RESEARCH ARTICLE

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Bimanual adaptation: internal representations of bimanual rhythmic movements

Abstract From tying your shoes and clipping your tie to the claps at the end of a fine seminar, bimanual coordination plays a major role in our daily activities. An important phenomenon in bimanual coordination is the predisposition toward mirror symmetry in the performance of bimanual rhythmic movements. Although learning and adaptation in bimanual coordination are phenomena that have been observed, they have not been studied in the context of adaptive control and internal representations—approaches that were successfully employed in the arena of reaching movements and adaptation to force perturbations. In this paper we examine the dynamics of the learning mechanisms involved when subjects are trained to perform a bimanual non-harmonic polyrhythm in a bimanual index finger tapping task. Subjects are trained in this task implicitly, using altered visual feedback, while their performance is continuously monitored throughout the experiment. Our experimental results indicate the existence of significant ($p < < 0.01$) learning curves (i.e., error plots with significantly negative slopes) during training and aftereffects with a washout period after the visual feedback ceases to be altered. These results confirm the formation of internal representations in bimanual motor control. We present a simple, physiologically plausible, neural model that combines feedback and adaptation in the control process and which is able to reproduce key phenomena of bimanual coordination and adaptation.

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Introduction

Human daily routine frequently involves coordinated bimanual movements. In many cases both hands are involved in the same task and demonstrate symmetry (Cohen 1971; Schoner and Kelso 1988; Mechsner et al. 2001; Swinnen 2002). The tendency toward mirror symmetry in movements has been studied under different conditions with a variety of movement types, and has been associated with homologous muscle activation (Schoner and Kelso 1988), callosal neural crosstalk (Marteniuk et al. 1984; Swinnen et al. 1991; Cardoso de Oliveira 2002), and perceptual symmetry (Mechsner et al. 2001). It is interesting to note that even amputees with phantom limbs maintain the tendency toward bimanual coupling (Franz and Ramachandran 1998).

One of the prominent paradigms for the study of bimanual coordination consists of rhythmic finger movements. This paradigm has been used to model one of the most important phenomena in bimanual rhythmic movements—the involuntary phase transitions that occur when the frequency of oscillations is increased. Initially these transitions were explained by a fixed dynamic model (Haken et al. 1985) that may represent interconnection between the muscles at the spinal level (homologous muscles). This model has been extended to accommodate several other conditions, e.g., different eigenfrequencies (Fuchs et al. 1996), hand dominance (Treffner and Turvey 1995), and physiological functionality (Beek et al. 2002; Peper et al. 2004). Subsequent recent research has also demonstrated that these coordination patterns are influenced by training and attention (Zanone and Kelso 1992; Klapp et al. 1998; Temprado et al. 2002).

The fact that the coordination patterns are changeable through training calls for the study of the mechanisms and system dynamics active during learning,

demanding the application of adaptive control theory and the notion of "internal representations" to the study of bimanual adaptation. These notions were successfully employed in the study of reaching movements (Shadmehr and Mussa-Ivaldi 1994; Mussa-Ivaldi 1999; Karniel and Mussa-Ivaldi 2003) and grip force modulation (Witney 2004), but in the arena of bimanual coordination even the term "bimanual adaptation" has not yet been used.

In this study we refer to the terms "internal model" and "internal representation" in the widest possible sense; we do, however, distinguish between pure feedback control and adaptive control, where the former does not include internal models.

The term feedback is used to describe information that is used for control and learning (see, e.g., Schmidt and Lee 1999). In order to distinguish between learning and real time control, we use the term "feedback control" in the engineering sense where it is used as a real time control signal. In engineering terminology (see, e.g., Karniel and Inbar 2000) feedback control is defined as a flow of information that changes the control signal based on the measured output signal. In an adaptive control system, the controller itself changes during task performance, a change that is much slower than the time constant of the slowest signal transduction pathway in the control loop, resulting in observable learning curves, aftereffects of learning, and washout. In pure feedback control the controller is fixed and unchangeable—only the control signals may change. (For further discussion about feedback and adaptation in the motor control system, see Bhushan and Shadmehr 1999; Kawato 1999; Karniel and Inbar 2000.)

If the controller undergoes changes that are based on changes in the environment, it essentially represents the environment. We believe that the term "internal model" is appropriate because it facilitates the next step of research that will be aimed at unraveling the structures of the internal representations, their learning and generalization capabilities.

So far, studies researching bimanual coordination and the training of difficult coordination patterns have concentrated on the achieved steady states, overlooking the dynamics of the learning process itself. Models that describe the observed phenomena of symmetry and phase shifts have been typically based on nonlinear coupled oscillator theory with representations of either dynamics equations or physiologically plausible neural networks (Schoner and Kelso 1988; Grossberg et al. 1997; Cattaert et al. 1999; Sternad et al. 1999; Swinnen 2002; Yu et al. 2003). The current models are based on a fixed unchangeable architecture that may employ feedback signals that are capable of generating phase shifts in the behavior but do not include gradual adaptive changes in the parameters or other types of internal representation.

Mechsner et al. (2001) found that bimanual symmetry might have origins at the perceptual level. In their experiments, subjects were able to perform difficult non-harmonic polyrhythms as well as various phase relations with both hands while presented with mirror symmetrical altered visual feedback. These observations point toward the ability of the brain to perform complex transformations between the desired perceptual goal and the required motor activity, essentially implementing an inverse model of the controlled system. In their experiments, Mechsner et al. did not examine the learning process and adaptation dynamics of the subjects to the presented altered feedback, but rather focused on the steady states which resulted from this training; therefore, internal models were not required for explaining their results. A subsequent study (Weigelt and Cardoso de Oliveira 2003) examined interactions between hands in bimanual reversal movements and distinguishes between coupling on the visual level and on the executional level. Using altered visual feedback, modifications in some of these coupling effects were made. Coupling at the visual level and executional level has also been addressed in other studies (Swinnen et al. 2003).

