

RESEARCH ARTICLE

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The role of synchrony and oscillations in the motor output

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Abstract There is currently much interest in the synchronisation of neural discharge and the potential role it may play in information coding within the nervous system. We describe some recent results from investigations of synchronisation within the motor system. Local field potentials (LFPs) and identified pyramidal tract neurones (PTNs) were recorded from the primary motor cortex of monkeys trained to perform a precision grip task. The LFPs showed bursts of oscillatory activity at 20–30 Hz, which were coherent with the rectified electromyographs (EMG) of contralateral hand and forearm muscles. This oscillatory synchronisation showed a highly specific task dependence, being present only during the part of the task when the animal maintained a steady grip and not during the movement phases before or after it. PTNs were phase-locked to LFP oscillations, implying that at least part of the coherence between cortical activity and EMG was mediated by corticospinal fibres. The phase locking of the PTNs to LFP oscillations produced task-dependent oscillatory synchronisation between PTN pairs, as assessed by the single-unit cross-correlation histogram. Recordings were also made from normal human subjects performing a precision grip similar to that used in the monkey recordings. Pairs of EMGs recorded from intrinsic hand and forearm muscles showed 20–30 Hz coherence, which modulated during task performance, being present only during periods of steady contraction. We suggest that these changes in EMG-EMG synchronisation reflect changing levels of synchronous drive from the corticospinal system. The generation of oscillations in the cortex is discussed in the light of results from a model of local cortical circuits. Other modelling work has shown that synchrony in the corticospinal inputs could act to recruit motoneurons more efficiently, producing more output force from a

muscle than asynchronous inputs firing at the same mean rate. A speculative hypothesis is presented on the role of synchronous oscillations in the motor system, which is consistent with experimental observations to date.

Key words Motor cortex · Monkey · EMG · Synchrony · Oscillations

Introduction

One hypothesis has dominated most neurophysiological research in the last fifty years. This is the assumption that the firing rate of a neurone codes the information transmitted and processed by that cell. However, more recent work has suggested an alternative to such rate coding: that the precise timing of cell discharges codes information (Abeles et al. 1993; Softky 1994; Mainen and Sejnowski 1995; Bair and Koch 1996). Such exact timing is defined relative to other spikes, either from the same cell (i.e. the inter-spike intervals are informative) or from other cells. There has been considerable debate in the recent literature over whether neurones should be seen as integrators of noisy, firing-rate input (Shadlen and Newsome 1994) or as sensitive detectors of precisely patterned input, being especially sensitive to spikes synchronised with millisecond accuracy (Softky and Koch 1992). In the latter view, the variability in cell discharge is not noise, but signal. In fact, these two possibilities represent not mutually exclusive possibilities, but extremes of an entire spectrum, depending on the accuracy with which spikes are detected (Rieke et al. 1997).

Work in the visual system has presented the most convincing evidence for a role of neuronal synchronisation in information processing. The known firing properties of cells in the visual cortex are best understood in terms of feature extraction, with different, parallel systems responding to orientation, motion and colour. Once an image has been decomposed into the constituent features, the problem remains of reconstructing a coherent whole from the disparate features. A number of groups have

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shown (see Singer and Gray 1995 for a review) that synchronisation between cells seems capable of solving this “binding” problem. Such synchronisation is often accompanied by oscillations at around 40 Hz; the oscillations become phase-locked between different cell populations to signal object binding.

In the motor system, there has been less work on neuronal synchronisation, perhaps because no clear hypothesis concerning its function has been proposed. In this article, we describe some recent results from our laboratory that address the functional significance of synchrony, and synchronous oscillations, in the motor cortex.

Materials and methods

Task

The motor task used in all of the experiments, with modifications as appropriate, was the precision grip task of Lemon et al. (1986). The manipulandum consisted of two spring-loaded levers, which were gripped by the finger and thumb in a classical precision grip posture (Napier 1980). The position of each lever was independently measured by potentiometers. Visual (human experiments) or auditory (monkey experiments) feedback of the lever position was provided to the subject, whose task was to maintain the levers within a target zone for a given time (the “hold period”). In over ten years of experience in using this type of manipulandum, we have gained considerable knowledge of the firing properties of identified corticospinal and cortico-motoneuronal cells during performance of this task in the monkey. Lately, our work has begun to address the role of synchrony in this task performance.

Multiple site recordings in awake behaving monkeys

We have recently established a multiple electrode recording laboratory, permitting us to record from up to 16 sites in the motor cortex simultaneously. This uses the Eckhorn microdrive (Eckhorn and Thomas 1993), which permits 16 glass-insulated platinum electrodes (diameter 80 μm) to be inserted into the cortex in a 4x4 grid with an inter-electrode spacing of only 300 μm . Each electrode can be independently positioned. The signals are amplified and filtered into two separate components; one, with bandpass from 10–250 Hz, yields the local field potential (LFP); the other, from 1–10 kHz, gives single-unit spikes. Neurones are identified during the experiment as pyramidal tract neurones (PTNs) by antidromic activation following stimulation through electrodes chronically implanted in the pyramidal tract (PT) at the medulla (Lemon 1984).

