CYCLIC H-REFLEX MODULATION IN RESTING FOREARM RELATED TO
CONTRACTIONS OF FOOT MOVERS, NOT TO FOOT MOVEMENT

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ABSTRACT

During rhythmic voluntary oscillations of the foot, the excitability of the H-reflex in the Flexor Carpi Radialis (FCR) muscle of the resting prone forearm increases during the foot plantar-flexion and decreases during dorsi-flexion. It is known that, when the two extremities are moved together, isodirectional (in-phase) coupling is the preferred form of movement association. Thus, the above pattern of the H-reflex excitability modulation may favour the preferred coupling between the two limbs. To gain some clues about its origin, FCR H-reflex excitability was tested before and after modifying the phase relations between the activation (EMG) of foot movers and foot movement, either by loading of the foot or by changing the movement frequency. After foot loading, the movement cycle was consistently delayed with respect to the onset of the EMG in Soleus (Sol) or Tibialis Anterior (TA) muscles. Simultaneously, the FCR H-reflex modulation advanced by that same amount with respect to the foot movement, thus remaining phase-locked to the EMG onsets. Similarly, when movement frequency was varied step-wise between 1.0 and 2.0 Hz, the foot movement was progressively delayed with respect to both the EMG onset (Sol and TA) and the FCR H-reflex modulation, so that the phase relation between the motor command to the foot and the H-modulation in the forearm remained constant. These results suggest that modulation of H-reflex in the forearm is tied to leg muscle contraction rather than to foot kinematics, and point to a central, rather than kinaesthetic, origin for the modulation.
INTRODUCTION

When trying to move two different body segments at the same time a number of constraints are experienced. For instance, several coplanar movements of the upper and lower limbs of one side (e.g. axial rotation of arm and leg, flexion-extension of hand and foot) are easily performed when the segments rotate in the same direction (in-phase) whereas coupling is difficult when they move in opposite directions (anti-phase) (Baldissera et al. 1982, 1991, 2000; Carson et al. 1995; Jeka and Kelso, 1995; Kelso and Jeka, 1992; Serrien and Swinnen, 1998; Swinnen et al. 1995).

The term nervous constraint, which is usually referred to factors, or situations, which limit the coupling repertoire (e.g. hindering or impeding non-isodirectional coupling of ipsilateral limbs) may however conceal, not a limit, but rather an obligation to produce a certain behavior. For instance, the clear-cut preference for isodirectional (in-phase) coupling of ipsilateral limbs may be sustained by nervous mechanisms that compel the limbs to “imitate” each other when they are moved simultaneously and, consequently, discourage other types of coupling, for instance in phase opposition.

In favor of this view, it was recently found that during the voluntary rhythmic flexion-extension movement of the ankle the H-reflex excitability in the resting forearm undergoes cyclic modulation (Baldissera et al. 1998). In the Flexor Carpi Radialis (FCR), with the forearm in prone position, modulation is characterized by an increase of the H-reflex amplitude during foot plantar flexion and a reduction during dorsi-flexion, whereas it is opposite in phase when the forearm is held supine (Baldissera et al. 2002). It was therefore argued that, when the two extremities are moved together, this pattern may favor the preferred in-phase (isodirectional) coupling (Baldissera et al. 1982, 2000) of the hand (either prone or supine) and foot.

To account for these findings, it could be postulated that afferent signals generated by the foot movement influence the reflex excitability in the cervical spinal segments. Further investigations however, uncovered that, during oscillations of the foot, the cortical motor area innervating the relaxed forearm muscles undergoes excitability fluctuations parallel to those occurring in forearm motoneurones (Baldissera et al. 2002) and that the former are possibly the cause of the latter. On this basis, it was proposed that centers elaborating the motor program for limb oscillations send parallel projections to the motor pathways to both limbs even when only one (e.g., the foot) is moved. In this contingency, the command directed to the foot is strongly activated while the collateral component directed to the resting hand is weakly excited. This would result in the movement of the foot and in the subliminal activation of the motor pathways directed to the resting hand. An alternative possibility, however, must be considered, i.e. that the spinal and cortical excitability changes may originate from kinesthetic afferent signals generated
by the foot movements and fed into the motor pathways directed to resting forearm. Indeed such a feedback action seems to be involved in the control of hand-foot coupling, when they both move, as a means to compensate for mechanical disparities between the two limbs. The latter control system apparently operates by anticipating muscular activation of the segment with greater inertia (Baldissera and Cavallari 2001). If a similar afferent feedback were also responsible for the excitability changes recorded in the forearm, then the H-reflex modulation should be tightly bound to the time-course of foot movement. Conversely, the hypothesis of a central common origin would predict that H modulation is temporally linked to foot EMG activity (i.e., the motor command) not to foot position.