Altered visual feedback (mainly in the form of Lissajous figures) has been previously used in bimanual coordination studies to facilitate learning of nontrivial phase relations (mostly a 90° offset) in bimanual rhythmic movements (Swinnen et al. 1993, 1997a, b; Lee et al. 1995; Debaere et al. 2003, 2004; Swinnen and Wenderoth 2004). In these functional and modeling studies, altered visual feedback was shown to facilitate production of otherwise difficult bimanual coordination patterns.

Hence, it is clear that coupling exists between hands, perhaps even distributed over several functional layers, but also that at least some of these couplings can be modified by training and practice. Altered visual feedback has been established as a viable means of intervening with bimanual coupling and facilitating the acquisition of various coordination patterns.

In this study, we try to address changes in bimanual coordination as a form of adaptation and learning of internal representations and look for the signatures of such processes as learning curves, aftereffects, and washout phenomena. We consider a bimanual finger tapping task and propose a simple model that reproduces the learning curves, the aftereffects, and the coupling phenomena. Parts of this study were presented in conferences (Karniel et al. 2003; Klaiman and Karniel 2004a, b).

Materials and methods

Participants

Ten male unpaid volunteers (ages: 22–29) participated in the experiment. All had normal or corrected to normal vision, were naive as to the purpose of the study, and gave their written informed consent. The experiments were approved by the local ethics committee and complied with the Declaration of Helsinki.
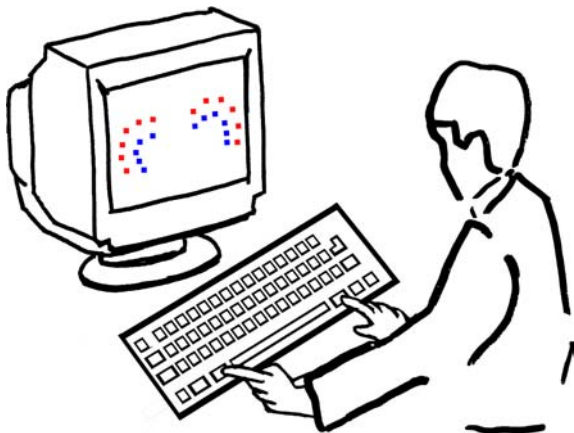
Task and apparatus

Subjects were seated in front of a computer monitor at a distance of approximately 50 cm, and asked to place their index finger on the CTRL keys of a standard computer keyboard (Fig. 1). A PC-based platform specifically designed for this purpose was programmed in Sun Java. The visual feedback consisted of four dotted arcs rotating in concentric pairs. Each pair of dotted arcs provided feedback for one of the hands. The outer (red) semicircles acted as target markers, and rotated with a constant speed in a path mirror-symmetrical to each other. The inner (blue) semicircles acted as user feedback markers, and rotated concentrically with the corresponding target marker in a speed proportional to the subject's inter-tap-interval (ITI) of the associated hand, i.e., the right circle would move faster if the subject tapped with his right finger at higher frequency. Angular velocity of the feedback markers was calculated with the formula

$$w = \frac{\pi}{14.4 \, \text{ITI}} \, [\text{rad/s}], \tag{1}$$

where w is the angular velocity of the marker and ITI is in seconds. The ratio between tapping frequency of each hand and the rotation speed of the corresponding visual feedback marker was chosen heuristically so that it was slow enough to comfortably follow, but fast enough to provide clear indication of tapping frequency. The goal of this visual feedback display was to "convert" the discrete tapping feedback into continuous visual feedback, which we could alter in order to facilitate learning. For example, if the tapping frequency of one hand is 2 Hz, the ITI is 0.5 s and the corresponding marker would complete a full circle in 14.4 s.

Subjects were instructed to focus their attention on the visual feedback displayed on the monitor and maximally match each hand's target marker with the corresponding user feedback marker, controlling the speed of the markers via the tapping frequencies of their fingers.
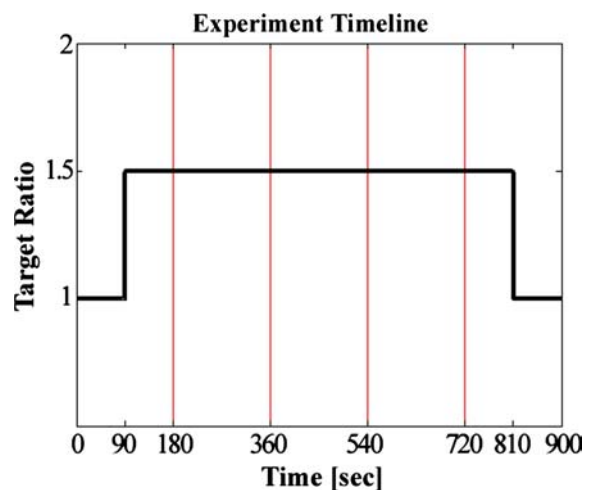
Data acquisition was performed through the software by recording the timestamps of all keyboard interrupts and distinguishing between right and left CTRL keys by the interrupt key-flag. The time resolution of the interrupt timestamp is 1 ms.