Simultaneous recording of large numbers of units in an awake behaving monkey presents considerable difficulties. Firstly, the time taken to position the electrodes next to cells may be so long that the patience of the experimental animal is exhausted before recordings can begin; in chronic monkey work, nothing is achieved without the co-operation of the animal. Secondly, monitoring activity on all channels simultaneously, and ensuring that it remains stable, with recordings from the same cell throughout, is beyond the processing capabilities of a single human operator. Finally, the sheer complexity introduced by multiple channels can easily lead to errors, such as moving the wrong electrode by mistake.

We have overcome these problems by designing a novel suite of computer software through which the entire experiment is controlled. A single PC, running the Windows operating system, displays the signals from each electrode, sets the pyramidal tract stimulation parameters and moves the electrodes. In such a system, errors due to confusing channels are rarely made, since an electrode is moved by clicking with a mouse on the window dis-

playing the signal. In this way, the experimenter is freed of much of the tedious detail of running the experiment.

In order to expand the number of channels which can be recorded simultaneously, this main control PC is networked to a number of “slaves”. These duplicate its functionality, displaying the signal from all channels and permitting the movement of any electrode. In our experience, a single experimenter can successfully monitor no more than two or three channels which have cellular activity on them. By using up to five such networked computers, each manned by a human operator, we have been able to record high quality data using the full 16 electrode array. Cells can be found rapidly at the start of a session, and small movements can be made during a recording to maintain stability. Although highly labour intensive, without such a system it would be impossible to find and maintain such a large number of channels of single-unit activity.

We aimed to record the activity of as many identified PTNs as possible. Antidromic identification (Evarts 1968; Lemon 1984) is of enormous value in permitting multiple single-unit recordings. Sudden movements of the animal can often cause changes in the size or shape of a recorded action potential. Following such changes, the PT stimulus can be briefly turned on. If the new potential responds with the same antidromic latency and current threshold, it is almost certain to be the same cell as was recorded before. A collision test (Lemon 1984) demonstrates that the tonic firing activity is composed only of the cell antidromically responding to the PT stimulus. The availability of such a rapid check that recordings have remained stable is invaluable.

Finally, in many single-unit recording laboratories, it is common practise to pass action potentials through a threshold crossing detector, and to digitise only the time of occurrence of the threshold crossings. When recording from 16 channels, it would be impossible to be certain of good discrimination on all electrodes throughout the recording. Therefore, we record the analogue waveform of all channels at a high sampling rate (24 kHz) using a 32-channel tape recorder (RX832, TEAC). The data can be transferred off-line to a PC, where spike discrimination is performed by customly written software using principle component and cluster analysis (Gerstein et al. 1983; Eggermont 1990). In this way, not only do we achieve high confidence in the unitary nature of discriminated spikes, but it is also often possible to discriminate several potentials from the recording of one electrode on the basis of differences in shape and amplitude. However, such software can never produce clean discrimination unless cells have clearly different action potentials with a high signal-to-noise ratio. Thus, careful monitoring of the recording on-line, with adjustments to the electrode position as necessary, is essential for success.

Results

Task dependence of motor cortical oscillations

It has been known for some time that the sensorimotor cortex can produce oscillatory activity in the 20–30 Hz range (Adrian and Matthews 1934). This can be seen in invasive surface recordings in animals and humans (Penfield 1954) and in non-invasive electroencephalographic (EEG) and magnetoencephalographic (MEG) recordings in man (Conway et al. 1995; Pfurtscheller et al. 1997; Salenius et al. 1997; Halliday et al. 1998), where it is commonly called the “mu” rhythm. Such field-potential oscillations represent synchronous oscillatory activity in a large number of cortical neurones. In such recordings, asynchronous activity is lost due to cancellation. We have investigated the task dependence of this rhythmic activity in monkeys trained to perform the precision grip task (Baker et al. 1997); an example of the results of this study is shown in Fig. 1.

