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The effect of motor-respiratory coordination on the precision of tracking movements: influence of attention, task complexity and training

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Abstract

Purpose: We investigated motor-respiratory coordination (MRC) in visually guided forearm tracking movements focusing on two main questions: (1) Does attentional demand, training or complexity of the tracking task have an effect on the degree of MRC? (2) Does MRC impair the precision of those movements? We hypothesized that (1) enhanced attention to the tracking task and training increase the degree of MRC while higher task complexity would reduce it, and (2) MRC impairs tracking precision.

Methods: Thirty-five volunteers performed eight tracking trials with several conditions: positive (direct) signal–response relation (SRR), negative (inverse) SRR to increase task complexity, specific instruction for enhanced attention to maximize tracking precision (“strict” instruction), and specific instruction that tracking precision would not be evaluated (“relaxed” instruction). The trials with positive and negative SRR were performed three times each to study training effects.

Results: While the degree of MRC remained in the same range throughout all experimental conditions, a switch in phase-coupling pattern was observed. In conditions with positive SRR or with relaxed instruction, we found one preferred phase-relationship per period. With higher task complexity (negative SRR) or increased attentional demand (strict instruction), a tighter coupling pattern with two preferred phase-relationships per period was adopted. Our main result was that MRC improved tracking precision in all conditions except for that with relaxed instruction. Reduction of amplitude errors mainly contributed to this precision improvement.

Conclusion: These results suggest that attention devoted to a precision movement intensifies its phase-coupling with breathing and enhances MRC-related improvement of tracking precision.

Key words: Entrainment; Phase coupling; Tracking precision; Attentional demand; Signal–response compatibility

Abbreviations

ANOVA	Analysis of variance
MRC	Motor-respiratory coordination
SRR	Signal–response relation

List of symbols

ΔA	Movement amplitude deviation
Δt	Phase deviation between tracking signal and movement
E	Tracking error
$m_{\max}$	Highest value of the movement signal per period
$m_{\min}$	Lowest value of the movement signal per period
$RP_{\max}$	Relative phase of $m_{\max}$ within inspiration or expiration
$RP_{\min}$	Relative phase of $m_{\min}$ within inspiration or expiration
s_0	Lowest value of the tracking signal per period
s_{100}	Highest value of the tracking signal per period
T_i	Time of inspiration
T_e	Time of expiration
T_{tot}	Time of total breath

Conditions

P1, P2, P3	Trials 1, 2, 3 with positive SRR
N1, N2, N3	Trials 1, 2, 3 with negative (inverse) SRR
S	“Strict” instruction to maximize tracking precision
R	“Relaxed” instruction: no particular attention to tracking precision required

Introduction

Limb movements, particularly rhythmical limb movements such as locomotion, are often coupled with respiration. Coupling or coordination means modulation of the temporal patterns of the related motor processes that may result in adoption of a common rhythm or a stable frequency ratio with a stable phase relation (entrainment). Coordination with breathing is not confined to locomotion but occurs with activities of every motor subsystem; it will further be referred to as motor–respiratory coordination (MRC). In MRC, the breathing rhythm is usually attracted by the rhythm of the concomitant movement (Kohl et al. 1981; Rassler et al. 1990; Siegmund et al. 1999; Ebert et al. 2000). This is not surprising as the rhythm of the non-respiratory movement is usually subject to a voluntary intention and hence, is more rigid than breathing rhythm. Rhythm and timing of breathing are finely regulated to meet metabolic demands with low energetic cost of respiratory work. These requirements might be compromised by modulation of the respiratory rhythm due to MRC. However, it has repeatedly been shown that MRC can persist even when the frequency of a non-respiratory movement changes over a wide range. In these situations, most subjects switch to other frequency ratios, thus avoiding extensive modifications of the respiratory pattern (Ebert et al. 2000). This is particularly evident during locomotor activities in specifically trained or experienced subjects (Amazeen et al. 2001; McDermott et al. 2003) and may improve their degree of MRC (Kohl et al. 1981; Sporer et al. 2007; Mahler et al. 1991; Bernasconi et al. 1995). A recent study has shown that specific frequency ratios have been learned within a short training interval of 20 minutes (Hessler and Amazeen 2014). Transition to other frequency ratios is considered to support the adaptation of subjects' ventilation to their metabolic demands and may reduce their oxygen consumption (McDermott et al. 2003; O'Halloran et al. 2012).

MRC, however, is not purely unilateral. The temporal pattern of a non-respiratory movement is affected by the respiratory rhythm (Rassler et al. 1990; Rassler and Kohl 2000). Attraction of a voluntary movement by the respiratory rhythm may compromise motor performance. In particular, this may have important consequences in fine motor actions such as precision

movements (Rassler et al. 1996; Rassler 2000). Precision movements play a more and more vital role in everyday life, e.g., for using smartphones or computers. They are often associated with a complex task requiring a high level of attention and concentration for successful performance. Hence, it is conceivable that precision of those movements can be impaired by MRC.