The finger tap times were registered by the software program and immediately updated the corresponding marker speed. This process was performed in a software loop and therefore the length of the delay was around 10 ms, which we assumed to be subliminal and negligible.

Experimental protocol

Prior to each trial the subjects performed a 1 min preliminary stage, in which they were able to try out the system with normal (i.e., unaltered) feedback and learn how the markers react to their increase or decrease of tapping frequency. The trial timeline (shown in Fig. 2) consisted of five separate stages with duration of 180 s each. Subjects were allowed a short break between the different stages. The short break was under 60 s and usually around 20 s. The break periods are not included in the data analysis. The first 180 s stage consists of 90 s with 1:1 target ratio followed by a step transition to 3:2 target ratio for an additional 90 s. The second, third, and fourth stages are training stages in which the target ratio is constant at 3:2. The fifth (last) stage consists of 90 s of 3:2 target ratio followed by a step transition to the original 1:1 ratio for an additional 90 s.

Execution of all bimanual rhythms by the subjects during the trial was implicit, i.e., they were not told what the target frequency was (or that there even was one),

Fig. 1 Experiment setup—subject seated in front of a computer keyboard and monitor displaying visual feedback. The outer arc markers' (*red*) speed represents the target tapping frequencies and the inner arc markers' (*blue*) speed represents subject tapping frequency

Fig. 2 The experiment timeline—The target ratio starts at a comfortable 1:1 ratio, it is then abruptly changes to 3:2 target ratio and finally returns to 1:1 ratio for the after-effect phase. Following each 180 s stage the subjects are allowed a short resting period

but rather instructed only to match the target markers with the feedback markers by constantly tapping their fingers. The non-harmonic polyrhythm target ratio was selected to be 3:2 since it has been shown in previous studies to be one of the easiest non-harmonic rhythms to learn (Deutsch 1983; Treffner and Turvey 1993).

In order to change the target-tapping ratio, the "gear" between ITI and feedback marker speed of the right hand was changed so that when the subject successfully followed the target markers he was performing the non-harmonic polyrhythm.

During the normal 1:1 target ratio stage, the target marker rotated at a frequency of five rotations per minute (i.e., 0.52 rad/s), and the feedback markers were configured so that the user was required to tap at a comfortable 2 Hz frequency in order to match the target markers' speed with the user feedback markers.

Data collection

The data collected from each trial consisted of two vectors of integers representing the time of each key press in milliseconds, counting from the beginning of the trial. To calculate the ITI, these vectors were numerically differentiated. The two ITI vectors were resampled on a uniform timeline with a 10 ms timescale and divided by each other to obtain the ratio of tapping frequencies. All data analysis was performed with the MATLAB 6.5 software package.

The model

We hypothesize that the acquisition of non-harmonic polyrhythms in bimanual coordination involves an adaptation such that an internal representation of the
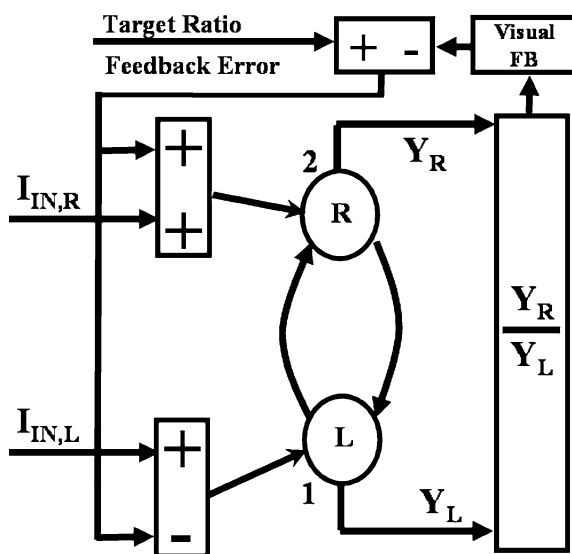

Fig. 3 Two coupled rate-based neurons with feedback signals

learned task is formed. Previous studies in this area make it clear that visual feedback plays an essential role in facilitating the internal representation of complex coordination patterns. We also know from previous studies that some sort of coupling exists between both hands and that visual feedback can help in modifying this coupling.

Our goal in the modeling study was to propose the simplest model that can account for these three phenomena. Coupling required at least two elements and visual information has to be fed back to these elements; therefore the two linearly coupled rate-based neurons in Fig. 3 represent a lower bound to our solution. We demonstrate below that this architecture is insufficient to explain our results and then present an extended model that was sufficient and successfully reproduced our observed results.

The firing rate of a neuron in this model can be described by any non-negative, monotonically increasing and bounded function $S(P)$, where P is the neural input. The input P to each of the two neurons consists of the external current, inter-neural connections, and from the feedback signal. The resulting sum can be written as

$$P_i = I_0 + K_{\text{FB}(i)}(T - S_1/S_2) + W_i \times S_{(i+1)\bmod 2}, \qquad (2)$$

where T represents the target spike rate ratio, W the inter-neural connection strengths, K_{FB} the feedback gain, and I the neuron index ($i = 1, 2$).