Experiments aiming at modifying the time (phase) relations between the motor commands and the subsequent movements of the foot can put the above predictions to the test and help to reveal to which of the two events (muscular activation or movement) the modulation is linked. In the present experiments we modified such phase relations by applying an external load to the foot and/or by changing the frequency of its oscillations (see Baldissera et al. 2001). With these experimental manipulations and following our standard protocol for testing the H-reflex modulation (Baldissera et al. 1998, 2002) we explored whether the modulation time-course is phase-linked either to movement or to muscular activation.

METHODS

Subjects (6) gave informed consent to the experiments, which were performed according to the Declaration of Helsinki and approved by the local ethics committee. Healthy adult volunteers of either sex, aged 20 to 60 (36.5 ± 11 SD) were seated in an armchair with the hand resting in prone position and the right foot fixed to a platform oscillating around the axis of the ankle. EMG was recorded from the two main movers of the ankle, Tibialis Anterior (TA) and Soleus (Sol) muscles. H reflex was evoked in the Flexor Carpi Radialis (FCR) with standard technique: stimulation of the median nerve with bipolar external electrodes placed at the elbow (square pulse duration 0.8ms) and recording from bipolar surface electrodes over the muscle belly.

Subjects followed a general experimental protocol (see Baldissera et al 2002), in which they were asked to perform sequences of 4-5 flexion-extension cycles of the foot about the ankle, starting at their own will and following a tempo of 1.66 Hz (600 ms period), imposed by a metronome. A beeping signal allowed the subject to start a new oscillations sequence. The interval between sequences lasted at least 8 seconds.

During each movement sequence, transit of the foot in front of a photocell generated a signal that was fed into a PC which, at the third signal, triggered the stimulator to elicit an H-reflex at
one of 5 different delays during the third movement cycle. At the same time, the potentiometric signal giving the foot angular position and the EMGs from the foot movers Tibialis Anterior and Soleus were recorded, A/D converted (sampling rate 250 Hz for the potentiometer signal) and stored for further analysis.

In the different experiments this protocol was repeated after modifying the experimental set-up and/or the procedures in the two following ways: i) a metal disk (weight 10 Kg, radius 14 cm, inertial momentum 98 gm$^2$) was applied concentrically to the axis of rotation of the foot platform; and, ii) oscillations were repeated at different frequencies between 1.0 and 2.0 Hz. Both modifications were utilized with the aim of altering the phase relations between muscle activity in foot movers and the resulting foot oscillations.

A series of 25 sequences was delivered in each trial. The corresponding 25 reflexes were divided in 5 groups. Within each group, the reflexes were evoked in a random sequence at 5 different delays from the photocell trigger, dividing in even parts the imposed oscillation period (e.g., 0, 120, 240, 360 and 480 ms for a 600ms period). H-reflex responses were amplified, filtered (pass-band 10 to 3000 Hz) and digitally converted (sampling rate 5 KHz). In order to attenuate long-term variability independent of the stimulus position in the cycle, peak-to-peak amplitude of each response was measured and expressed as the deviation (in µV) from the mean of the 5 responses of its own group. This value was then averaged with those obtained at the same delay in the other groups of reflexes.