MRC has been found during fine motor actions such as hand, finger, head or eye movements, and even during sole rhythmical sensory input (Wilke et al. 1975; Haas et al. 1986; Sammon and Darnall 1994; Temprado et al. 2002; Rassler and Raabe 2003) indicating that MRC is not primarily dependent on mechanical relations or metabolic demands. In contrast, timing-related factors such as movement velocity, movement rate or breathing rate have a marked influence on MRC (Rassler and Kohl 1996; Ebert et al. 2000; Amazeen et al. 2001; Temprado et al. 2002; Mc Dermott et al. 2003; O'Halloran et al. 2012). Moreover, MRC can be stabilized when several muscle groups act synchronously or when a rhythmical sensory signal paces the movement rhythm (Rassler et al. 1990; Ebert et al. 2000; Hoffmann et al. 2012). Variability of the movement rhythm is reduced in these situations. In addition, the synchronous (or almost synchronous) action of the non-respiratory rhythms can amplify their attractive effect on the respiratory rhythm. Particularly, when a visual signal has to be tracked by finger or hand movements, oculo-manual coordination may additionally support MRC. A study comparing eye–hand tracking vs. eye-alone tracking of a visual target demonstrated that an addition of hand movements markedly improved tracking performance (Gauthier et al. 1988). In sinusoidal tracking movements with appropriate target frequencies, MRC could exceed 50% of total recording time (Ebert et al. 2000).

Visually guided tracking tests are a suitable model for studying precision movements. Tracking a visually presented target as accurately as possible by hand or forearm movements requires a high degree of attention and concentration, particularly when the task is highly complex. With training, tracking precision can be optimized although attentional demand is often reduced. However, little is known on the role of MRC on the performance of precision tracking movements. The present study was designed to investigate (1) whether

factors such as task complexity, attentional demand and training would affect the degree of MRC in a forearm tracking test and (2) whether the degree of MRC has an influence on the precision of tracking movements. Task complexity was modulated by varying the compatibility between tracking signal and tracking response (signal–response relation, SRR). Positive or direct SRR means a less complex task while complexity increased with inverse or negative SRR. Trials with positive and negative SRR were repeated for several times to study short-term training effects. Attentional demand was modified by instruction, that was, either a strict demand for maximum tracking precision or the information that tracking precision was not important. We hypothesized that high complexity of the motor task (i.e., tracking with negative SRR) might impair MRC while training would improve it. Increased demand for precision was expected to focus subjects' attention to the tracking task and thus, to stabilize MRC. On the contrary, if subjects knew that precision was not important, reduced attention might destabilize MRC. Further, we assumed that tracking precision would be compromised in periods of MRC.

Methods

Subjects

Experiments were performed in 35 voluntary healthy subjects (16 female, 19 male, aged 23 ± 2.6 years). None of them had neurological or motor disorders. Three subjects had allergic airway disorders but were completely free of symptoms at the time of the experiment. All subjects but two were right-handed; the two left-handed subjects regularly used their right hand for writing. Informed consent was obtained from all individual participants prior to the experiment. The study has been approved by the local ethics committee and has been performed in accordance with the ethical standards laid down in the Declaration of Helsinki.

Experimental set-up

Subjects were seated at a table looking onto a 17" monitor (Philips 107E20) at a distance of 70 cm. To guarantee fixed and comfortable head position, the chin was supported and the forehead was leaned against a horizontal bar. Both tracking signal and forearm movement were displayed on the screen as vertical bars in different colors. The tracking signal bar moved upwards and downwards according to a sinus function at a frequency of 0.3 Hz. This target rate was chosen according to previous results demonstrating that most stable entrainment patterns with a ratio between movement and breathing rates of 1:1 were observed at 0.3 Hz (Ebert et al. 2000).

When subjects put their forearm straight on the table, the angle between upper arm and forearm ranged between 130° and 150°. Their elbow was supported on a small upholstered pad on the table. The lower and upper visible margins of the movement bar represented angles between forearm and table surface of 10° and 45°, respectively, while the required movement amplitude ranged between 18° and 36°. Subjects were instructed to move their right forearm in order to match the tracking signal with the movement bar as precisely as possible. With this experimental setup subjects had to design exactly their movement amplitude to avoid large overshoots.

Forearm movements were measured using a goniometer that was attached to the radial side of upper arm and forearm. The goniometer signal was digitalized using DasyLab 3 software (Datalog, Mönchengladbach, Germany). This software also generated the tracking signal and movement bars presented on the screen.

Breathing was recorded using a Fleisch pneumotachograph (G. Hertel, Lengenfeld, Germany). Subjects breathed room air through a face mask. The breathing signal was also digitalized with DasyLab but was not visualized to the subjects.

Study protocol

After subjects were seated and equipped with measuring facilities, breathing at rest was recorded for 5–7 min. After that, they had the opportunity to practice tracking movements for

about 5 min in order to familiarize with the signal and the tracking task. The tracking experiment consisted of 8 trials lasting 5–6 min each with a resting interval of 3 min between trials. In the first six trials, tracking was performed three times with positive (P1–P3) and three times with negative SRR (N1–N3) in alternating order. Positive SRR means that upward movement of the tracking signal bar had to be responded by upward movement of the forearm, i.e., forearm flexion, and downward movement of the signal corresponded with forearm extension. With negative SRR, upward movement of the tracking signal was associated with upward movement of the movement bar on the screen but this had to be produced by downward forearm movement, i.e., extension. In the last two trials, subjects performed tests with positive SRR but with specific instructions. With the “strict” instruction (S), subjects were required to be more attentive to their tracking precision to surpass the results from the preceding trials. With the “relaxed” instruction (R), subjects were informed that high tracking precision was not required in this trial and would not be evaluated. Subjects were allocated randomly to group 1 (trial sequence P1–N1–P2–N2–P3–N3–S–R, $n = 18$) or group 2 (trial sequence N1–P1–N2–P2–N3–P3–R–S, $n = 17$).

