 5.2$ (mean ± SD) artifact-free epochs were obtained for each subject in the six movement and six tone tasks.

To obtain the time sequence without phase distortion, a zero-phase-shifting FIR (finite impulse response) filter was applied for each epoch for each electrode, producing a frequency sequence of 4-Hz bins between 8 and 40 Hz. Event-related covariance was computed for each electrode-pair at each 4-Hz frequency bin by using a 64-ms time window with a shifting step of 32 ms from the beginning to the end of the epoch. Then the covariance matrices were averaged over the epochs. Ordinary correlation matrices were computed from the following equation

$$R_{xy}(f) = C_{xy}(f)/\sqrt{(C_{xx}(f)C_{yy}(f))}$$

where $C_{xx}(f)$ and $C_{yy}(f)$ represent the autocovariance for $x$ and $y$, and $C_{xy}(f)$ the covariance between $x$ and $y$. Because the power of oscillations at centrofrontal areas is suppressed during movement, occipitoparietal oscillations spreading to the centrofrontal areas could be relatively predominant and cause false high coupling of the centrofrontal areas (Florian et al. 1998; Mima et al. 2000). To remove this volume conducted effect from the occipitoparietal area, partial correlation was finally obtained after removing the linear effect from the OZ electrode, according to the following equation

$$R_{xy}(f) = (R_{xy}(f) - R_{xz}(f)R_{yz}(f))/\sqrt{(1 - R_{xz}(f)^2)(1 - R_{yz}(f)^2))}$$

where $R_{xy}$, $R_{xz}$, $R_{yz}$ are correlations. The correlation is expressed as a real number between $-1$ to 1, with 1 ($-1$) indicating perfect linear positive (negative) association and 0 indicating complete absence of linear association.

The event-related power change (ERpow) was obtained by subtracting the autocovariance in the tone task from that in the movement task after logarithmic transformation of autocovariance to obtain a normal distribution (Halliday et al. 1995); note that a decrease in ERpow means increased activation of the cortical region. The event-
related correlation change (ERcor) was computed by subtracting the hyperbolic inverse tangent transformed correlation in the tone task from that in the movement task. Hyperbolic inverse tangent transformation was employed to remove the effect of distance between two electrodes in the correlation (Farmer et al. 1993; Gerloff et al. 1998; Rosenberg et al. 1989).

According to the relationship between brain structures and electrode locations (Gerloff et al. 1998; Homan et al. 1987) and taking distortion and spread of EEG signals over the scalp, regions of interest (ROIs) were set up in the left (LSM1) and right (RSM1) sensorimotor areas and medial frontal area (MFC) for the ERpow (Fig. 1A). For the ERcor analysis, connections of interest (COIs) were also defined in these three areas, making all pairwise combinations (Gerloff et al. 1998): the LSM1-MFC, LSM1-RSM1, and RSM1-MFC (Fig. 1B). ERpow for each ROI was created by averaging the power of each electrode. Likewise, the correlation from each pair of electrodes was averaged to give ERcor for each COI.

To select an appropriate EEG band for the analysis, mean frequency maps across eight subjects were created for the six rate tasks, in which time was plotted on the x axis with 32-ms bins and frequency on the y axis with 4-Hz bins. For the later analysis, the frequency ranges that showed the decreased ERpow (high activation) and increased ERcor (high coupling) were selected.

To separate uncorrelated patterns in the ERpow and ERcor signals, principal components were computed from the covariance matrix for the alpha and beta ERpow and ERcor, after interpolation to obtain the same number of data sets in the time series for the six rate tasks.

Statistics

To evaluate the difference in performance during the different movement rates, a one-factorial ANOVA with a factor of RATE (6 rates) followed by post hoc t-test with Bonferroni’s correction was done on peak EMG amplitudes, CV of ITI, discrepancy, and mean phase shift from tone to movement.

RESULTS

Behavioral change with increasing movement rate

As shown in Table 1, no main effect of RATE was present for the EMG amplitude (F = 0.22, P = 0.95 by 1-factorial ANOVA), CV of ITI (F = 1.77, P = 0.14), and discrepancy (F = 0.43, P = 0.83). Figure 2A shows the change in movement timing relative to tone with increasing movement rate. For 0.5 to 1 Hz, movements were executed around tone onset (−0.25 to 0.25 cycle: synchronization). By contrast, for 3 and 4 Hz, most movements were performed with a half cycle lag (−0.75 to −0.25 cycle: syncopation). Two-hertz movements were transitional but closer on average to syncopation. Cumulative density analysis (Fig. 2B) clearly separated these two different behavioral patterns, shifting from synchronization to syncopation between 1 and 2 Hz. In the mean phase shift for eight subjects, there was a significant difference between slow and fast rate groups (Fig. 2C), but within each group, no difference was found. Slow and fast movements are likely categorized into synchronized and syncopated motor modes, respectively.