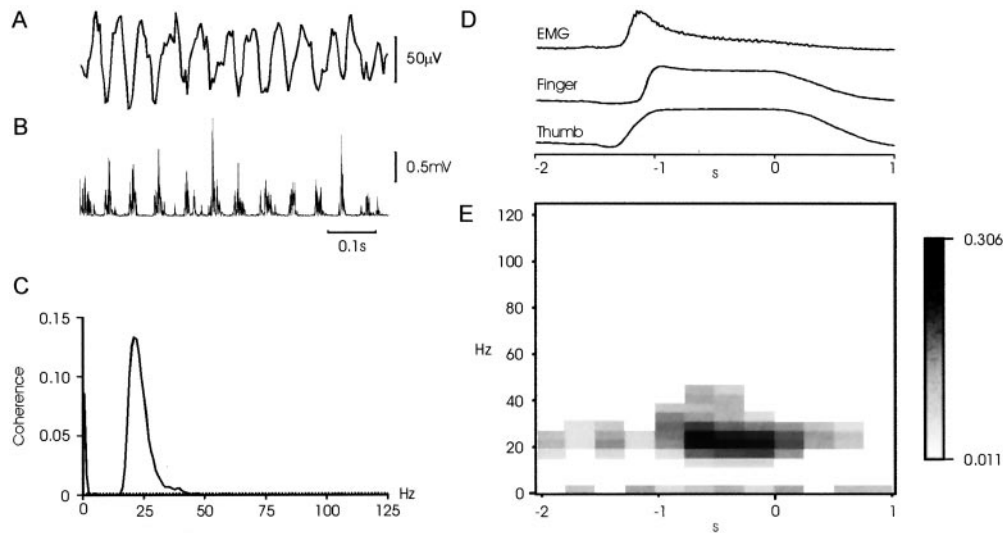


Fig. 1. **A** Cortical slow-wave recording from primary motor cortex of a macaque monkey performing a precision grip task. **B** Simultaneously recorded rectified electromyograph (*EMG*) from the adductor pollicis muscle. Clear oscillations can be seen in the cortical recording, which are phase-locked to bursts in the *EMG*. **C** The coherence calculated between slow-wave and rectified *EMG*, using all data available from one recording session. The peak around 25 Hz indicates consistent phase locking between the two signals in this frequency band. The dotted line just above abscissa is the theoretical significance level for the coherence ($P < 0.05$). **D** Variation during the task of the rectified adductor pollicis *EMG* and the finger and thumb lever-position signals. Analysis has been time-locked to the end of a successful hold period of the precision grip task (0 s). **E** Variation in coherence with task performance. The abscissa shows time during task performance. The ordinate shows coherence frequency. The grey scale indicates how the coherence between cortical signal and *EMG* varies with time, using the scale on the right. **D** and **E** averaged from 274 successful trials of the task

Figure 1A shows a short section of LFP recording from an electrode placed in the hand area of the motor cortex. Such recordings frequently showed bursts of oscillations at around 20–30 Hz. In Fig. 1B, a simultaneously recorded rectified electromyograph (*EMG*) from the adductor pollicis muscle is shown. Clear bursts could be seen in the *EMG*, which appeared to be synchronised with the cortical LFP. In Fig. 1C the coherence between LFP and *EMG* is plotted. Coherence is a measure of correlation between two signals in the frequency domain; it is mathematically bounded between zero and one (Rosenberg et al. 1989). A peak in coherence is visible in Fig. 1C, which rises above the theoretical significance level (shown by a dotted line) for frequencies around 25 Hz. This is in agreement with previous work measuring coherence between MEG or EEG and *EMG* in man (Conway et al. 1995; Halliday et al. 1998) or which has shown that averages of *EMG* triggered by cycles of LFP oscillations exhibit damped oscillations (Murthy and Fetz 1992).

The calculation of Fig. 1C used all available data from one recording session. It was, however, of interest to determine whether the oscillations showed any task-

dependent modulation. Figure 1E presents an analysis of this question. The data were divided into small sections aligned to the end of the hold period in our task. Coherence was then calculated separately for all sections with a given timing relative to this, averaging across trials. This produced a time-frequency map of coherence, displayed using a grey scale. For reference, Fig. 1D presents averaged rectified *EMG* and the finger and thumb lever-position signals over the same time period as that used for Fig. 1E. The 20–30 Hz coherence peak was limited to the central part of the task, when the animal was holding the levers in the target zone and waiting for the reward signal.

The coherence demonstrated in Fig. 1C indicates that oscillatory activity can be propagated from cortex to the *EMG* of contracting contralateral muscles. A strong candidate for transmission of oscillatory activity is the corticospinal pathway, which makes monosynaptic corticomotoneuronal connections in primates (Porter and Lemon 1993). Evidence for involvement of the corticospinal tract is shown in Fig. 2. The peaks of LFP oscillations in the cortex were identified, and histograms constructed of the timing of simultaneously recorded PTN spikes relative to the oscillation phase (Pinches et al. 1997). Figure 2A gives two examples of such histograms. The cells discharged throughout the cycle, but with a clear sinusoidal modulation. This was quantified by fitting a cosine curve. The distribution of the phase of peak firing (Fig. 2B) and the strength of phase locking (Fig. 2C) are plotted for 11 PTNs. The mean phase of PTN cell firing was 10.9° . The phase locking strength was quantified as the ratio of synchronised to unsynchronised spikes. PTNs were strongly phase-locked to the oscillations, with a mean ratio B/A (defined in Fig. 2C) of 0.32.