After completion of all tests subjects were questioned about their motivation for the tests and their attention and fatigue during the experiment. All subjects stated that they were attentive and highly motivated to perform the tracking tests at their best and did not notice fatigue.

Parameters

All signals (tracking signal, goniometer signal and pneumotachogram) were digitalized at a sample rate of 100 Hz. An example of the resulting signal curves is shown in Fig. 1a. The time course of breathing was assessed as time of inspiration (T_i), time of expiration (T_e) and time of a total breath (T_{tot}). The main parameter of tracking precision was the tracking error (E) with low E values reflecting high tracking precision. E means the area between tracking and goniometer signals measured as the sum of differences between the signals. For each movement period, we determined E_{up} between the lowest (s_0) and the highest (s_{100}) value of the tracking signal, and E_{down} between s_{100} and the following s_0 (Fig. 1b). The amplitude of

the tracking signal reached from $s_0 = -2$ V to $s_{100} = +2$ V corresponding to angles between forearm and table surface of 18° and 36° , respectively. Additionally, we performed a cycle-by-cycle analysis of amplitude and phase deviation of the tracking movement. Movement amplitude deviation (ΔA) is the difference between $m_{\min}$ and s_0 ($\Delta A_{\min}$) and between $m_{\max}$ and s_{100} ($\Delta A_{\max}$) with $m_{\min}$ representing the lowest and $m_{\max}$ the highest value of the movement signal in the actual period. Phase deviation (Δt) between tracking signal and movement was calculated as the absolute phase difference between the time points of $m_{\min}$ and s_0 ($\Delta t_{\min} = |t_{\min} - t_0|$) and of $m_{\max}$ and s_{100} ($\Delta t_{\max} = |t_{\max} - t_{100}|$) in this period, respectively (Fig. 1b). Outliers exceeding the individual mean by more than three-fold were discarded.

Motor–respiratory coupling

For coupling analysis, we determined the relative phase of $m_{\max}$ ($RP_{\max}$) and $m_{\min}$ ($RP_{\min}$) within inspiration or expiration (marked by index i or e, respectively; Fig. 1a). The relative phase means the difference between the time points of $m_{\max}$ or $m_{\min}$, respectively, and the start of inspiration (0_i) or expiration (0_e) related to T_i or T_e . Periods of at least five subsequent breaths with $RP_{\max}$ or $RP_{\min}$ being distributed over less than 25 % of T_i or T_e were classified as coupled breaths and considered to represent MRC. The degree of coupling was assessed as the percentage of coupled breaths within each trial.

Additionally, we analyzed the distribution of $RP_{\max}$ and $RP_{\min}$ over breath duration to detect the preferred phase-relationship. Values of $RP_{\max}$ and $RP_{\min}$ were classified into groups of 5 % of T_i or T_e . The main peaks of the RP distribution were determined as those two adjacent groups with the highest frequency of $RP_{\min}$ and $RP_{\max}$, respectively. The main peaks of trial P1 that was considered to represent the baseline condition, were compared to the corresponding groups of all other trials to assess the effect of task condition on the preferred phase-relationship.

Finally, the effect of MRC on tracking precision and on breathing time course was assessed. For this analysis, we included all trials containing 25 – 75 % of coupled breaths (Table 1) and

performed an intra-trial comparison of respiratory and movement parameters between coupled and non-coupled breaths.

Statistical analysis

Results are presented as means $\pm$ SEM. Differences across conditions were tested for significance using Friedman repeated measures analysis of variance (ANOVA) on Ranks with a post-hoc pairwise multiple sample comparison according to the Student–Newman–Keuls Method. Additionally, a two-way ANOVA on Ranks was performed to investigate possible interaction effects on tracking parameters between the factors SRR (positive, negative) and repetitions (1–3). The distributions of RP were tested for homogeneity using the Brandt–Snedecor Chi-square test. Intra-trial comparisons between coupled and non-coupled breaths were performed using a Wilcoxon matched pairs signed rank test. p-values < 0.05 were considered to be significant.

Results

Degree of MRC

In general, most of the subjects ($n = 15$, 43%) presented poor MRC with less than 25 % of coupled breaths. In 12 subjects (34 %), we found moderate MRC (26-50 % of coupled breaths), and 6 subjects (17 %) presented good MRC (51-90 % of coupled breaths). Strong coupling, that is, stable entrainment, was observed in two subjects (6 %) with more than 90 % of coupled breaths. The overall degree of coupling was 34 ± 4 % (Table 1). None of the conditions had a significant influence on the degree of MRC. Although MRC was slightly reduced in the first trial with negative SRR, this was not significant and was completely abolished with a second and third repetition.

Phase-relationship between breathing and tracking movement

The preferred phase-relationship was a coincidence between phase transitions in both processes, i.e., start of inspiration or expiration and start of forearm flexion or extension. With positive SRR (P1), the predominant phase-relation was start of forearm flexion immediately before or after start of expiration (25 % of all RP_{min} ranging between 95 % T_i and 5 % T_e). The great majority of RP_{max} ranged in late expiration (37 % of all RP_{max} ranging between 80 and 90 % T_e , Fig. 2). With repetitions, this main peak became lower (P2: 35 %, P3: 31 %, $p < 0.05$, data not shown). A significantly different distribution was obtained with negative SRR (N1): Both RP_{min} (start of extension) and RP_{max} (start of flexion) presented two peaks, one around the start of expiration (RP_{max} 18 %, RP_{min} 13 %) and the other one in late expiration (RP_{max} 19 %, RP_{min} 24 %, Fig. 2). The late expiration peaks changed significantly only during the second repetition (N3) in a differential way: the RP_{max} peak increased (N3: 24 %, $p < 0.05$), and the RP_{min} peak decreased (N3: 21 %, $p < 0.05$, data not shown).