From Eq. 2 (using $i = 1$ without loss of generality) we can now extract K_{FB} as

$$K_{\text{FB}} = \frac{P_1 - I_0 - S_2(P_2)W_{1,2}}{T - \frac{S_1(P_1)}{S_2(P_2)}}. \qquad (3)$$

Denoting the output ratio as $r = S_1(P_1)/S_2(P_2)$, and assuming a finite current with a maximum value of M, input $P_i < M$, neural excitation $S_i(P_i) > 0$ (both hands are tapping), and W constant (i.e., exclusive use of feedback in the control scheme), one can see that in order to achieve any target ratio while keeping the synapse strengths constant, the system would need an infinite loop gain,

$$\lim_{r \to T} K_{\text{FB}} = \infty. \qquad (4)$$

This result is not physiological and furthermore, we know that the 1:1 ratio is inherently stable and does not require feedback to be performed.

Therefore we conclude that the architecture in Fig. 3 is too simple and needs to be expanded. A natural choice for such an expansion would be to use pulse coupled neurons, e.g., Leaky-Integrate-and-Fire (LIF) neurons. Pulse coupled neurons are known to have synchronization capabilities (Masuda and Aihara 2001) which would allow the model to describe the predominant phenomena of tendency toward the stable 1:1 ratio and phase locking (Cohen 1971; Schoner and Kelso 1988; Mechsner et al. 2001; Swinnen 2002), which would now be inherently built in the system. In order to include any

type of adaptation or learning (that were clearly observed in our experiments), the synapse weights must be changeable. A final enhancement to accommodate physiological constraints would be to add two inhibitory neurons to the network so that every single synapse would be either excitatory or inhibitory, but not both, i.e., would follow Dale's principle (Dale 1935).

It should be noted that adding each of the improvements to the simple model uniquely improves the model in one particular way, but still leaves other demands such as physiological plausibility or description of major system qualities unaddressed. Adding the changeable synapses to the model in Fig. 3 facilitates the observed learning process but still leaves the basic flaw of rate-based models, which is the inability to accurately describe phase preference and synchrony.

The neuronal network in our model (Fig. 4) consists of four interconnected units. Two of these are primary input-output units, which are excitatory and cross-coupled. They receive the external input currents and error feedback currents while providing output to the external world in the form of spike trains. The other two are inhibitory units, which provide contralateral inhibition to the primary input-output neurons.

This model represents neuron cells or cell populations in the central nervous system (CNS), and its components follow the dynamics of LIF-spiking neuron equations. The network model proposed is consistent with a family of network configurations known as recurrent on-center off-surround networks. This type of network design is common in the CNS (Kuffler 1953; Von Bekesy 1968; Grossberg 1982; Kandel et al. 1991) and has been previously used to describe various aspects in neural control of bimanual coordination (Pearson 1993) and specifically involuntary shifts between in-phase and anti-phase movement patterns (Grossberg et al. 1997).

In consistency with the LIF model, the neuronal membrane voltages in our model (Fig. 4) are characterized by the following equation:
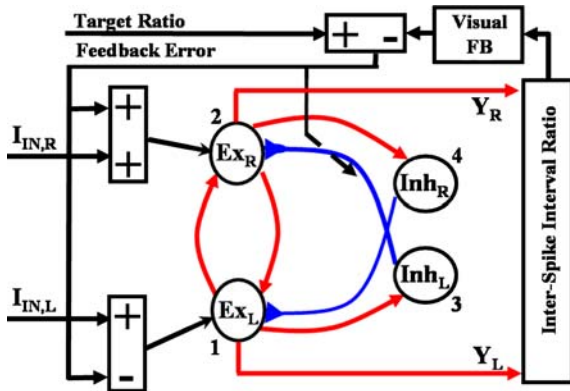
$$\tau_m \frac{dV(t)}{dt} = -V(t) + R\,I(t), \tag{5}$$

where τ_m is the membrane time constant, $V(t)$ the membrane potential vector, $I(t)$ the neuron input current vector, and R the membrane resistance. When the membrane potential of a certain neuron i, $V_i(t)$, crosses the threshold potential V_T, a spike is generated and the membrane potential is reset to the resting potential V_R.

The input current for each neuron follows the dynamics in the following equation:

$$I(t) = I_{IN}(t) + K_{FB} \times e(t) + W(t)\,S(t) + \Delta N(t), \tag{6}$$

where $I_{IN}(t)$ is the external input current vector, $K_{FB} = K_{FB0}\,[1\ \text{-}1\ 0\ 0]^T$ the feedback coefficient vector, $e(t)$ the feedback error, calculated as the difference between the target ratio and the network's output inter-spike-interval ratio,

$$S_i(t) = \left\{ \begin{matrix} 1 & V_i(t) = \text{SPIKE} \\ 0 & \text{ELSE} \end{matrix} \right.$$

(i.e., $S_i(t) = 1$ if a spike occurred in neuron j in the last sample time), $W(t)$ the synaptic connectivity matrix [i.e., $W_{i,j}(t)$ is the synapse strength from neuron j to neuron I], $N(t)$ a normally distributed noise vector, and Δ the noise amplitude.

A simple algorithm is used to update the synapse strengths in the learning process, using the feedback control signal as the error to be minimized in a way similar to feedback error learning architecture (Kawato et al. 1987).

$$\frac{\partial W_{i,j}(t)}{\partial t} = -\mu U_{FB}(t), \tag{7}$$

where μ is a learning rate constant and $U_{FB}(t) = K_{FB0} \times e(t)$, the feedback control signal.

Results

Due to the fact that subjects were unpaid and that it was explained to them that under the Helsinki convention rules they were eligible to withdraw from the experiment at any time, two subjects decided to exercise that right, stopped tapping during the experiment and were extracted. One of the subjects did not show improvement in task performance (possibly due to lack of attention) and was excluded from the data analysis. The rest of the subjects (seven subjects) were able to learn the 3:2 tapping ratio, demonstrating reduction in task performance error during training and the resultant aftereffect.