In order to obtain a more effective modulation linked with foot movement, in all experiments, except those describing the effects of changing movement frequency, the FCR H-reflex was facilitated by short-latency conditioning by transcranial magnetic stimulation, a procedure that enhances the modulation amplitude but does not affect its time-course (Baldissera et al. 2002, Fig. 3). For this purpose, the subject’s head was restrained by a fitted support and a stereotactic apparatus held an 8-shaped coil, connected to a magnetic stimulator (Magstim 200, maximal power 2.2 T), over the cortical focus for TMS activation of forearm muscles. To induce facilitation of the H-reflex in FCR (Baldissera and Cavallari 1993; Gracies et al. 1994), TMS was delivered 2-3.5 ms after median nerve stimulation, i.e. during the facilitation rising-phase, as determined in each subject by testing 3-4 conditioning-test intervals. The TMS intensity was just below (80-95%) of the threshold for evoking CMAPs (Cortical Muscle Action Potentials) at rest (usually 50-60% of maximal output).

The facilitated H-response thus represents the sum of a peripheral (Ia) and a central (corticospinal) component, which are both modulated in parallel during foot oscillations (Baldissera et al. 2002).
For each experimental condition, 3-4 trials were repeated in each subject. During each recorded (third) cycle, movement period was measured and found to never deviate between cycles by more than 5%. The ensemble-average of the (third) foot oscillations of all trials was then calculated and fitted by a four-parameter sine wave function, whose parameters were calculated by minimizing the sum of the squared differences between the observed and predicted values (Marquardt-Levenberg algorithm, SigmaPlot®), and its period estimated.

Starting from the position data, collected with a sampling interval \( t \) of 4 ms, movement velocity and acceleration were calculated as the first and second derivatives of the position \( y \):

\[
\dot{y} = \frac{y(i+1) - y(i-1)}{2t} \quad \text{and} \quad \ddot{y} = \frac{\dot{y}(i+1) - \dot{y}(i-1)}{2t}
\]

The two derivatives were also fitted by sine-wave functions with the same period of movement. Thereafter, all records (ensemble-average of movement and integrated EMGs) were normalized to the cycle period, as were also the 5 delays at which the H reflex was tested. This allowed the changes in the H-reflex to be displayed together with all other parameters as a one-cycle diagram. Onset of EMG bursts was defined by visual inspection on the averaged records.

Significance of H-reflex modulation within each subject and condition (loading or frequency) was evaluated by one way ANOVA. Significance level for all tests was \( p<0.05 \). In order to allow immediate phase matching between the excitability changes occurring in forearm motoneurones and foot movement (and its derivatives), the reflex data were then fitted by a sine-wave function with the same period as that of the movement. To attenuate the influence of background variability on the sinusoidal correlation with the independent variable (delay in the period) the best-fit determination coefficient, \( R^2 \), was calculated on the mean reflex values for each delay.

Comparisons of phase delays between different conditions were performed by paired-sample \( t \) test.

**RESULTS**

Correlation between H-reflex modulation in forearm muscles and dynamic parameters of foot movement.

Fig.1 illustrates, for one of the 6 subjects, an example of the H-reflex modulation (mean change of the H-reflex amplitude at 5 delays during the foot movement cycle, see Methods) occurring in the resting FCR during oscillations of the ipsilateral foot at about 1.6 Hz. In this figure, the ensemble-average of the foot position (pos), its first and second derivatives (vel and
acc), the integrated EMGs from the foot movers (TA and Sol) as well as the 5 delays at which the H reflex was tested, are all displayed on the same abscissa, normalized to the period of the movement cycle.

Note that the rising phase of the H-reflex modulation coincided with the EMG burst in Sol and the declining phase with the EMG burst in TA. The reflex data were significantly fitted (Fig. 1A, dotted line, \( p<0.001 \)) by a sine-wave function with the same period as that fitting the movement (Fig. 1B, dotted line). Determination coefficient \( (R^2) \) for the best-fit of the 5 mean values was 0.96.

The sinusoidal nature of both the foot movement and the associated modulation of the H-reflex allowed us to easily estimate the phase relation existing between the modulation and the parameters of movement dynamics (position, velocity and acceleration). In this subject, the sine function fitting the modulation led the movement sine-wave (flexion positive) by a phase angle \( (\Delta \Phi) \) of 74°, thus almost approaching the velocity sine-wave (dashed line). The rising phase of the H reflex modulation is therefore temporally related to both the rising phase of movement velocity and the period of Sol EMG activation. Similar results were obtained in all 6 subjects. On one hand, the relation with velocity may suggest that modulation is produced by the discharge of receptors signaling this parameter of foot movement. On the other hand, however, the linkage to Sol activation may support the “central” hypothesis, i.e. that the reflex modulation originates from a collateral action to the resting “isodirectional” muscle FCR during Sol contraction.