The finding that PTNs are phase-locked to cortical oscillations, which are themselves coherent with contralateral *EMGs*, implies that an oscillatory synchronisation should be seen in spike-triggered averages of rectified *EMG*, and this has been demonstrated (Baker et al. 1997). Such effects are, however, weak and should not

Fig. 2. **A** Example of phase locking of two pyramidal tract neurones. Cell discharge during periods of oscillation is plotted versus oscillation phase, Θ , in 10° bins. The *line* shows a best fit curve: $A+B \cos(\Theta+\Phi)$. **B** Distribution of the phase of maximum cell discharge, Φ , across the same population. **C** Distribution of the ratio of synchronised to asynchronous spikes, B/A , in a population of 11 cells. The *inset* shows graphically the interpretation of this ratio

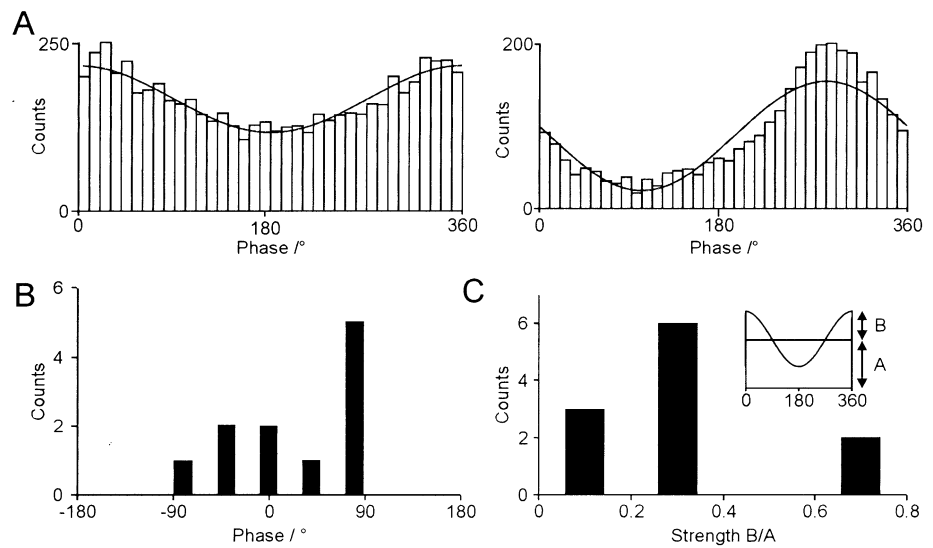
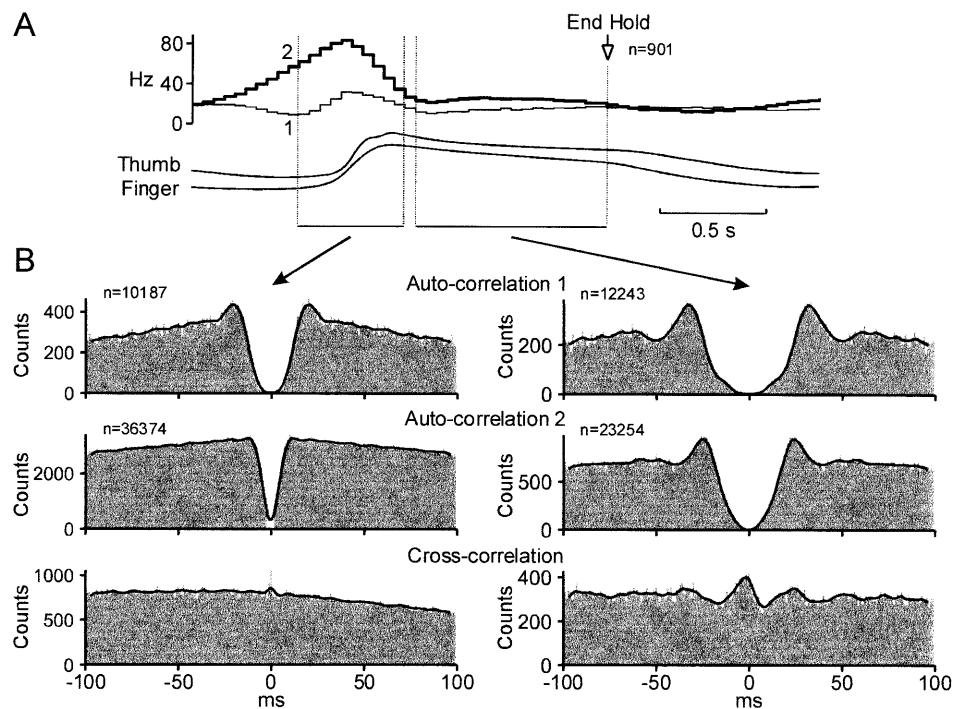


Fig. 3A, B Example of modulation of synchrony between pyramidal tract neurones (PTNs) during task performance. **A** Firing rate of two PTNs (labelled 1 and 2) during the precision grip task. Histograms have been aligned to the end of the hold period (*open arrow*) and are averages from over 901 trials. *Beneath* are shown averaged finger and thumb lever-position signals. **B** Auto- and cross-correlation histograms selectively compiled using spikes from the movement and hold phases of the task (periods shown by *dotted lines* in **A**). The *overlain lines* are smoothed versions of the histograms. Cell 1 shows a tendency towards oscillatory discharge in both periods, although at a higher rate during the movement phase; cell 2 oscillates only during the hold phase. The cross-correlation in the movement phase shows a narrow central peak, whereas in the hold there is a broad central peak with oscillatory side lobes