With reduced attentional demand (condition R), the distribution of RP_{max} and RP_{min} was almost the same as in trial P1 (34 % of all RP_{max} ranged between 80 and 90 % T_e ; 27 % of all RP_{min} ranged between 95 % T_i and 5 % T_e). With the “strict” instruction, the distribution was similar but two additional small peaks developed (8 % of RP_{min} between 80 and 90 % T_e and 6 % of RP_{max} between 95 % T_i and 5 % T_e , Fig. 2)

Precision of tracking movements

No differences in tracking precision were observed between group 1 and group 2.

Influence of task conditions: Tracking movements were performed more precisely with positive SRR (P1: E_{up} 0.42 ± 0.01 V, E_{down} 0.38 ± 0.01 V) than with negative SRR (N1: E_{up} 0.48 ± 0.02 V, E_{down} 0.49 ± 0.02 V, $p < 0.001$). Note that E_{up} is the tracking error of flexion when SRR is positive, and of extension when SRR is negative, i.e., inverse. Training did not significantly improve tracking precision in each of the two conditions (Fig. 3a). The differences in tracking precision were mainly an effect of phase deviation between tracking signal and movement (Δt), which was smaller with positive than with negative SRR. With

positive SRR, training had no effect on Δt . However, in the condition of negative SRR, Δt significantly decreased with repetitions (Fig. 3b). A significant interaction between the factors SRR and repetition existed for $\Delta t_{\max}$ ($p = 0.008$). In both conditions, the amplitude of forearm flexion (i.e., $\Delta A_{\max}$ with positive SRR, $\Delta A_{\min}$ with negative SRR) was more precise than that of forearm extension, and this did not change with repetitions (Fig. 3c).

Tracking errors were significantly smaller when subjects were requested to maximize their tracking precision (condition S: $E_{\text{up}} 0.35 \pm 0.01$ V, $E_{\text{down}} 0.31 \pm 0.01$ V). In contrast, when subjects were informed that their tracking precision had no particular value (condition R), tracking errors were significantly greater ($E_{\text{up}} 0.54 \pm 0.04$ V, $E_{\text{down}} 0.53 \pm 0.05$ V, $p < 0.001$) than in condition S and even than in condition P1. When subjects received the “strict” instruction, they mainly reduced their amplitude deviation ($\Delta A_{\max} 0.02$ V, $\Delta A_{\min} 0.09$ V) while phase deviation changed only slightly compared to condition P1. With the “relaxed” instruction (condition R), subjects produced a greater amplitude deviation than in the P and S conditions but significantly decreased their phase deviation (Fig. 3b, c).

Influence of MRC: The main finding of this study was that MRC was associated with higher precision of tracking movements. In coupled breaths, the tracking error E was significantly reduced in all conditions. This difference was particularly strong in the condition with negative SRR and remained stable with repetitions. The “strict” but not the “relaxed” instruction was also associated with higher precision in periods of MRC (Fig. 4).

Improved tracking precision mainly resulted from a reduction of amplitude deviation. With positive SRR, $\Delta A_{\max}$ was significantly lower in coupled than in non-coupled breaths, this means, the amplitude of forearm flexion was more precise in periods of MRC. This effect diminished with repetitions; there was no significant difference in trial P3. In the negative SRR condition, a smaller $\Delta A_{\min}$ in coupled breaths also indicated that flexion amplitude was more exactly restrained in MRC periods. This difference, however, was not significant and did not change with training. When enhanced tracking precision was requested (condition S), flexion amplitude ($\Delta A_{\max}$) was significantly reduced in coupled breaths but this effect was

completely absent in the “relaxed” condition (R). Phase deviation ($\Delta t_{\max}$ and $\Delta t_{\min}$) was similar in coupled and non-coupled breaths in all conditions (Table 2).

Temporal breathing pattern

Influence of tracking movement and task conditions: At rest, breathing rates varied from 7.6 to 21.3 min⁻¹ (mean 14.8 ± 0.6 min⁻¹) with T_i being 1.7 ± 0.09 s, T_e 2.6 ± 0.11 s and T_{tot} 4.3 ± 0.20 s. With the start of an additional tracking movement, breathing rate significantly increased to 18.3 ± 0.4 min⁻¹ ($p < 0.001$). Breath duration was shortest in the first trial (T_i 1.3 ± 0.05 s, T_e 2.0 ± 0.05 s, T_{tot} 3.3 ± 0.09 s) irrespective of the SRR type. In the condition of positive SRR (P2, P3), T_i , T_e and T_{tot} increased with training towards resting level. With negative SRR, only T_i increased with training while T_e and T_{tot} remained in the same range as in N1.

When highest tracking precision was required (condition S), T_{tot} was also shorter than at rest but was significantly longer than in trial P1. With the “relaxed” instruction, T_i and T_e and consequently, T_{tot} were longer than in P1 and N1 but they were not significantly different from breathing at rest or in condition S (Fig. 5).