In order to have further elements that help clarify this point, we verified whether the link between H-modulation and foot movement described above persists when the relations between the movement (which remains the same) and its motor command are modified.

**Modifications of the phase relation between muscular activation and foot movement**

Application of a rotating inertial load to a voluntarily oscillating limb increases the delay with which movement follows muscular activation. Moreover, the delay is frequency-dependent and increases when the oscillation frequency increases (Fig. 2E, see also Baldissera and Cavallari 2001). The changes in the phase relations between the TA EMG and the foot movement produced either by loading the foot with a rotating mass or by modifying the oscillation frequency are exemplified in Fig 2. In this example, the phase difference between the onset of the TA EMG and the onset (bold arrow) of the foot dorsi-flexion, increased by about the same amount either when, at 1.66 Hz, the foot was loaded with a balanced rotating mass (inertial momentum 98 gm\(^2\)) (compare B and D) or when, with the foot loaded, the frequency was changed from 1.0 to 1.66 Hz (compare C and D). Frequency-related changes of the EMG-movement delay between 0.8 and 3 Hz are illustrated in Fig.2E, for both the unloaded and loaded
conditions (open and filled circles, respectively). To be consistent with the phase measurements regarding the H-reflex modulation (see Figs.1 and 5), here we measured the phase difference between movement and EMG ($\Delta \Phi'$) not from the movement onset, as previously done (Baldissera and Cavallari 2001) but from the oscillation midpoint (vertical dotted line in A).

On the basis of the above effects of frequency and loading on coupling between muscular activation and movement, the H-reflex modulation was measured after connecting a rotating mass to the foot support and different rhythms of foot oscillations were examined between 1 and 2 Hz.

**Effect of foot loading on H-reflex modulation**

Figure 3 A-D illustrates, for a representative subject, the change induced by foot loading on the phase relation between the modulation of the FCR H-reflex and the foot movement. In both conditions H-reflex modulation was significantly fitted (A: $p<0.04$; B: $p<0.0001$) by a sine wave function ($R^2 = 0.81$ in A and 0.97 in B). However, while in the unloaded condition the rising phase of the H-modulation started just before plantar flexion (A), after foot loading it was shifted forward, starting at the beginning of dorsi-flexion (B). In this subject, the advance of the H-modulation on movement was thus increased by 76°, from 53° (foot unloaded) to 129° (foot loaded). Note however that, in parallel with the shift of the H-reflex modulation, loading had produced a comparable forward shift of the TA EMG with respect to the movement, so that the modulation ascending phase still coincided with the period free of TA activity, i.e. the period of Sol contraction. Similar results were obtained in all 6 subjects, shown cumulatively in Fig.3 E-F. Sinusoidal fitting of the individual reflex data was always significant, $p$ ranging between $<0.001$ and $<0.05$. Determination coefficient, $R^2$, was 0.81, 0.96, 0.75, 0.79, 0.92, 0.78; and 0.97, 0.92, 0.88, 0.57, 0.92, 0.74 for the loaded and unloaded conditions, respectively. Sinusoidal fitting of the cumulative reflex data was highly significant ($p<0.0001$, determination coefficient, $R^2$, 0.78 for unloaded and 0.62 for loaded data). The overall advance of the H-modulation on movement was increased by 90°, from 62° (foot unloaded) to 152° (foot loaded).

Whatever the reason for the phase advance observed in the H-reflex modulation after loading, its mere occurrence implies that is not linked to movement or its derivatives, which are not modified by load application. Therefore, modulation could not be attributed to any specific feedback mechanism based on kinesthetic afferences, monitoring the foot position, velocity or acceleration.