Activation and functional coupling of motor cortical areas in the different movement rates

For all six different movement rates, an event-related change in the ERpow and ERcor was detected in the four frequency bands. With regard to the difference of ERpow between the beta1 (16–20 Hz) and beta2 (24–28 Hz), these two bands were separately distributed in the time-frequency map (Fig. 3, top). The ERpow at beta1 band was most remarkable at the LSM1, whereas the beta2 modulation was more obvious than the beta1 at the MFC and RSM1. Postmovement synchronization (ERS), which is regarded as postprocessing of motor act (Pfurtscheller et al. 1996, 1997; Toma et al. 2000), was present around 20 Hz; the beta1 band accompanying ERS likely reflects motor function. With regard to ERcor, an increase was observed within the beta1 band (Fig. 3, bottom), consistent with the previous studies (Andres and Gerloff 1999). Taking the ERpow and ERcor findings into consideration, we selected beta1 band as an index for motor function in the later analysis.

Figure 4 shows an event-related change in the band-power and correlation in slow (1 Hz) and fast (4 Hz) movements in a single subject. It is noteworthy that, even for the fastest movement (4 Hz), modulation of the activation and coupling are present, although small. Compared with 1 Hz, both activation and coupling were larger and sustained at the 4 Hz rate.

In Fig. 5, mean ERpow (A) and ERcor (B) across eight subjects were time-locked to each movement for the six rates. For all six rates, the largest power decrease at the alpha and beta1 bands was observed at the LSM1; the MFC showed a moderate decrease; and the reduction at the RSM1 was smallest. The largest increase in correlation at the alpha and beta1 bands was seen at the LSM1-MFC, followed by the LSM1-RSM1; and the RSM1-MFC had the smallest correlation. In all ROIs (LSM1, MFC, and RSM1), maximal decrease of ERpow was larger for faster movement rates, particularly 3 and 4 Hz at the LSM1 (Fig. 5A).

In addition, ERpow for 2–4 Hz showed no rebound above baseline (0 level; Fig. 5A). Similarly, ERcor for 2–4 Hz did not return to baseline as a result of the sustained coupling (Fig. 5B). At the alpha band, peaks of the ERpow and ERcor locked to movements were no longer identified for the 3- and 4-Hz rates. The alpha band did not show smooth patterns for both ERpow and Ercor because we selected the time window of 64
ms to focus on beta range rather than alpha. Within a 64-ms window, a half cycle of alpha wave exists, whereas one cycle is present for beta wave. Thus correlation values were better stabilized for beta than alpha, resulting in smoother temporal evolution patterns (Fig. 5).

Sustained elevation for movement rates of 3 and 4 Hz in ERcor was most obviously observed at the LSM1-MFC (Fig. 5B). Moreover, these two areas, the LSM1 and MFC, showed continuous activation for 3 and 4 Hz (Fig. 5A). According to the PCA, EEG findings separated between 1 and 3 Hz, with 2 Hz being transitional. In Fig. 6, distinct patterns in EEG for slow and fast movement were demonstrated by PCA. ERpow at the LSM1 and MFC showed two significant principal components; the first component demonstrated greater and more sustained decrease in ERpow and was associated with 3 and 4 Hz, whereas the second component had a clear temporal modulation, which was strongest with 0.5, 0.75, and 1 Hz. Likewise, ERcor of the LSM1-MFC had two significant components: 3 and 4 Hz contributed to the first sustained component, whereas 0.5, 0.75, and 1 Hz were related to the second component with greater temporal modulation. ERcor of the LSM1-RSM1 and ERpow of the LSM1 and RSM1 showed a similar tendency but were not clearly separated into two PCA patterns, i.e., 0.5–1 Hz and 3–4 Hz. ERcor of the RSM1-MFC and ERpow of the RSM1 and MFC did not show such separate patterns. In all COI and ROI, PCA for the alpha band did not show such two separate patterns of modulations in the ERpow and ERcor.

**DISCUSSION**

Analysis with the event-related EEG band-power and correlation is useful to investigate cortical activation and functional coupling in rapid repetitive movements, allowing simultaneous good time and frequency resolution. By employing event-related EEG band-power and correlation techniques, we comprehensively demonstrated activation and functional linkage of motor cortices associated with each single movement in different movement rates.