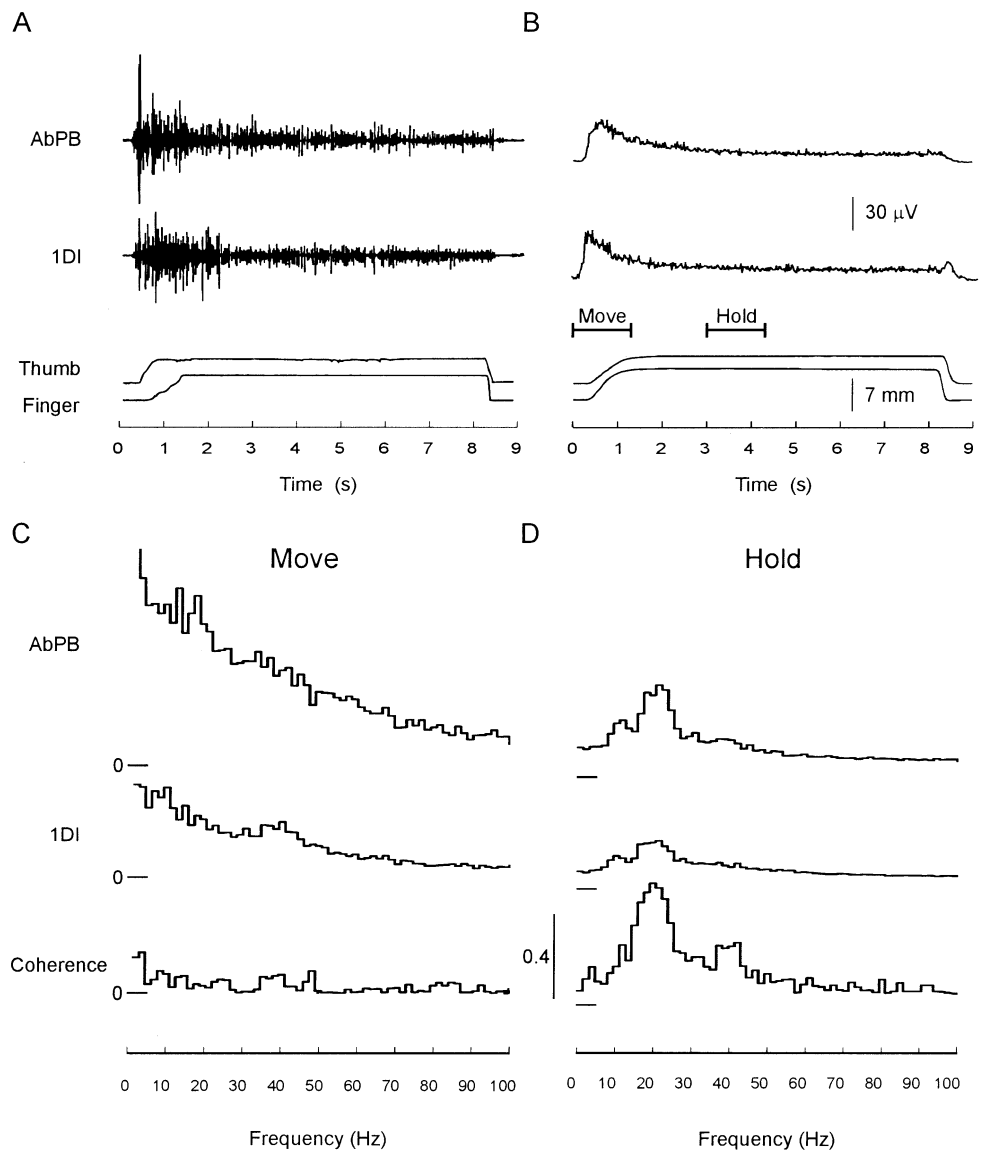


be confused with the narrower, stronger post-spike facilitation which is used to identify cortico-motoneuronal (CM) cells (Fetz and Cheney 1980; Lemon et al. 1986; Baker and Lemon 1998).

If many PTNs become phase locked to 20–30 Hz oscillations during the hold phase of the precision grip task, they must necessarily fire synchronously with each other (Murthy and Fetz 1996b). This will have the effect of changing the cross-correlation between cell pairs, depending on the part of the task analysed. Figure 3 indicates that this is indeed the case and that profound task-dependent changes in PTN-PTN synchrony can occur. Figure 3A presents the modulation in firing rate of two PTNs with task performance. This has been calculated

aligned to the end of the hold phase of the precision grip task and averaged over a large number of trials. Both cells showed a considerable increase in their firing during the initial movement of the levers into target, followed by a lower, tonic level of firing during the hold. Figure 3B shows the auto-correlation and cross-correlation histograms, calculated separately for spikes falling in each of these two periods. Cell 1 showed a tendency towards periodic discharge in both regions, although at higher rates in the movement than in the hold phase. Cell 2 had periodic discharge only during the hold. The cross-correlation histogram calculated during the movement had a narrow central peak, consistent with a branched fibre common input to the two cells which was active at