The phase difference ($\Delta \Phi$) between the best-fit sine waves of the H-modulation and the foot movement (H Mod-Mov delay), was measured as indicated in Fig. 4A. Individual $\Delta \Phi$ values are
plotted in Fig. 4C by small symbols (open = foot unloaded, filled = foot loaded) and their means by the large upper symbols. Mean values are significantly different from each other \( (p<0.001, \text{ paired } t \text{ test}) \) changing from \( 63° \pm 15° \text{ SD} \) (foot unloaded) to \( 141° \pm 41° \) (foot loaded). Having been obtained by averaging the individual \( \Delta \Phi \)s, these mean values are slightly different from \( \Delta \Phi \)s obtained by fitting the cumulative data points (Fig 3E-F).

Figure 4 also illustrates the phase relations between H-reflex modulation and activation onset in TA and Sol muscles, before and after loading. These relations were measured as the phase delay \( (\Delta \Phi''') \) between the H-modulation and the EMG onset, as illustrated for the TA EMG in Fig 4 B (H Mod-TA delay). Their individual and mean values are plotted in Fig. 4D. It is apparent that values of \( \Delta \Phi''' \) for either Sol or TA are mostly the same after loading (filled symbols) as they were before loading (open symbols) and that the mean values of the data in the two conditions (large upper symbols) are not different from each other \( (\Delta \Phi''') \text{ TA: unloaded} = 136° \pm 24° \text{ SD} ; \text{ loaded} = 142° \pm 30° ; p > 0.44, \text{ paired } t \text{ test. } \Delta \Phi'\prime \prime \text{ Sol: unloaded} = -10° \pm 29°; \text{ loaded} = -12° \pm 24°; p > 0.75). \)

In conclusion, loading of the foot modifies the phase relations of the H-reflex modulation with foot movement, while its relations with TA and Sol muscle contractions remains unmodified.

**Effects of changing movement frequency**

The FCR H-reflex modulation was measured at 4 different oscillation frequencies, ranging between 1 and 2 Hz, in 5 subjects. In this range, the effects of frequency on the EMG-movement delay are much larger after loading than before (cfr. Fig. 2); thus, the tests were performed in the loaded condition. In the subject of Fig. 5, the four step increase of the oscillation frequency (A to D) induced a progressive forward shift of both the modulation curve and the onset of TA and Sol EMGs with respect to movement, so that the phase relations between H-reflex modulation and EMG onsets remained virtually unvaried. The phase delays \( \Delta \Phi \) (H Modulation-Movement delay), \( \Delta \Phi' \) (Movement-TA EMG delay) and \( \Delta \Phi''\prime (H \text{ Modulation-TA EMG and } -\text{Sol EMG delays}) \) were measured between the 4 reference points indicated by vertical arrows in panel A of Fig.5. The respective values are plotted in Fig.6, A to C, for 5 subjects: individual values are shown by filled triangles and dashed lines and their means by large open symbols. Plot A shows how the phase delay between the foot oscillation and the H-modulation \( (\Delta \Phi) \) increased significantly with frequency, while plot B illustrates the parallel decrease of \( \Delta \Phi', \) i.e., the phase delay between mid-flexion (movement reference point) and the onset of the TA EMG. The simultaneous reciprocal changes of the two above delays results in the lack of change of both
ΔΦ’’TA and ΔΦ’’Sol, i.e. the phase differences between the H-modulation and the onsets of TA and Sol muscle activation respectively (Fig. 6C, circles and squares).

**DISCUSSION**

Altogether, the results of both “loading” and “frequency” experiments indicate that the modulation of FCR H-reflex during foot oscillations is linked to the timing of muscular activation, since in all conditions excitability rises during Sol contraction and declines during TA contraction. Conversely, the correlation with the time course of the movement parameters changes in the different conditions. These results do not support the hypothesis that the reflex modulation occurring in the resting forearm flexor is produced by afferent signals related to the foot kinetics. They are instead in line with the hypothesis that, when lumbar motoneurones are supraliminarily activated to produce foot movements, a central subliminal command is collaterally conveyed to forearm motoneurones. This same conclusion was reached in a recent study (Baldissera et al. 2002) which showed that the modulation was larger when the H-reflex was facilitated by TMS (at short latency) than when it was unconditioned and that the modulation disappeared when the reflex was evoked during the cortical “silent period” induced by TMS. All these results combined suggest a cortical origin for FCR H-reflex modulation, which would depend on activity fluctuations occurring in the cortical motor area to the forearm motoneurones during voluntary foot oscillations.