Initially, the subjects performed the 1:1 tapping ratio easily and rather accurately, tapping in both fingers at the same rate and almost at the same time. During the early learning phase, the subjects kept tapping 1:1 and in order to track the target arc markers they occasionally corrected by tapping faster in the right hand or slower in the left hand to obtain a mean ratio of 3:2. After practice the fluctuations around the target ratio became smaller

Fig. 4 The augmented neural network, consisting of four Leaky-Integrate-and-Fire neurons with feedback signals and synapse adaptation

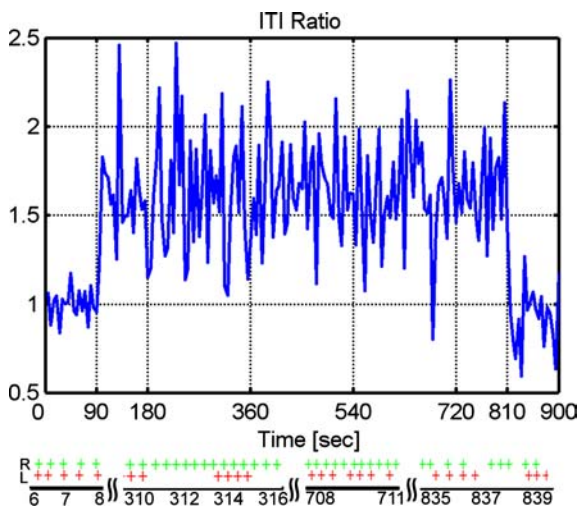as subjects gradually acquired the target 3:2 tapping ratio.

Due to the boring nature of the experiment, the subjects were only presented with a relatively short period (12 min) of training. Although they showed a significant learning curve, i.e., improvement in task performance, they reached only a preliminary stage of task acquisition and probably did not achieve automaticity during this short training phase.

In the last stage, when the target tapping ratio returned to 1:1, a similar phenomenon was observed where the subjects did not perform the 1:1 ratio easily and immediately but rather fluctuated around the 1:1 ratio in order to track the target arc markers. The tracking task was performed with reasonable accuracy; however, the variance in the tapping ratio was much larger than the variance in the first block before the training phase. It is important to note that the time scale of the reduction in these fluctuations was measured in units of minutes whereas the tapping occurred in time scale of seconds excluding simple feedback control oscillations, indicating an adaptation process and an aftereffect of adaptation.

An example for single subject measurements of tapping ratio and tap times during the trial is presented in Fig. 5.

Learning curves

In order to determine if a learning process took place during the trial, while the subjects were attempting to perform the tar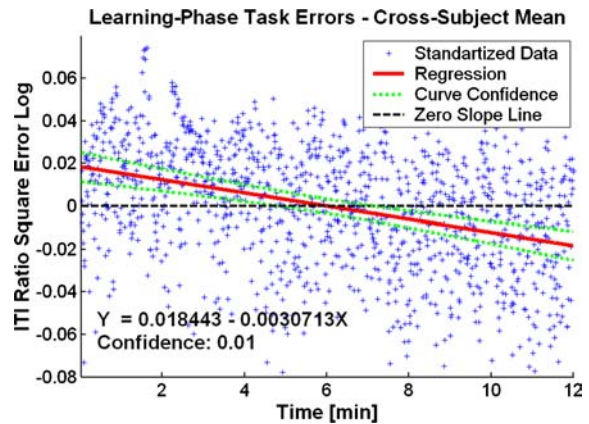get non-harmonic polyrhythm, we examined the square error of subject tapping frequency ratio, i.e., the difference between the target ratio and ITI ratio, squared. For detection of learning we considered the entire duration in which the target ratio was set to 3:2. This time period accumulates to a total of 720 s. We postulated that if negative error curves were observed in the experiment data, this would mean that a constant decrease in error took place and that this decrease could only be achieved via a learning mechanism. From the regression analysis we calculated the learning curve exponential time constant to be of an order of several hundreds of minutes; the time scale of this process is significantly longer than any physiological feedback loop delay in the human control system.

It is important to note that the term learning implies different things for different researchers; specifically, we wish to clarify that by using the term learning curves we do not intend to imply that the augmented feedback was removed. The learning curves in this section describe the acquisition of a new visuomotor mapping. We use the Engineering terminology where the terms adaptation and learning are used in contrast to feedback as described in the introduction.

Regression analysis results clearly indicated a negative curve on all of the subjects' square error log values during the training phase of the trial with $p < 0.05$ for each subject (both for the raw data and in normalized data) and with $p < {<}0.01$ for cross-subject mean data (Fig. 6). In order to perform inter-subject analysis, the experimental data were standardized by subtracting the mean and dividing by the standard deviation. The nor-

Fig. 5 The (*top*) ITI ratio of a single subject during the experimental trial. (*bottom*) raster plots of left and right hand tapping times in base stage, early learning stage, late learning stage and aftereffect stage. As can be seen from the plot, the relatively short training period does not enable the subject to perfectly learn the target ratio. Still, even in this short period of training, we did observe statistically significant learning *curves* and clear aftereffects of learning

Fig. 6 Learning *curve* by linear regression of cross-subject mean log of square ITI ratio error data in the duration of the training phase of the experiment, when target ratio is 3:2. In order to perform inter-subject analysis, experimental data were standardized by subtracting the mean and dividing by standard deviation (mean and standard deviation were calculated for each subject for the whole duration, 12 min, of the training phase). A significant ($p < {<}0.01$) *negative curve* can be observed, indicating that the error is being decreased through training. This figure summarizes the data analysis that was also performed separately per subject. A significant ($p < 0.05$) *negative curve* was observed for every subject for the *raw data* and the normalized data

malization was performed separately for the training phase and for the aftereffects phase.