Fig. 4. **A** surface electromyograph (EMG) and the positions of finger and thumb levers during one trial of the precision-grip task performed by a human subject with visual feedback of lever position on a computer screen. *AbPB* Abductor pollicis brevis, *1DI* first dorsal interosseous. **B** Rectified EMG and lever position signals averaged over 50 trials, aligned to the trial onset. The bars define two analysis periods: “Move” and “Hold”. **C, D** Power spectra for each EMG recording, and coherence between them, for the “Move” and “Hold” periods of the task. Peaks around 20 Hz are clearly visible in all measures in **D**, but not in **C**



this time (Perkel et al. 1967). By contrast, the hold phase histogram showed a broad central peak, with oscillatory side lobes, presumably caused by phase locking of both cells to the global motor cortical rhythm. Similar synchronisation of motor cortical cells during periods of cortical oscillatory activity has also been reported by Murthy and Fetz (1996b).

Non-invasive recordings in humans

An important finding in our work in monkeys has been that time-resolved measures of coherence derived from pairs of EMG recordings from different muscles show a similar task dependence to that seen between cortical LFP recordings and EMG. This presents the opportunity to study task-related changes in oscillations in more detail in man using nothing more invasive than surface EMG recordings.

Figure 4 shows the result of an experiment with a single human subject. EMGs were recorded from two intrinsic hand muscles whilst the subject performed the precision grip task with a longer hold period than used in the monkey experiments. Figure 4A illustrates raw data from one trial of this task, with data averaged across 50 trials presented in Fig. 4B. Two sections, of 1.28 s duration, were defined from these averages and are designated “Move” and “Hold” in Fig. 4B. Data from these two periods were analysed separately across trials. Figure 4C and D show the power spectrum of each EMG and the coherence between them. Neither power spectrum shows a peak at 20 Hz during the movement period, whereas this is clear for those calculated during the hold phase. There is also high coherence between the two signals at this frequency in the hold phase, showing that a proportion of power at this frequency results from a common input to the motoneurone pools.

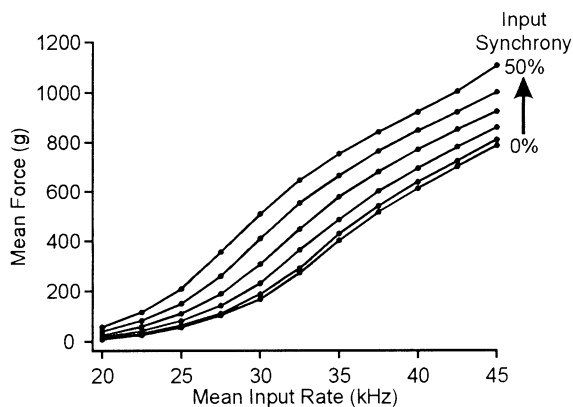


Fig. 5 Effect of input synchrony on the force output of a simulated muscle and motoneurone pool. Input was quantified as the mean number of 100- μ V EPSPs arriving at a motoneurone per second. Higher force is produced at a given rate with increased synchronisation in the input

Data from non-invasive work in man therefore agrees with recordings in the monkey in showing that 20–30 Hz motor rhythms are confined to periods of steady contraction and are abolished during movements.

Computer modelling

Role of oscillations

It is tempting to view synchronisation at the cortex as solely subserving a role in *cortical* processing. However, the data of Figs. 2 and 3 demonstrate that the cortical output to the pyramidal tract is itself considerably synchronised during periods of oscillations. It is well known that a synchronous input can be more efficient in recruiting the cells to which that input projects than an asynchronous input (see Abeles 1991; Murthy and Fetz 1994) – indeed, this is the main reason for the current interest in cortical synchrony. It is then of interest to determine what effect the synchrony in the descending cortico-motoneuronal fibres might have on motoneurone recruitment.

This issue has been addressed using a computer model (Baker 1997). It simulates a pool of biophysically realistic motoneurones, which, following their discharge, generate motor-unit action potentials and twitch forces. The action potentials, when summed, produce a simulated EMG, and the twitches sum to produce a total force output of the muscle. The model has been successfully used to investigate the contribution of cortical synchrony to the production of post-spike facilitation in spike-triggered averages of rectified EMG (Baker and Lemon 1998).

Figure 5 shows the results of simulations which sought to determine the effect on motor output of a synchronous, descending command to the motoneurone pool. Input to the motoneurones consisted of simulated EPSPs. The number of EPSPs per time step was Poisson

distributed, with a mean which varied sinusoidally with time at 25 Hz. The ratio of synchronous to asynchronous spikes was calculated as in Fig. 2D and expressed as a percentage. Figure 5 shows the force output produced by the simulated muscle, as a function of the mean rate of input. The different curves present the results for simulations with varying amounts of input synchrony. It can be seen that the presence of synchrony in the descending input markedly increases the force output for a given input. Thus, the use of a synchronous descending command could be a means by which a given force could be produced with as low an input firing rate as possible.