However, an afferent contribution to the H-reflex modulation cannot be completely excluded: being correlated with muscle contraction, modulation might be produced by discharges from Golgi tendon organs that, through their cortical projections (McIntyre 1984), may induce the excitability changes in the motor cortex relayed to forearm motoneurones. In this case too, however, modulation of forearm motor excitability would reflect the time course of the motor command to the foot, not that of the foot movement.

The action of muscle spindles could instead be ruled out, since recordings from their afferent fibers during voluntary movement in man (Jones et al. 2001) showed that their discharge was linked to lengthening of the parent muscle, not to γ drive, and well encoded the joint position. Thus, being correlated with movement kinetics, signals from spindles should not be involved in the generation of the observed H-reflex modulation.

Other considerations contrast an afferent origin. Assuming that the H-reflex modulation is produced by a composite afferent signal, including position, velocity and acceleration components, either from a single receptor type or from different kinds of receptors, it might be postulated that the three components ought to be affected to a different extent by the movement
manipulations we employed. For example, if the reflex modulation is partly dependent on a velocity signal, then a forward phase shift of modulation on movement is expected (and actually occurs) when the movement frequency increases. Conversely, no similar effect is expected after loading, since loading leaves the movement period unchanged and, if anything, it smooths the movement profile, thus filtering local velocity and acceleration components. Nevertheless, after both frequency increase and loading, H-reflex modulation is markedly shifted forwards.

A further line in support of the hypothesis of a central origin for the forearm excitability modulation comes from a comparison with results of experiments in which hand-foot coupled movements were perturbed by loading the hand. In this condition, an afferent feed-back mechanism, likely based on measuring the hand-foot asynchrony induced by loading, compensates for the added inertia and helps to maintain coupling of limb oscillations (Baldissera and Cavallari 2001). Since this compensation is mainly implemented by anticipating the EMG onset in one limb with respect to the other, it cannot be responsible for excitability modulation described here in the forearm, which instead remains strictly linked to the activation of the foot EMG. In the present experiments loading of the foot was indeed ineffective in modifying the phase relations between muscular activation in the leg and excitability changes in the forearm.

As suggested in the Introduction, the time-course of H modulation would favor isodirectional coupling when the hand and foot are oscillated together. Should this view be correct, one would expect the excitability modulation in resting forearm motoneurones to match the requirements of isodirectional coupling. In particular, i) a parallel modulation, but opposite in phase, should be present in the hand extensors; and ii) modulation in FCR should reverse in phase when the hand positions is changed from prone to supine. Both these predictions have been confirmed experimentally (Baldissera et al. 2000, 2002).

As for the neural substrates of isodirectional coupling, recent findings have shown strong functional interactions between the foot and hand areas of the motor cortex during coupled movements of the two limbs (Liepert et al.1999). These intracortical connections could in principle explain the link observed between the hand and the foot, but they still do not clarify how the principle of isodirectionality is maintained when the hand position is changed from prone to supine. Interestingly, Kakei and colleagues described “extrinsic-like neurons”, principally in the ventral premotor cortex but also in the primary motor cortex of the macaque, so called because they appear to encode the movement of the wrist in a frame of extrinsic spatial coordinates, independently of the forearm position (Kakei et al. 1999; Kakei et al. 2001). Neurons with these properties, inserted in the network responsible for hand-foot coupling, would indeed encode the movements of the two limbs in absolute spatial coordinates irrespectively to the pattern of muscle activation.
Modulation of reflex excitability in one limb during voluntary movements of another limb has been described by several authors in recent years, though in contexts different from the one considered here. During active pedaling with one leg, the soleus H-reflex in the contralateral resting limb undergoes a profound modulation (Brooke et al. 1992) which is absent during passive pedaling movements, a condition in which the Sol H-reflex is tonically depressed (McIlroy et al. 1992; Cheng et al. 1998; Collins et al. 1993). Voluntary oscillations of the whole arm (Hiraoka 2001) as well as passive oscillations of the forearm (Hiraoka et al. 1999) have both been reported to modulate the Sol H-reflex excitability in a phase dependent way. Further, elevation of the arm is preceded and accompanied, in most subjects, by a burst in Biceps Femoris EMG and a complete silence in Soleus EMG, the latter being accompanied by a strong depression of the Sol H-reflex (Kasai et al. 1996) ascribed to a mixture of central and peripheral mechanisms (Kawanishi et al. 1999). These influences of arm movements on the leg muscles were explicitly discussed as being “anticipatory postural activities” (Marsden et al. 1978; Marsden et al. 1981 Cordo and Nashner 1982; Bouisset and Zattara 1987; Zattara and Bouisset 1988), a category to which also the crossed inter-leg relation quoted above (Brooke et al. 1992) may possibly be ascribed, aimed at realizing a fixation chain for trunk stabilization during one-leg pedaling. Finally, modulation of the FCR H-reflex has been reported to occur during voluntary oscillations of the contralateral hand (Carson et al. 1999) and this may also be expression of postural activities, for instance aimed at stabilizing objects during bimanual manipulation.