Influence of MRC: In periods of MRC, breaths tended to be shorter than in non-coupled breaths. This was mainly due to a reduction of T_i . Only in condition R, T_e was significantly shorter than in non-coupled breaths. A significant reduction of T_{tot} was observed only in conditions P3 and R while in all trials with negative SRR and with “strict” instruction breath duration remained at the same level as in non-coupled breaths (Table 3).

Discussion

Effects of task conditions on MRC

MRC is a common phenomenon during rhythmical movements in animals and humans, but stable entrainment is not always achieved. In the present study, only two subjects presented

stable entrainment in all tests while about 75 % of all subjects showed MRC in less than 50 % of all recorded breaths. This distribution is in accordance with previous findings in various types of rhythmic non-respiratory movements (van Alphen and Duffin 1994; Rassler and Raabe 2003; Hoffmann et al. 2012).

Contrasting to our hypothesis, there were no significant differences in the degree of MRC across the conditions. A recent study on coordination between breathing and rhythmic arm movements showed that cognitive loads and instructions induced shifts in frequency ratio and relative phase, which, however, did not necessarily result in more stable coordination patterns (Hessler and Amazeen 2009). In the present study, we found large interindividual differences. For instance, a comparison between conditions N1 and P1 showed that 15 subjects improved their MRC degree in condition N1 indicating that enhanced attention and movement control prevailed and thus, may have promoted MRC. In contrast, 14 subjects had a lower degree of MRC in N1 than in P1; in seven of them, the difference was 15 % or even more. These results indicate that task complexity, attentional demand and training exert heterogeneous effects on MRC. In particular, attentional demand is modified by other conditions: it is supposed to increase with higher task complexity but to decrease with training. Moreover, the degree of MRC mainly estimates occurrence and stability of entrainment, corresponding to von Holst's absolute coordination (von Holst 1939). Interactions that are not strong enough to achieve entrainment [so-called relative coordination (von Holst 1939)] may remain undetected with this criterion but can be brought to light by distribution of the relative phase.

Coordination is associated with adoption of a certain phase relationship, which often consists in coincidence of "anchor points", that is, points of maximum angular excursion (Byblow et al. 1994). In MRC, start of a movement phase preferably coincides with start of inspiration or expiration (Haas et al. 1986; Rassler et al. 1990; Rassler 2000; Ebert et al. 2002; Temprado et al. 2002). Several studies reported a preference of coupling with the transition from expiration to inspiration (Kohl et al. 1981; Amazeen et al. 2001) while others found coupling of movement with expiration onset to be the preferred and most stable phase relationship

(Wilke et al. 1975; Temprado et al. 2002). The latter corresponds with our present finding that subjects in a tracking task with positive SRR preferentially started flexion of the forearm at the beginning of expiration. One might argue that mechanical interactions would promote expiration during forearm flexion with the elbow supported. Indeed, in rowing, certain phase relationships between stroke and breath are advantageous with respect to ventilation and breathing pattern (Siegmund et al. 1999). However, the range of flexion angles required in the present experiment and the very low work load of the tracking movements preclude a relevant mechanical interaction.

The second main peak in late expiration is rather considered to be a secondary peak. This is illustrated by the following rough calculation: With a tracking signal rate of 0.3 Hz, one movement cycle (flexion + extension) lasts 3.3 s on average. As expiration is usually longer ($T_e = 2.0$ s on average in coupled breaths) than inspiration ($T_i = 1.4$ s on average in coupled breaths), forearm extension starts about 1.7 s after start of expiration, i.e., after 85 % T_e on average. This pattern was typical for situations with lower task complexity and attentional demand (positive SRR, second or third repetition, “relaxed” instruction). When the tracking task was more complex such as in conditions with negative SRR, subjects adopted a four-peak pattern, that is, they tended to couple each half-period of the forearm movement with one of the respiratory phase transitions. The augmented complexity of this tracking task requires increased attention and, more specifically, a higher degree of conscious control to each phase of the movement. This can amplify the attracting effect of the tracking movement on breathing rhythm as reflected in the two additional peaks in relative phase distribution. A study on multifrequency ratios in MRC demonstrated that highly compatible visual feedback can improve task performance while less compatible displays may even compromise performance (Hessler et al. 2010). Negative SRR impairs eye–hand coordination and thus, may interfere with the coupling between breathing and arm movement. Studies on MRC during piano playing illustrate this discrepancy. When experienced pianists played a simple piece without thumb passages, phase coupling between the first keystroke in a bar and start of inspiration or expiration was frequently observed (Ebert et al. 2002). On the contrary,

when arpeggios with thumb passages were to play, meaning a much more complex movement, MRC occurred very scarcely (Nassrallah et al. 2013). Performing highly complex movements can impede the development of MRC or even stable entrainment. This may be advantageous as a lower degree of MRC allows greater flexibility in adapting movement performance to the complex requirements of the motor task.

The additional two peaks in the relative phase distribution also appeared when highest accuracy was requested (condition S) but they were smaller than those in the conditions with negative SRR (cf. Fig. 2). The increased attentional demand associated with this instruction had a less specific effect on motor control than complexity of the task. As the tracking signal in this condition moved in parallel with the forearm, a strategy of coupling only one reference point in movement (preferably start of flexion) with one reference point in breathing (preferably start of expiration) was favored, while the tighter coupling pattern (half-period by half-period) occurred less frequently than in a highly complex task.