Observation of the subjects during the trial gave an additional clue as to the nature of the learning process. We observed that subjects would initially correct the error by tapping either extremely fast or extremely slow with one of the hands, thus generating either very high or very low ITI ratios, and overshooting the target markers. In later stages of the trial the subjects were less extreme in their correction maneuvers and stayed closer to the target markers.

Aftereffects

Our hypothesis suggests that in addition to the learning curve, a secondary consequence of the learning process exists. If an internal representation of the task, body, or external world is acquired during performance and practice under specific conditions, it should be expected that when these conditions are changed this internal representation would need to adapt to allow optimal performance in the newly formed conditions. When the new task at hand is difficult and unfamiliar to the subject, the phenomenon observed is the aforementioned learning curve, which accounts for the gradual adaptation to the new environment; but when the environmental transition is made from a newly learned task to a more predominant stable task, a quicker transition would be visible. The first erroneous behavior after the return to the normal, well-known, condition is called an aftereffect of learning and the transition back to normal behavior is called the washout of the aftereffect. The learning curves, the aftereffects, and the washout curves are evidence of the internal representation. Aftereffects have been previously noticed in other motor tasks such as adaptation to force perturbations during reaching movements (Shadmehr and Mussa-Ivaldi 1994; Lackner and DiZio 1994; Karniel and Mussa-Ivaldi 2003).

In our experimental trials, subjects transitioned between a symmetric 1:1 ITI ratio target and a 3:2 non-harmonic ITI ratio target. We observed the learning and hypothesized that the learning curves represent an adaptation process and a plastic change within the internal representation. Such a change is not expected to have an immediate washout and therefore an aftereffect is to be expected.

In order to test this prediction we compared subject performance of the trivial 1:1 ratio before and after the 3:2 training stages of the trial (see Fig. 7). The comparison was done between square errors of tapping ratio (i.e., the same parameter used for learning curve analysis). The results indicated a significant ($p << 0.01$) difference between tapping ratio errors before and after the training stages.

These results confirm our prediction that an internal representation for the production of bimanual polyrhythms has been established or modified during the 3:2 tapping ratio training stage and thus deterioration in

performance of the natural 1:1 rhythm occurred when the natural feedback conditions are reintroduced.

Regression analysis of the aftereffect stage tapping ratio square error revealed a negative learning curve with steeper descent than the one observed during the learning of the 3:2 ratio (Training: -0.052 vs. Washout: -0.13). These slopes correspond to time constant in the order of hundreds of minutes for the learning phase and tens of minutes for the washout phase. The reduced time for the washout compared to the learning was expected, as in this stage the subject is trying to relearn the predominant 1:1 tapping ratio (Fig. 8).

Model simulations

The values of model parameters used in the simulations are: $dt = 0.01$, $I_{IN} = [1.7; 1.7; 0; 0]$, $K_{FB0} = 0.2$, $V_R = 0$, and $V_T = 1$. For convenience, we have normalized the timescale so that $R = 1$ and $\tau_m = 1$. Simulations have shown that the network can be trained by simultaneous change of multiple synapses but, on grounds of simplicity, we focus here on the case where only one of the synapses is changed during the learning process. Starting synaptic values were set to zero, except for the following: $W_{1,2} = W_{2,1} = 10$; $W_{3,1} = 45$, and noise amplitude was set to $\Delta = 2$. Both learning curves and aftereffects produced by the model simulations (Figs. 9, 10) closely match the ones observed in the experimental study (Figs. 6, 7). One should note that the rather monotonic reduction of mean square errors does not imply smooth transition from one tapping ratio to the other (1:1–3:2 and back). Our model contains nonlinear interactions that prefer harmonic polyrhythm and also include the feedback component that can generate the proper mean tracking and the observed fluctuations in the tapping ratios.
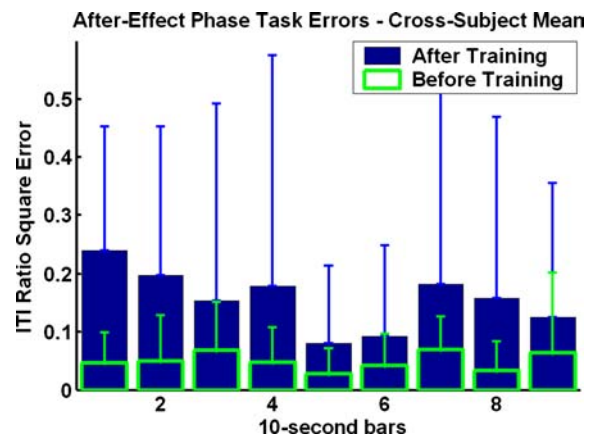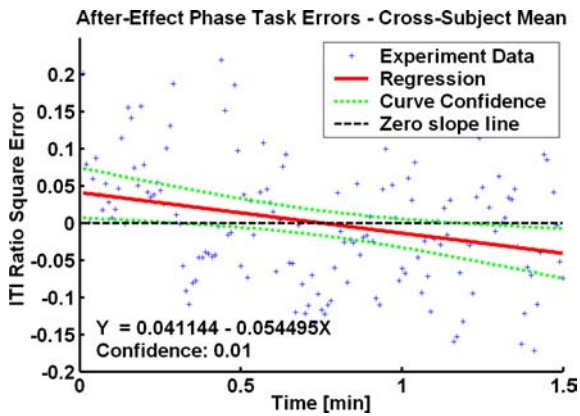