If synchronisation and firing rate together determine the force which a muscle produces, it would be possible to explain one otherwise puzzling finding from the literature. In a study which correlated CM cell discharge rate with force produced during a steady isometric precision grip, Maier et al. (1993) showed that 18% of the CM cells *decreased* their firing rate with *increasing* force. Similarly, Cheney and Fetz (1980) demonstrated that some CM cells decrease their firing rate during a constant force hold. If the decreased firing rate coincided with increasing synchrony, the product could still be the observed maintained, or even elevated, force level.

Source of oscillations

Oscillations are a feature commonly seen in cortical activity, both in visual and motor areas. The mechanisms by which such local oscillatory activity can be generated are as yet unknown. Gray and McCormick (1996) recorded from a population of cortical pyramidal neurones in visual cortex which they termed “chattering cells”. These cells had intrinsic membrane properties which led to periodic bursting behaviour, with the inter-burst frequency ranging from 20–70 Hz. These cells could, therefore, play a role in the generation of the 40 Hz oscillations seen in visual cortex. It is not known whether such cells are found in motor cortex or whether their intrinsic frequency is lower to be appropriate for the slower oscillations commonly encountered there.

An alternative way in which oscillations could be produced is by the cooperative activity of the cortical network. A recent modelling study, partly from our laboratory (Pauluis et al. 1998), has shown that a realistic network of cortical neurones can produce local oscillatory activity in response to aperiodic input. The generation of oscillations is crucially dependent on the activity of the inhibitory interneurones, which appear to pace the activity of the whole network. In networks where inhibition is weak, oscillations are unstable and will soon die away. Changes in the inhibitory conduction delays, and in the time course of IPSPs, both affected the frequency of the network oscillations. By contrast, the excitatory cells do not seem so critical. Networks wholly without pyramidal cells could produce stable oscillations, although they required a stronger external driving input. Changes to excitatory parameters did not greatly influence the

network frequency. These results agree with the modelling work of Bush and Sejnowski (1996) and Wang and Buzsáki (1996) using smaller networks, as well as the experimental work of Traub et al. (1996), and suggest an important asymmetry between excitatory and inhibitory cell populations. It is, of course, likely that both intrinsic cell properties and network dynamics function together to generate local circuit cortical oscillations.

Discussion

In considering the functional importance of motor cortical oscillations, it is tempting to attempt parallels with the visual system, where experimental and theoretical evidence is accumulating in favour of the idea that they act to subserve binding of the disparate features of the visual scene into a unified percept. As in the visual system, the motor system is characterised by a number of different cortical areas, which are to some extent specialised for different functions. It is possible that synchronous oscillations are used, as in the visual cortex (Engel et al. 1991), to permit reliable communication between different motor areas (Donoghue et al. 1998). There may be useful parallels between the synthetic functions of the visual and motor cortices; however, the motor cortex also has an important analytic role. It must convert a unified, goal-directed motor plan into the temporal activity of the many muscles which must carry it out.

Even within the motor system, care must be taken not to consider synchrony, and synchronous oscillations, as a single phenomenon performing one function. Our work on oscillations in the motor system has focused on the 20–30 Hz band, although oscillations can also be seen at 8–10 Hz (Vallbo and Wessberg 1993) and 40 Hz (Piper 1907; Brown 1996) in the motor output; sometimes, the three frequency bands occur simultaneously (McAuley et al. 1997). In addition, there is a range of pathological tremors seen in clinical practice, which tend to occur at low frequencies (below 6 Hz; see Deuschl et al. 1996 for a review). At the cortex, oscillations at around 10 Hz (Pfurtscheller and Neuper 1992; Toro et al. 1994b; Stancak et al. 1997) and 40 Hz (Pfurtscheller and Neuper 1992; Salenius et al. 1996) can be seen as well as the 20–30 Hz oscillations discussed here. Finally, 20–30 Hz cortical oscillations may not be caused by a single generator. Pfurtscheller et al. (1997) provided evidence that one component of the 20 Hz EEG recorded over sensorimotor cortex was motor in origin, whilst another was a harmonic of 10 Hz rhythms, thought to originate from somatosensory cortex (Salmelin and Hari 1994; Salenius et al. 1997).

The existence of two distinct types of 20 Hz rhythm in sensorimotor cortex could explain the apparent contradiction between data from different laboratories on their task dependence. On the one hand, we have shown that 20 to 30 Hz oscillations appear most strongly during the hold phase of the precision grip task and disappear

during movements. This agrees with much former work: just before movement, there is an “event-related desynchronisation” of the EEG and MEG in this frequency range (Toro et al. 1994a; Pfurtscheller et al. 1996; Salenius et al. 1997; Manganotti et al. 1998). Donoghue et al. (1998) similarly showed oscillations predominantly confined to the period before a movement was produced. Pfurtscheller et al. (1996) demonstrated a post movement synchronisation of EEG following movements, which they interpreted as a sign of “idling” in the motor cortex.

