Relationship between improvements in motor performance and changes in anticipatory postural adjustments during whole-body reaching training

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Abstract

Anticipatory postural adjustments (APAs) provide postural stability and play an important role in ensuring appropriate motor performance. APAs also change in various situations. However, it is unknown whether changes in APAs during repetitive movement training contribute to improvement in motor performance. This study aimed to investigate the relationship between improvement in motor performance and changes in APAs during repeated reaching training, as well as the learning effects on APA changes. Sixteen healthy subjects (23 ± 2 years of age) stood barefoot on a force platform and reached as quickly and accurately as possible to a target placed at their maximum reach distance immediately following a beep signal in a reaction time condition. Whole-body reaching training with the right arm was repeated 100 times for three consecutive days. Motor performance and APAs were evaluated on the first day, after discontinuation of training for one day, and again at three months. In addition, reaching with the left arm (untrained limb) was tested on the first and the fifth training day. Body position segments were measured using three-dimensional motion analysis. Surface electromyography of eight postural muscles in both lower limbs was recorded. Kinetics data were recorded using the force platform. Whole-body reaching training induced not only improvements in motor performance (e.g. increased peak hand velocity), but also changes in APAs (e.g. earlier APA onset and increased amplitude). These changes were strongly correlated with and occurred earlier than improvements in motor performance. The learning effects on APAs were retained after the discontinuation of training and were generalized to the untrained limb. These results suggest that change in APAs contributes to improvement in motor performance; that is, the central nervous system may be able to adapt APAs for improvement in motor performance.

Keywords: focal learning, reaching movement, anticipatory postural adjustment, muscle activity, motor performance

1. Introduction

Motor learning is a set of processes associated with practice or experience leading to relatively permanent changes in performance parameters and electromyographic activity for movement (Schmidt, 1988). Repetitive training in a motor task leads to improvements in motor performance, which is defined in terms of accuracy, force, reaction time, movement time, and peak velocity (Singer, 1968; Winstein & Schmidt, 1990). In particular, a reaching movement to touch or grasp an object is a motor task commonly used to investigate motor learning mechanisms, and is an important action in daily life. Postural stability is well known to influence the performance of reaching movements. For example, when sitting subjects pushed a bar in front of them with maximal force as rapidly as possible, the push force was enhanced by limiting the area of contact between the thigh and seat (Le Bozec & Bouisset, 2004). The peak hand velocity during an arm pointing task in an erect posture increased when the base of support size was enlarged (Yiou, Hamaoui, & Le Bozec, 2007). Thus, postural control including postural stability may be a major factor for improvements in motor performance.

Changes in postural control are also induced through practice or repeated experience. For example, postural sway and postural responses to repeated rotational or horizontal support surface perturbation clearly decrease after a few cycles when the amplitude of the perturbation is constant (Horak, Diener, & Nashner, 1989; Nashner, 1976). Repeated perturbation training to induce a loss of balance during gait using a low-friction moveable platform (Bhatt, Wening, & Pai, 2006; Pai, Wang, Espy, & Bhatt, 2010), during treadmill stepping over an obstacle with minimal foot clearance and without visual information about the obstacle, which appears with predictable timing (Lam & Dietz, 2004), or during gait on an unexpected soft support surface embedded in hard walkway (Bierbaum, Peper, Karamanidis, & Arampatzis, 2010) leads to rapid adaptation of lower limb reactive responses. In addition, postural stability while standing is improved during the learning of arm movement tasks (Galgon, Shewokis, & Tucker, 2010; Patton, Lee, & Pai, 2000). However, the relationship between improvements in motor performance and changes in postural control are unclear. That is, it remains unknown whether positive changes in postural control by repetitive motor training (e.g. the increased amplitude and prolonged duration of postural muscle activity) lead to improvements in motor performance, and whether the learning processes of postural control are similar to those of motor control.

To perform functional and accurate arm movement while standing, postural compensations for predictable perturbations created by self-initiated movements, such as raising an arm (Bouisset & Zattara, 1987) or releasing a load (Aruin & Latash, 1995), are required (Cordo & Nashner, 1982; Oddsson & Thorstensson, 1987). In this regard, APAs are observed as changes in postural muscle activity (Kaminski & Simpkins, 2001; Santos, Kanekar, & Aruin, 2010) and center of pressure (COP) displacements (Yiou et al., 2007) prior to the onset of a focal movement. The roles of APAs are to reduce postural disturbance due to a forthcoming perturbation (Bouisset & Zattara, 1981) and create a driving force to initiate forward whole-body movement when the reaching movement is directed to a target placed at a distance greater than arm length while standing (Oddsson & Thorstensson, 1987; Stapley, Pozzo, & Grishin, 1998; Tyler & Karst, 2004). Several studies reported that the central nervous system (CNS) adequately modulates anticipatory postural responses to compensate for focal movement performance depending on the amount of bodily support provided for stability (Friedli, Hallett, & Simon, 1984; van der Fits, Klip, van Eykern, & Hadders-Algra, 1998), the difference in target size and distance (Bonnetblanc, Martin, & Teasdale, 2004; Kaminski & Simpkins, 2001), and growth (Assaiante, Mallau, Viel, Jover, & Schmitz, 2005; Schmitz, Martin, & Assaiante, 2002). Furthermore, some studies have reported a relationship between APAs and motor performance. During pointing in a standing posture, the larger the base of support was, the higher the amplitude of anticipatory COP shift, and peak hand velocity increased accordingly (Yiou et al., 2007). During pointing combined with a leg flexion, the maximal velocity of the pointing was reduced when it was initiated during APAs of a leg flexion task (Yiou, 2005). In particular, Yiou and Do (2001) demonstrated involvement of APAs in the improvement in motor performance. Speed performance of fencers during complex athletic movements (touche and lunge) was improved compared to non-fencers when the touche was initiated during the APAs of the lunge. Thus, APAs must contribute strongly to improvements in motor performance. Although APAs modulate many aspects related to motor performance, it remains unclear whether APAs change during repeated movement training and whether such a change in APAs contributes to improvement in motor performance.