Fig. 7 Cross-subject mean ITI ratio square errors in 1:1 target ratio performance before and after training, averaged over 10 s intervals. Also shown are the positive $p = 0.01$ confidence intervals

Fig. 8 Learning *curve* by linear regression of cross-subject mean log of square ITI ratio error data in the duration of the aftereffect phase of the experiment, when the target ratio is 1:1. A significant ($p < 0.01$) *negative curve* can be observed, indicating that the *error* is being decreased
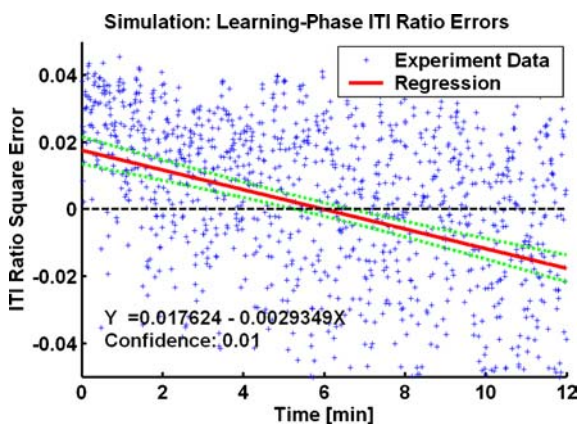
Fig. 9 Learning *curve* by linear regression of model simulation results. *Data* is the log of square ITI ratio error data in the duration of the training phase of the simulation, when target ratio is 3:2. A significant ($p < < 0.01$) *negative curve* can be observed, indicating that the error is being decreased
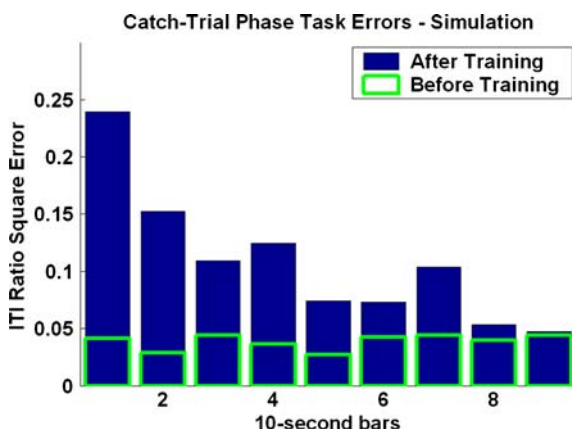
Fig. 10 Model simulation results of ITI ratio square errors in 1:1 target ratio performance before and after training

Discussion

A simple visuomotor transformation was used in this study to facilitate the training of bimanual tapping non-harmonic polyrhythms for the purpose of observing the learning dynamics of these difficult bimanual coordination patterns.

The experimental results provide new evidence for the existence of internal representations of bimanual, coordinative motor tasks. The first piece of evidence consists of a gradual decrease in task performance error, visible in the training stage of the trails. These findings suggest that a learning process occurs in the human motor control system during the training period of the experiment. The second piece of evidence includes the observed aftereffects and washout at the time when the visuomotor transformation is removed and the tapping target is reverted to one that subjects could easily perform before the training stage (1:1 tapping ratio). These aftereffects are apparent both by comparison between task performance of the easy rhythm before and after polyrhythm training, and by negative curves in task performance errors in the aftereffect phase. Combined with the learning curves in the training stage, these aftereffects are unequivocal evidence for the existence of an adaptive process that could be referred to as an internal representation of a learned task in the nervous system.

The aftereffects were observed when the task target was abruptly changed back to the 1:1 ratio, similar to the removal of perturbation in a catch trial. The time scale of learning and the presence of aftereffects distinguish between temporary boosts in performance that disappear when feedback is removed and adaptive change of internal representation. Only the latter will show aftereffects that last long after the change in the feedback regime.

In Zanone and Kelso (1992), and related studies (e.g., Lee et al. 1995; Swinnen et al. 1997), the disruption of dominant phase relations after learning of a novel phase relation is addressed. Our paradigm, although somewhat related to these studies, is considerably different in that it does not address relative phase relations between the hands explicitly but rather addresses frequency ratios, in which the relative phase is a constantly changing variable.

One should note that in this study we addressed only the distinction between feedback and adaptation and did not continue to explore long-term practice that may invoke skill learning (see Karniel and Inbar 2000 for discussion about the hierarchy of learning and adaptation). It might be possible that the observed aftereffects are present due to the short nature of the experiment (Lee et al. 1995), in which only the preliminary phase of learning has been done, and automaticity has not yet been achieved. It is obvious that humans can learn various tasks without one canceling another (e.g., we can learn to tap-dance and still be able to ride a bicycle a

minute later); multiple model architectures were proposed to address this capability (Wolpert and Kawato 1988; Karniel et al. 2001). However, in the first stage of learning, in some cases, a single model is adjusted (Karniel and Mussa-Ivaldi 2002) and the new task disrupts the previously known patterns as manifested in the aftereffect we observed. According to this theory, one may expect that in a long exposure to a single condition, e.g., the 2:3 ratio, the aftereffect in returning to the 1:1 ratio would be more significant; however, after practice in switching between 1:1 and 2:3, the aftereffect might be reduced. One can also expect the internal representation of 1:1 ratio to be more stable and therefore more difficult to modify and easier to return to after shifting to another representation, and indeed, we see this gap in the time scales in our results. In any case, this aftereffect, be it temporal or of a more permanent nature, consolidates the theory that the coordination control mechanism in the CNS undergoes some sort of task-related restructuring which we call the acquisition of an internal representation.