Effects of task conditions on breathing pattern and tracking precision

Effects on breathing pattern: Starting a movement is associated with an initial acceleration of breathing, even if the additional metabolic load is negligible. Bell and Duffin (2006) observed a rise in breathing frequency of more than 20 % at the onset of passive rhythmic leg movement, which was in the same range as that found in the present study at the start of forearm tracking movement. Increased mental activity elicits an increase in breathing rate, which is more pronounced when particular attention is required. Just opening the eyes significantly increased breathing rate by 6 % while starting to read a text induced a further increase of additional 6 % (Shea et al. 1987). The extent of this increase depended on the difficulty of the cognitive task (Mehler et al. 2009). In contrast, relaxation is associated with a decrease in respiratory frequency (Blumenstein et al. 1995). In our study, we observed the largest increase in respiratory frequency (i.e., decrease in T_{tot}) in conditions P1, N1 and S, which were the conditions with the highest attentional demand. Repetitions familiarized the subjects with the tracking task as reflected in a re-increase in T_{tot} , particularly in P2 and P3.

The lowest demand for attention and concentration was expected in condition R when subjects were informed that their tracking precision was of minor importance. In this trial, average breath duration was longer than in all other tracking trials and was only insignificantly lower than at rest.

Effects on tracking precision: Both attentional demand and complexity of the tracking task affected tracking accuracy. Enhanced complexity of a task with negative SRR (conditions N1–N3) impaired tracking precision although intense attention and concentration of subjects to this task has been expected and was confirmed by a marked reduction in T_{tot} . Specifically, phase deviation was enlarged in these trials. Repetitions induced a slight decrease of tracking errors in conditions N2 and N3, which was based on a significant decrease in phase deviation. Although training has been shown to improve the precision of pursuit tracking movements of both eyes and hand (Gauthier et al. 1988), two or three runs were not sufficient to achieve a significant improvement of tracking precision. With repetitions, subjects may have developed a certain routine and thereby, reduced their attention. In tests with positive SRR, repetitions (P2, P3) did not reduce tracking errors at all. In situations with high attentional demand but lower task complexity such as in condition S, tracking precision was significantly better than in all other test conditions. In this condition, subjects reduced tracking errors by reduction of amplitude errors but on the cost of greater phase deviation. In contrast, when subjects were allowed to be less attentive to their tracking precision (condition R), they produced greater tracking errors and, particularly, amplitude deviations while phase deviations were significantly lower than in the other conditions. This indicates that instructions manipulating the required tracking precision mainly focused subjects' attention to the amplitude rather than to timing and phase of the movement. Correspondingly, during learning of precision forearm movements, amplitude-related parameters needed more time to reach plateau values than time-related parameters (Flament et al. 1999). In voluntary limb movements, activation of synergistic muscles is organized by amplitude-dependent regulation of contraction velocity so that the time to contraction peak remains constant, which is a highly economic strategy to achieve high movement precision. The motor program

encodes the amplitude of the voluntary movement by neural activity to the antagonistic muscles (Freund 1983). Correction of the movement amplitude requires continuous adjustment of the neural activity to flexor and extensor muscles. This was performed more successfully in conditions with higher attentional demand. In addition, it should be considered that reduction of amplitude deviation may be supported, to a minor portion, by anatomical features such as contact of the forearm with the biceps muscle, which are mainly relevant for limitation of forearm flexion.

Effects of MRC on breathing pattern and tracking precision

In contrast with our hypothesis, this study showed that in periods of MRC, precision of tracking movements was even higher than without coupling. This means that the performance of such fine motor actions is not compromised by the respiratory rhythm. This corresponds with the results of two previous studies on MRC and tracking precision under conditions of increased respiratory drive using mild hypercapnia. These experiments aimed at reducing the subordination of breathing to a non-respiratory movement and, in turn, enhancing the influence of breathing on this movement. In contrast to the hypotheses of these studies, tracking performance was not impaired by respiratory influences but a more sensitive response of breathing to sensorimotor stimuli was found under hypercapnia (Rassler et al. 1999). In periods of MRC, breathing was more regular under hypercapnic conditions resulting in longer and more stable MRC periods compared to normocapnia (Ebert et al. 1998).

In the present study, we observed only marginal changes in breath duration within periods of MRC. This confirms previous findings demonstrating that MRC predominantly reduces variability of breathing rhythm (Ebert et al. 1998; Ebert et al. 2000). The most pronounced coordination-related changes in breath duration were found in conditions P3 and R. In these conditions, attentional demand was lowest as reflected by longer breath duration.

In contrast, the transition from rest to the first experimental run was accompanied by a substantial increase in breathing rate. Although in the first trial, average breath duration was 3.3 s, thus perfectly matching the target rate, this initial increase did not immediately result in entrainment. This fully confirms previous findings (Rassler et al. 1996; Ebert et al. 2002; Rassler and Raabe 2003). However, only slight modulations in breath duration were then sufficient to entrain the respiratory rhythm to that of the tracking movement. As a consequence, entrainment is possible without impairing the homeostatic function of breathing. Significant changes in breathing pattern, which are associated with significant changes in ventilation and oxygen uptake, may occur in periods of coordination. In a previous study, we observed that coordination-related increases or decreases of the respiratory rate were accompanied by increases and decreases, respectively, of ventilation despite compensatory changes in tidal volume. However, those periods were usually short and did not substantially affect breathing pattern and oxygen uptake over a longer interval of time (Rassler and Kohl 2000). Our present results rather indicate that the interaction of breathing with tracking movement is beneficial for tracking performance. In all conditions except for the “relaxed” condition, tracking errors were significantly smaller in periods of MRC. As this effect decreased with repetitions in conditions with positive (P3) but not with negative SRR (N3), we assume that subjects’ attention to the tracking task is involved in this MRC-associated improvement of tracking precision. In addition, restriction of flexion amplitude and hence, of amplitude errors, considerably contributes to enhanced tracking precision in periods of MRC. The strongest restriction of flexion amplitude was observed in condition S – a condition with high attentional demand but lower task complexity. This finding confirms our notion that the degree of attention significantly amplifies the effect of MRC on tracking precision.