Power decreases in both alpha and beta bands generally increased with rate, but the dependence on rate was not absolute (Fig. 5), perhaps because of the small number of subjects in our study. EEG power change in alpha band may reflect predominantly sensory function, whereas beta band EEG

![Figure 2](http://jn.physiology.org/)
power likely correlates with motor function (Salmelin and Hari 1994; Salmelin et al. 1995). In addition, postmovement beta synchronization, which is related to idling or resetting of motor cortices, is seen around 20 Hz (Pfurtscheller et al. 1996, 1997; Toma et al. 2000), again suggesting an important role of 20-Hz rhythm for motor control. With regard to the functional coupling of motor cortical areas, Andres and Gerloff (1999) demonstrated an important role of the low beta oscillation (13–21 Hz). In the present study, we selected low beta band (16–20 Hz) for the analysis and further confirmed its role for motor function.

In the present study, absolute correlation values of movement tasks were from about 0.5 to 0.8. However, control (tone) tasks with no movements also showed relatively high correlation values of about 0.5 probably because of volume conduction effect, especially when the distance between two electrodes is small. In addition, signals from reference electrodes may have contaminated the recordings, leading to relatively high correlation values in control tasks. Thus subtracting the correlation values of a control task from a movement task led to values of approximately 0.2–0.3 (Fig. 4 or 5).

**Task performance**

The most remarkable finding in the task performance was a shift of movement timing relative to an auditory cue from...
synchronization to syncopation between 1 and 3 Hz. For 0.5–1 Hz, movements were near the tone, and each movement was individually controlled. For 3 and 4 Hz, movements were performed with about a half-cycle lag; i.e., syncopation. The syncopated operation implied that the rhythm of movements rather than each individual movement may be controlled in the fast-rhythmic operation. In fact, the subjects had no time to prepare for the next movement in response to a rapidly presented cue because a couple of hundred milliseconds are needed to react to an external cue (Evarts et al. 1981; Wilson 1925).

In the study by Mayville et al. (1999), subjects were instructed to repeat index finger flexion, keeping 1:1 relationship
with tones in syncopated (anti-phase) manner. They found a spontaneous switch of motor modes from syncopation to synchronization at about 2 Hz. Instruction of our study was different: the subjects were asked to just keep pace with tone; the subjects were neither requested to execute movements coincident with the tones nor in anti-phase manner. Thus the subjects may have implicitly chosen their own strategy to conduct the different rate movements, and the results showed a change in behavior from synchronization to syncopation between 1 and 3 Hz. In both studies, 2 Hz seems to be the critical rate for transition between different strategies to time movement with an external cue.

Task difficulty measured by the coefficient of variation (CV) showed no significant difference among six rate tasks; error was the same for all six rates, i.e., about 10% of nominal ITIs. In addition, muscle force as assessed by EMG did not change for the six rates. Therefore it is unlikely that parameters such as task difficulty and muscle force may have affected difference in the behavioral and EEG findings, although the possibility that movement amplitude, velocity, or acceleration may have

![PCA Diagram](image)

**FIG. 6.** Principal component analysis (PCA) for activation and coupling of LSM1 and MFC. Both activation (ERpow) and coupling (ERcor) show 2 significant components: 1 with clear modulation locked to movements is associated with 0.5- to 1-Hz movements, whereas the other sustained component is linked to 3 and 4 Hz with 2 Hz being transitional. SD of eigenvector of 8 subjects is shown, and the rate that exceeded the SD was regarded as significantly contributing to each principal component.
Movement rate effect on motor cortical activation

Dampening in the EEG band power and subsequent rebound above the baseline are called event-related desynchronization (ERD) and synchronization (ERS), respectively (Chatrarian et al. 1959; Gerloff et al. 1998; Pfurtscheller et al. 1997; Toma et al. 2000; Toro et al. 1994); ERD represents cortical activation, whereas ERS is regarded as a transient cortical idling or resetting. For the ERPs in slow-repetitive movements, activation (ERD) of the motor cortical areas was immediately followed by transient deactivation (ERS). In contrast, for fast-repetitive movements, motor cortical areas showed continuous activation without deactivation.

In neuroimaging studies, two types of rate-dependent activation of the contralateral SM1 have been described. Rao et al. (1996) and Schlag et al. (1996) observed a linear relationship between percent change in MR signal intensity and tapping rates between 1 and 5 Hz, corresponding with the PET study by Blinkenberg et al. (1996). Similar to our findings of a stepwise change are the PET and fMRI results from Sadato et al. (1996) and Jäncke et al. (1998).

Regarding the SMA, rate-dependent activation was unclear in previous studies using fMRI (Schlag et al. 1996) as well as PET (Blinkenberg et al. 1996; Sadato et al. 1996). The anterior part of the SMA, or pre-SMA (Luppino et al. 1993), is more activated during complex movement tasks (Kawashima et al. 1999; Picard and Strick 1996). Multiple features, such as movement complexity and additional motor demands accompanying movement rate tasks, may involve activation of the pre-SMA and probably caused inconsistent findings with regard to SMA activation in these previous studies. The present study, with similar task difficulty among the different rates, showed positive dependence of the MFC activation with movement rates.