Anticipatory postural activities are aimed to prepare a fixation chain connecting the moving segment to a firm support, or to produce a counter-movement that contrasts the postural unbalance produced by the main body action. When explicitly manifest, they are characterized by the parallel activation of muscles in different body segments, are scaled with the intensity of the prime movement (Aruin and Latash 1996) and can be reduced or abolished when the biomechanical context is modified (Aruin et al. 1998). Further, their timing and spatial distribution may vary when the surround conditions or some feature of the movement (e.g., direction) are changed (Aruin and Latash 1995; Nashner and Forssberg 1986). This allows one to imagine that, even when a manifest intervention of the anticipatory postural activities is not required, subthreshold effects may nevertheless take place. In this view, the positive and negative constraints characterizing ipsilateral limb coupling might indeed be the expression of some underlying postural mechanism.
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Figure 1. Cyclic modulation of FCR H-reflex during voluntary oscillation of ipsilateral foot

A, absolute deviations of the H-reflex size from its mean value over the whole cycle, occurring at five different delays during voluntary oscillations of the foot. Each point represents the average (± SE) of 15 responses evoked at that delay. Dotted line describes the sinusoidal function, with the same period as the foot movement, that fitted the mean data best (correlation coefficient, R² = 0.96).

B, average of all records of the foot angular position (pos) and the calculated velocity (vel) and acceleration (acc) of the foot movement, together with the rectified EMGs from Tibialis Anterior (TA, thick continuous line) and Soleus (Sol, thin continuous line) muscles. The dotted line superimposed on the position record describes the sine-wave function fitting the average position record best (R² = 0.99). Its period (π = 532 ms) was utilized for normalizing to 1 cycle the time-scale of all parameters. The phase of the best-fit sinusoids for the movement and for the H-reflex modulation was measured and their difference (ΔΦ) calculated. Positive values of ΔΦ indicate that the movement sinusoid lagged the modulation sine wave. Pf = plantar flexion, Df = dorsi-flexion
Fig. 2. Effects on phase relations between muscle contraction and foot movement exerted by inertial loading of foot and/or increasing movement frequency.
Each graph shows the average records (10 movements) of the foot angular position and integrated EMG from TA muscle. Abscissa, one cycle. A, foot unloaded, oscillation frequency 1 Hz; $\Delta \Phi' = 107^\circ$. Distance between the vertical dotted lines = $\Delta \Phi'$. B, increasing the movement frequency to 1.66 Hz induced a small decrease in $\Delta \Phi'$ (97°). C, loading the foot, at the frequency of 1 Hz, also has a small effect on $\Delta \Phi'$ (103°). D, a large reduction of $\Delta \Phi'$ (5°) is instead obtained when the foot oscillating at 1.66 Hz is loaded (B to D) or when the loaded foot increases its oscillation frequency from 1.0 to 1.66 Hz (C to D). Bold arrows in B,C, D indicate onset of foot dorsi-flexion. E Phase relations between the onset of the TA EMG and the midpoint of the foot oscillation measured at different frequencies. Foot unloaded (open circles) and loaded (filled circles). Thin arrows indicate the changes from B to D and C to D.
Figure 3. Effect of foot loading on the phase relations between cyclic modulation of FCR H-reflex and voluntary foot oscillations.