Conclusions

In contrast to our first hypothesis, complexity or attentional demand of a rhythmical tracking movement does not affect the degree of its coupling with breathing. However, the present results clearly show that these factors induce a switch in phase-coupling strategy to a tighter

coupling pattern. When higher attention to the motor task is demanded, either by instruction or – even more – by task complexity, a tendency to couple both movement “anchor points” to both respiratory phase transitions has been observed. Although phase coupling is an important property of coordination, this tighter coupling pattern does not necessarily increase the degree of MRC, i.e., the number of entrained breaths.

Moreover, the results of the present study demonstrate that – contrasting to our second hypothesis – MRC does not impair but even improves the precision of tracking movements. MRC-related precision improvement was mainly achieved by reduction of movement amplitude, thus limiting amplitude errors. This effect was greater in conditions with high overall tracking precision, i.e., conditions with lower complexity of the tracking task but normal to high attentional demand (P1, P2, S). Requiring maximum attention improves the precision of visually guided tracking movements, and this may be enhanced in periods of MRC.

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Compliance with ethical standards

Conflict of interest

The authors declare that they have no conflict of interest.

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Figures and Tables

Fig. 1

Fig. 1: a) Example of recorded signals. Parameters of motor–respiratory interaction: RP, relative phase: difference between the start of inspiration (0_i) or expiration (0_e) and t_{max} ($RP_{max,i}$ and $RP_{max,e}$) or t_{min} ($RP_{min,i}$ and $RP_{min,e}$). b) Parameters of tracking movement: E, tracking error: sum of differences between tracking signal and goniometer signal (movement); E_{up} , tracking error determined from minimum (s_0 , t_0) to maximum (s_{100} , t_{100}) within a period of tracking signal; E_{down} , tracking error determined from s_{100} , t_{100} to s_0 , t_0 ; Δt , phase deviation: absolute phase difference between tracking and goniometer signals; Δt_{min} , absolute phase difference between t_{min} and t_0 ; Δt_{max} , absolute phase difference between t_{max} and t_{100} ; ΔA , amplitude deviation: difference between maxima and minima, respectively, of tracking and goniometer signals; ΔA_{min} , difference between m_{min} and s_0 ; ΔA_{max} , difference between m_{max} and s_{100}

Fig. 2

Fig. 2: Distribution of relative phase (RP) in conditions P1, N1, S and R. RP is the difference between the start of inspiration (0_i) or expiration (0_e) and $t_{\max}$ ($RP_{\max}$, black columns) or $t_{\min}$ ($RP_{\min}$, gray columns), given in percent of T_i or T_e , respectively (cf. Fig. 1a)

Fig. 3

Fig. 3: a) Tracking error E [V], b) phase deviation Δt [ms], c) amplitude deviation ΔA [V]. Data are given as means $\pm$ SEM. Significance marks: * significant vs. corresponding P; + significant vs. N1; # significant vs. P1; $\square^{*}$ S significant vs. R

Fig. 4

Fig. 4: Tracking error E [V] in non-coupled (black columns) and coupled breaths (white columns). Data are given as means $\pm$ SEM. Asterisks mark significant differences between non-coupled and coupled breaths: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

Fig. 5

Fig. 5: Time course of breathing: time [s] of inspiration (T_i), expiration (T_e) and total breath (T_{tot}). Data are given as means $\pm$ SEM. Significance marks: * significant vs. rest; # significant vs. P1; + significant vs. N1

Table 1: Frequency of coupling (in % of all recorded breaths)

Subject	P1	P2	P3	N1	N2	N3	S	R	Ind.mean
1	91%	99%	100%	97%	99%	100%	89%	88%	95%
2	9%	46%	38%	0%	24%	42%	52%	90%	38%
3	98%	91%	94%	77%	92%	90%	99%	97%	92%
4	10%	0%	27%	11%	28%	18%	26%	0%	15%
5	0%	0%	0%	0%	0%	0%	43%	0%	5%
6	0%	24%	14%	21%	32%	28%	0%	7%	16%
7	23%	79%	65%	37%	47%	55%	57%	24%	48%
8	0%	0%	38%	37%	42%	56%	65%	0%	30%
9	5%	60%	59%	34%	46%	44%	25%	39%	39%
10	95%	94%	94%	10%	55%	83%	91%	84%	76%
11	5%	33%	30%	7%	0%	28%	69%	33%	26%
12	88%	71%	82%	40%	87%	79%	68%	84%	75%
13	43%	62%	20%	47%	60%	28%	48%	26%	42%
14	0%	10%	12%	0%	41%	16%	27%	15%	15%
15	12%	0%	0%	8%	23%	27%	14%	13%	12%
16	80%	93%	91%	75%	73%	78%	27%	69%	73%
17	53%	46%	16%	43%	77%	73%	11%	21%	42%
18	82%	87%	61%	83%	91%	57%	70%	26%	70%
19	44%	20%	27%	38%	0%	11%	0%	12%	19%
20	12%	7%	0%	13%	21%	14%	16%	19%	13%
21	67%	24%	9%	41%	29%	39%	17%	43%	34%
22	0%	5%	5%	0%	0%	5%	0%	0%	2%
23	0%	22%	26%	0%	5%	0%	5%	21%	10%
24	15%	0%	0%	57%	0%	16%	14%	15%	15%
25	7%	7%	22%	0%	0%	0%	0%	14%	6%
26	0%	14%	0%	0%	0%	47%	11%	11%	10%
27	78%	65%	81%	11%	14%	16%	24%	80%	46%
28	58%	63%	64%	61%	70%	67%	39%	0%	53%
29	33%	13%	9%	0%	10%	0%	25%	0%	11%
30	0%	0%	5%	6%	0%	0%	6%	10%	3%
31	0%	0%	5%	0%	0%	0%	5%	0%	1%
32	67%	7%	7%	52%	49%	26%	29%	14%	31%
33	46%	53%	55%	54%	86%	63%	66%	57%	60%
34	47%	15%	22%	28%	8%	14%	42%	46%	28%
35	39%	31%	23%	57%	33%	23%	16%	56%	35%
Mean	34%	35%	34%	30%	36%	36%	34%	32%	33,9%
SEM	6%	6%	5%	5%	5%	5%	5%	5%	4%