By contrast, Murthy and Fetz (1992; 1996a) reported that oscillations occurred when the monkey performed fine manipulative movements with the hand in the absence of visual feedback. The existence of two fundamentally different types of 20 Hz oscillations might explain these apparently conflicting findings. Oscillations in somatosensory cortex have been proposed to play a role in texture discrimination by acting as a “phase-locked loop” (Ahissar 1998); the rhythms seen in motor cortex during fine manipulative movements (Murthy and Fetz 1992; 1996a) could be similar to these and perhaps permit efficient communication between somatosensory and motor cortices. By contrast, the oscillatory activity which we and others have seen, which is abolished on movement, may have a more purely motor function. It is quite possible that multiple underlying phenomena may be responsible for activity which overtly appears similar in electrophysiological recordings.

Toro et al. (1994b) showed that, whilst there were clear changes in 8–12 Hz power in the EEG when subjects made multi-joint arm movements, the power at 20–30 Hz remained unchanged. There was no event-related desynchronisation as in other studies. This may reflect a particular role for 20–30 Hz oscillations in the control of distal movements; it is worth noting that in this study, whilst subjects produced movements of a joystick by proximal muscle activation, they gripped the joystick itself with the hand in a steady manner throughout.

The concept of cortical oscillations as an “idling” rhythm (Pfurtscheller et al. 1996) is difficult to apply to motor control. In our task, the subjects, both human and monkey, were not at rest, but actively maintaining the levers of the precision grip manipulandum in a target window. In the task of Donoghue et al. (1998), oscillations were seen before the trained movement was produced; however, during this time, the animal was required to maintain a stable position with the hand. The important distinction would, therefore, appear to be between static and dynamic phases of motor performance. The question then arises as to what functional role such oscillations could play and why they are confined to periods without dynamic movements. One possibility could be the following speculative hypothesis.

The simulation data presented in Fig. 5 demonstrate that an oscillating descending command is more efficient at recruiting motoneurons, in the sense of requiring the lowest input firing rate for a given output. However, the output neurones of the cortex are deeply embedded in

the network by a dense array of interconnections. If they are to show oscillatory, highly synchronous firing, then so must most of the surrounding motor cortex. Synchronous oscillations of the entire network are, in such a view, a by-product of the use of an oscillating descending command.

Such widespread oscillations will have a considerable effect on cortical processing, since each cell will tend to fire at one defined phase of the oscillations (Fig. 2). This will limit the range of times over which spikes can fire, reducing the amount of information that can be carried. Viewed from an information-theory point of view, an oscillatory firing pattern is highly predictable, and, thus, the "surprise" value of the signal is limited. It is possible that this reduction in cortical processing capacity is unacceptable, except during periods of low computational load. At the start of the precision grip task, the subject must shape the hand, grasp the levers and move them correctly into the target zone; at the end, the levers must be released and the hand removed from the manipulandum. The processing required for this may exceed that which can occur in the presence of synchronous oscillations. By contrast, during the hold period, all that is required is the maintenance of the steady motor output established early in this period. The information processing which this needs may be low enough to permit simultaneous oscillatory activity, with the concomitant increase in efficiency of motoneurone recruitment that an oscillatory descending command gives. Such an hypothesis is in agreement with our observations on the task dependent modulation of 20–30 Hz oscillations, both in monkey and in man (Figs. 1, 3 and 4).

In conclusion, our recent results, and those of other laboratories, from monkey chronic recording, human non-invasive studies and computer simulation could be explained if there is a moment-by-moment trade-off between synchronous oscillations with efficient output on the one hand, and high processing capacity on the other. However, a number of points require further investigation and clarification. The first is the finding that the phase at which PTNs fire during the oscillations shows some variability, although its mean is close to 0° (Fig. 2C). We would expect different cortico-motoneuronal cells with convergent inputs to the same motoneurone pool to fire in a more tightly phase-locked manner, if synchrony is to act to recruit motoneurons efficiently. This clearly needs more extensive investigation in a larger population of cells than we have analysed in our preliminary study. Secondly, the reason for the oscillation frequency being 20–30 Hz is unclear. It could be a limitation of cortical design, although visual cortical circuits are capable of somewhat higher frequencies. Alternatively, this band may represent the most efficient frequency of input synchronisation for driving motoneurons; this should be tested by further modelling work.

Cortical oscillations are not all-or-nothing phenomena; when present, their amplitude can vary, presumably due to changes in the number of cells participating in the oscillations and their degree of phase locking. If cortical

processing and oscillations are to some extent incompatible, we predict that, in a task requiring an intermediate level of processing, between the hold and movement phases of the precision grip task there would be an intermediate level of synchronous oscillations.

Finally, synchrony in the cortex is not all oscillatory in nature. Non-oscillatory, stochastic, synchrony is also found, as demonstrated by the narrow peaked cross-correlation histogram in Fig. 3B for the movement period. Such synchrony is not seen in non-invasive field potentials, such as MEG and EEG, due to cancellation of biphasic action potential waveforms. Understanding its role in motor performance requires further multiple single-unit recording. Such stochastic synchrony has recently been claimed to show task related changes that are independent of the modulation in firing rate of the units recorded, suggesting that it may form another dimension for information coding beyond the firing rate (Riehle et al. 1997).

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