A and C, modulation of the FCR H-reflex (open circles), foot angular position (pos) and EMG activity in TA muscle (TA) during oscillations with the foot unloaded. Same symbols and display as in Fig 1. Dotted lines represent sinusoidal functions with identical period, fitting the foot movement and the H-reflex modulation best. The phase difference between the two sinusoids (\(\Delta \Phi\)) is 53° (H-modulation leading). B and D, same parameters as in A and B, but obtained after inertial loading of the foot (close circles). Note that the \(\Delta \Phi\) has increased to 129°. E and F, H-reflex modulations of all (6) subjects during oscillation of the unloaded (○) and loaded (●) foot. In each subject, besides period normalization and alignment to the midpoint of the movement cycle, data were normalized in size to the amplitude of the respective best-fit sine wave. Note the change in \(\Delta \Phi\) between the unloaded (62°) and loaded (152°) conditions.
Figure 4. Changes induced by foot loading on phase relations of FCR H-reflex modulation with foot movement and activation of foot movers, respectively.

A and B, diagrammatic sketches illustrating the way of measuring phase differences $\Delta \Phi$, between the sinusoid fitting the H-reflex modulation (dotted line) and foot oscillation (continuous line), and $\Delta \Phi''$TA, between the H-reflex modulation and the onset of the EMG burst in TA muscle. $\Delta \Phi''$Sol was measured in the same way.

C, values of $\Delta \Phi$ obtained in the 6 subjects of Fig. 3, before (open circles) and after (filled circles) loading the foot with a rotating mass, are vertically ordered according to the value in unloaded conditions. Uppermost large symbols indicate their means ($\pm$ SD). D, values of $\Delta \Phi''$Sol (squares) and $\Delta \Phi''$TA (circles) obtained, in the same experiments as in C, before (open symbols) and after (filled symbols) foot loading. Again, mean values of $\Delta \Phi''$ (± SD) are indicated by the large symbols.
Figure 5. Effect of changing frequency of foot oscillations on phase relations between cyclic modulation of FCR H-reflex and foot movement.

A to D, each letter corresponds to a different frequency of foot voluntary oscillations (in Hz) as indicated in the insets. Same symbols as in the preceding figures. Foot was loaded with a rotating mass. The phase differences $\Delta \Phi$ (H modulation - movement), $\Delta \Phi'$ (movement - TA EMG) and $\Delta \Phi''$ (H modulation - TA EMG and Sol EMG) were measured between the 4 reference points indicated by vertical arrows in each panel. As frequency increases from 1.0 to 2.0 Hz, $\Delta \Phi$ increases progressively, $\Delta \Phi'$ decreases progressively while $\Delta \Phi''$Sol and $\Delta \Phi''$TA remain virtually constant. Determination coefficient $R^2$ of sine-waves fitting the H-modulation best was 0.77 (A), 0.93 (B), 0.79 (C) and 0.91 (D); $p$ always $<0.01$. 
Figure 6. Frequency of foot voluntary oscillations affects phase relations of H-reflex modulation with foot movement, not with muscle contraction

All graphs have a common abscissa, i.e. the nominal movement frequency (metronome rhythm). On each plot, individual data from 5 subjects are indicated by filled triangles and large open symbols, connected by a continuous line, giving their mean values ± SD. Insets on the right show how $\Delta\Phi$, $\Delta\Phi'$ and $\Delta\Phi''$ are measured. When the frequency of foot oscillations increments (common abscissa) $\Delta\Phi$ increases significantly (A) $\Delta\Phi'$ decreases correspondingly (B) while $\Delta\Phi''$TA (circles) and $\Delta\Phi''$Sol (squares) remain constant (C). Linear regressions of all data in C gave $p>0.5$; $R^2 = 0.021$ for TA and $p>0.48$; $R^2 = 0.027$ for Sol.