Shaded fields represent trials chosen for direct comparison of respiratory and movement parameters between coupled and non-coupled breaths. Ind.mean: average individual coupling frequency

Table 2: Phase deviation (Δt) and amplitude deviation (ΔA) in non-coupled (nc) and coupled (c) breaths

	$\Delta t_{\max}$ (nc) [ms]	$\Delta t_{\max}$ (c) [ms]	$\Delta t_{\min}$ (nc) [ms]	$\Delta t_{\min}$ (c) [ms]
P1	71 ± 17	79 ± 19	69 ± 14	62 ± 14
P2	74 ± 17	70 ± 16	66 ± 16	71 ± 11
P3	63 ± 11	76 ± 13	49 ± 11	51 ± 9
N1	105 ± 11	86 ± 12	90 ± 13	105 ± 11
N2	85 ± 13	76 ± 12	102 ± 17	100 ± 13
N3	83 ± 10	$46 \pm 9^*$	82 ± 12	64 ± 15
S	69 ± 11	89 ± 15	54 ± 8	52 ± 8
R	50 ± 11	46 ± 6	32 ± 9	56 ± 18

	$\Delta A_{\max}$ (nc) [mV]	$\Delta A_{\max}$ (c) [mV]	$\Delta A_{\min}$ (nc) [mV]	$\Delta A_{\min}$ (c) [mV]
P1	95 ± 16	$39 \pm 17^*$	-74 ± 29	-49 ± 14
P2	102 ± 27	$26 \pm 17^*$	-86 ± 21	-64 ± 23
P3	146 ± 37	84 ± 36	-137 ± 25	-119 ± 20
N1	104 ± 31	114 ± 24	-31 ± 26	0 ± 20
N2	85 ± 28	108 ± 35	-16 ± 36	20 ± 23
N3	79 ± 29	105 ± 30	-52 ± 43	-11 ± 32
S	65 ± 26	$-7 \pm 16^*$	-107 ± 21	-126 ± 17
R	139 ± 56	113 ± 48	-197 ± 37	-216 ± 51

Data are given as means $\pm$ SEM. Asterisks mark significant differences between non-coupled and coupled breaths with $p < 0.01$

Table 3: Time of inspiration (T_i), expiration (T_e) and total breath (T_{tot}) in non-coupled (nc) and coupled (c) breaths

	T_i (nc) [s]	T_i (c) [s]	T_e (nc) [s]	T_e (c) [s]	T_{tot} (nc) [s]	T_{tot} (c) [s]
P1	1.45 ± 0.12	1.33 ± 0.05	2.16 ± 0.10	2.00 ± 0.04	3.60 ± 0.20	3.33 ± 0.03
P2	1.41 ± 0.05	1.34 ± 0.02	2.09 ± 0.06	1.99 ± 0.02	3.47 ± 0.08	3.33 ± 0.01
P3	1.68 ± 0.17	1.57 ± 0.15 *	2.19 ± 0.14	2.08 ± 0.16	3.88 ± 0.29	3.65 ± 0.29 *
N1	1.34 ± 0.05	1.33 ± 0.03	2.00 ± 0.04	2.01 ± 0.03	3.34 ± 0.08	3.34 ± 0.01
N2	1.47 ± 0.08	1.39 ± 0.05 *	2.07 ± 0.08	1.97 ± 0.05	3.53 ± 0.08	3.36 ± 0.01
N3	1.53 ± 0.15	1.53 ± 0.18	2.16 ± 0.10	2.09 ± 0.12	3.70 ± 0.23	3.62 ± 0.29
S	1.50 ± 0.09	1.37 ± 0.03 *	2.12 ± 0.10	1.98 ± 0.02	3.63 ± 0.18	3.35 ± 0.03
R	1.48 ± 0.04	1.42 ± 0.05 **	2.18 ± 0.05	2.02 ± 0.05 *	3.66 ± 0.05	3.44 ± 0.08 **

Data are given as means $\pm$ SEM. Asterisks mark significant differences between non-coupled and coupled breaths (* $p < 0.05$, ** $p < 0.01$)