It is an experimentally validated fact that symmetric 1:1 tapping is a very stable tapping pattern, specifically with zero-phase or anti-phase relations between the hands (e.g., Cohen 1971; Kelso et al. 1979; Haken et al. 1985; Zanone and Kelso 1992). A more recent study measured human activities in a normal daily routine and discovered that most of our day-to-day actions are bimanually mirror-symmetric (Howard et al. 2004). This would suggest that the internal representation of symmetric bimanual coordination has practically years of training (in daily performance) and should therefore be very stable. In contrast, bimanual non-harmonic polyrhythms, and the 3:2 ratio in particular, are very rare in everyday actions, so it would be safe to say that this task is practically unlearned in the human control system. Therefore it is not surprising that the slope of the washout curve is much steeper than that of the learning curve.

The distinction between feedback and adaptation in control theory is made in two categories. The first concerns the changes occurring in the control system. While in adaptive control schemes actual system elements (parameters) are changed, in feedback control only the signals in the system change. The second differentiation method between adaptation and feedback, especially in physiological neural systems, is via the timescale of the process. In contrast to feedback loops in neural systems, which take up to a few seconds, adaptation of neural systems is a more lengthy process, requiring minutes to hours or even longer periods of time. The lengths of time in which the learning and washout occur in the experiments (tens of seconds to minutes) are far longer in duration then the visuomotor feedback loop latency (well known to be under 1 s). This significant difference in timescales of physiological feedback latency and learning processes effectively rules out the possibility of exclusive use of feedback in control of bimanual rhythmic movement and in learning of new bimanual coordination patterns.

Although feedback does not seem to be the exclusive mechanism behind acquisition of new bimanual coordination patterns, countless studies have shown that it plays a major role in the learning process. We have shown that feed forward control and adaptation are also present in the human control system, which governs bimanual movements. The roles and interactions between feedback and adaptation in the CNS are still mostly unknown and more experimental and analytic work is needed to determine the exact relations between these two mechanisms, although one can definitely conclude that they are complexly entwined.

A simple physiologically plausible neuronal model was developed after analytic exclusion of the possibility for a simpler neural model. The results obtained from the simulations closely match the data from the experimental trials. The model incorporates several key aspects of the bimanual coordination system. Primarily, 1:1 ratio synchronization and transitions from anti-phase to in-phase bimanual patterns, which are prominent phenomena in bimanual coordinated movements, are inherent to pulse coupled neuronal networks. Secondly, a feedback signal was used in the model to reflect the important role of visual and other types of feedback in the acquisition of new coordination patterns (Mechsner et al. 2001; Weigelt and Cardoso de Oliveira 2003). Finally, a simple learning algorithm applied to the neural network by changing synaptic connection strengths implicitly implemented an internal model of the target task in a way which may resemble processes related to learning of new coordination patterns in the CNS.

Our model captures the tendency for symmetry and synchrony between the limbs and at the same time the capability to adapt to altered feedback. It successfully combines dynamic learning with phase synchronization and ratio preference in a simple physiologically feasible framework, which we believe can be extrapolated for understanding and modeling of bimanual adaptation in particular and perhaps other multi-actuator human performance.

In executing the experimental protocol described herein, we have asked ten subjects to participate and removed three subjects from the data analysis, two of who asked to be withdrawn from the experiment and one who did not manage to learn the task. It is important to note that we do not think the subjects removed from the data analysis represent the percentage of the population not able to learn bimanual polyrhythms, but rather portray lack of motivation, perhaps caused by the voluntary nature of the experiment. We believe that, with sufficient motivation and time, the vast majority of the population would be able to learn this task through the interface described in this paper. Note that with this interface, a task that is extremely difficult (but possible) for untrained individuals (Deutsch 1983; Summers et al. 1993; Treffner and Turvey 1993) becomes relatively easy to learn for most subjects. With further investigation of the internal

representation, such interfaces and carefully designed altered feedback might be employed to develop new techniques for motor training in order to simplify the learning of complex tasks. It might also be possible employ these findings in order to devise diagnostic tools for revealing motor dysfunctions and other types of brain pathologies (Swinnen and Wenderoth 2004). Future work on this subject should include examination of the learning process during longer periods of training, acquisition of automaticity in task performance, and examination of the aftereffect phenomenon after long training and in the absence of feedback.

To conclude, by examining subject behavior during the process of learning novel bimanual coordination patterns, our study extends previous bimanual coordination studies, focused mainly on steady-state performance of bimanual tasks. Observation of these learning stages and the aftereffects of learning constitutes strong evidence that internal representations are used in the learning and performance of bimanual rhythmic movements. Furthermore, we suggest a simple model, which inherently contains fundamental aspects of bimanual coordination such as phase locking (Masuda and Aihara 2001) and transitions (Grossberg et al. 1997). Our model accounts for the adaptation as well as the coupling phenomena. Altogether, this study extends the notion of internal models beyond the well-studied area of reaching movements and may provide a new framework for future research of internal models in bimanual adaptation and other natural motor behaviors.

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