Movement rate effect on motor cortical coupling

In the present study, for slow repetitive movements functional coupling between the motor cortical areas was immediately followed by transient decoupling. By contrast, motor cortical areas, particularly contralateral SM1 and MFC, showed sustained coupling for fast-repetitive movements, suggesting less attention to each individual movement.

With the Fourier transform algorithm that has been frequently used to measure cortical functional coupling in the frequency domain (Busk and Galbraith 1975; Sklar et al. 1972), time resolution is incompatible with frequency resolution. For example, to obtain data every 64 ms, the frequency resolution is considerably reduced to about 16 Hz, making it impossible to distinguish alpha and beta bands. By contrast, the present event-related correlation analysis in the time domain enabled us to see dynamic cortical coupling and decoupling associated with rapid repetitive movements by setting up the compatibility of high-temporal (64-ms time window with shifting step of 32 ms) and high-frequency (4 Hz) resolution. With this technique, a change in cortical oscillation, though small, was observable even for the 4-Hz movement, which is indicative of a dynamic ability of cortex to respond to a rapid repetitive task. Even though rCBF is saturated at 2-Hz movement as reported in a previous PET study (Sadato et al. 1996), it does not imply that a cortical response reaches steady-state in an electrophysiological measurement.

Phase difference between signals from two cortical sites during functional tasks is typically reported as being nearly zero in field potential measurements (Bressler et al. 1993; Roelfsema et al. 1997) as well as in human scalp EEG (Rodriguez et al. 1999; T. Matsuoka, T. Mima, K. Toma and M. Hallett, unpublished observations). Correlation is more sensitive to a phase difference than coherence and thus is very sensitive to detect modulation in cortical coupling associated with rapid repetitive movements. The fact that cortical oscillations of the motor areas have nearly zero phase suggests the possibility that the deep structure like thalamus may synchronously drive these motor cortical areas, or alternatively, global synchronization involving motor cortico-cortical networks may be present (Lopes da Silva et al. 1980; Roelfsema et al. 1997).

Dual motor control modes in separate rate ranges of movement

The fact that both task performance and EEG findings fell into two categories between movement rates of 1 and 3 Hz appears to relate behavior and neural mechanisms (Freund and Hefter 1993; Kunesch et al. 1989; Logigian et al. 1991; Mayville et al. 1999). For a movement rate of less than 1 Hz, deactivation and decoupling are presumably needed for cortical idling to execute next movement so that the brain controls each individual movement separately. For movement rates of 3 Hz and more, activation and decoupling are absent, suggesting that motor cortices are not reset to prepare for the next movement; the brain may not control each individual movement separately but rather the rhythm of movements. This fact may be reflected in the task performance, where movement was conducted as coinciding with tone (sensory guidance) for slow-repetitive movements but it was carried out as syncopating with tone (sensory monitoring) for fast-repetitive movements.

Some studies suggested that two separate time-keeping systems with preferred rates are present in the brain. By means of optoelectronic movement recording system, Kunesch et al. (1989) showed that manipulative finger movements involved in active touch as performed during object exploration cluster around low frequencies (1–2 Hz). In contrast, movements of the hand and fingers such as writing, typing, or hammering are executed at distinctly higher frequencies (4–8 Hz). The two types of sensorimotor integration, sensory guidance and sensory monitoring, are likely involved in the different movement frequencies. However, it may be also true that two motor modes represent a continuum of possible performances rather than distinct categories. Slow and fast rhythmic operations overlap and can be transformed voluntarily and gradually into each other.

Studies in patients with neurodegenerative conditions and aged individuals indicate that neural mechanisms may differ between slow and fast rhythmic movements. Parkinson’s disease patients can produce auditory-paced frequencies of 1 and 2 Hz, but at higher cue frequencies, their movements are slower or faster (“hastening phenomenon”) than the cue (Logigian et al. 1991). Slowness during fast repetitive movement

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was also reported in aged people (Nagasaki et al. 1988). In Huntington’s disease, rapid repetitive movement becomes irregular at about 4 Hz (Heftel et al. 1987).

It is known that humans make rhythmic movements at two preferred frequencies, but the physiology of this has not been understood. Using EEG methods to explore cortical activity, we discovered that the brain uses two different mechanisms in the two different frequency ranges. In addition, the present study has value in the technical dimension because it shows the two different frequency ranges. In addition, the present study has value in the technical dimension because it shows the frequency content of common synaptic inputs to motoneurons studied during voluntary isometric contraction in man. J Physiol (Lond) 470: 127–155, 1993.