Therefore, this study aimed to determine the involvement of APAs in improved motor performance during repetitive reaching movement training. We examined the correlation between improvements in reaching performance and changes in APAs during a repetitive whole-body reaching task while standing, and the temporal relationship between changes in APAs and reaching performance improvements. We also examined whether the training effects were retained after discontinuation of training. Because postural stability may lead to improvements in motor performance, we hypothesized that changes in APAs would contribute to reaching performance improvements and that these training effects could be retained.

2. Methods

2.1 Subjects

Sixteen healthy subjects (8 men and 8 women; mean age, 22.6 ± 2.1 years; height, 165.7 ± 9.5 cm; weight, 58.8 ± 7.0 kg) participated in this study. None of the subjects had a previous history of orthopedic, neurological, or musculoskeletal disorders. All subjects were right-handed, as assessed by the Edinburgh Handedness Inventory (Oldfoeld, 1971). Before participation, all subjects provided written informed consent, as approved by the ethics committee of Hokkaido University Faculty of Health Sciences.

2.2 Experimental protocol

The subjects stood barefoot on a force platform (Kistler Type 9286A, Winterthur, Switzerland) with their feet shoulder-width apart and their arms hanging naturally at the sides of the body (Figure 1A). To enable standardization of subsequent trials, the foot positions were marked by vinyl tape attached to the force platform surface. A small target (20-mm diameter) was positioned at shoulder height on the front of the body on the mid-sagittal plane (Figure 1A). The target distance was placed at approximately the maximum reach distance of each subject according to the functional reach test described by Duncan, Weiner, Chandler, & Studenski (1990), which was determined on the first training day. A force sensor was attached to the target, which permitted the measurement of pushing force and termination time of the reaching movement. The subjects were asked to reach toward the small target with the right arm after hearing a brief beep sound. The beep signal occurred at a random interval of 2–5 s after the subjects had assumed a natural upright standing posture (Kaminski & Simpkins, 2001). The subjects were asked to perform the reaching movement as soon as possible immediately following the beep signal in a reaction time condition, and as quickly and accurately as possible. To ensure that the reaching movement started from the identical standing posture in each trial, an investigator confirmed that both toes were located on the vinyl tape, and that the initial COP position during static standing posture was located at approximately 45% of the foot length from the heel (Murray, Seireg, & Sepic, 1975). A failed trial was defined as one in which a force sensor (FlexiForce, Nitta Corporation, Osaka, Japan) attached to the small target was pushed with a force greater than 3 N, the subject was unable to touch the target, or the subject's heel moved more than 2 cm during the reaching movement. Before the experiment, the subjects were told about the conditions for a failed trial. When a trial was failed, the subjects received immediate feedback from the investigators.

To examine learning effects on performance and APAs during repetitive reaching training, training with the right arm was repeated 100 times per day over three consecutive days including the first training day. The subjects also performed the reaching task after discontinuation of training for one day (day 5) and again at three months. To examine training effects on the untrained arm (left), 10 of 16 subjects (5 men and 5 women; mean age, 23.0 ± 2.5 years; height, 162.5 ± 8.5 cm; weight, 55.7 ± 6.3 kg) were also asked to perform reaching movements with the left arm on the first and fifth days (Figure 1B). To assess learning effects, the training session on each day was divided into groups of 10 trials. The first 10 trials, trials 11–20, trials 51–60, and the last 10 trials on the first training day were defined as Baseline, Early, Middle, and Late, respectively. In addition, the first 10 trials on the fifth training day and after three months were defined as Short learning and Long learning, respectively. The first 10 trials with the left arm on the first training day and on the fifth training day were defined as pretest and posttest, respectively. The subjects had never practiced reaching training prior to this study. They had 30 s of rest after each trial and 2 min of rest every 10 trials to prevent any effects of fatigue. The temperature and humidity in the laboratory were maintained at approximately 22°C and 50%, respectively, to prevent changes in physiological parameters due to environmental factors.

2.3 Experimental measurements

Movements were recorded using a three-dimensional motion analysis system (Motion Analysis Corporation, Santa Rosa, CA, USA). To derive the trajectory of the center of mass (COM) and joint angle magnitudes, 27 reflective markers (20-mm diameter) were placed at the following anatomical landmarks (Winter, 1990): top of the head; auricle of the ear; acromion process; lateral humeral epicondyle; radial styloid process; head of the third metacarpal bone; iliac crest; anterior superior iliac spine; xiphoid process; angulus inferior scapulae; inferior angle of the ribs; greater trochanter; and knee, ankle, and head of the fifth metatarsal. All marker locations were bilateral, except for the top of the head, xiphoid process, and angulus inferior scapulae. Six cameras were used to record the positions of these markers. Marker position data were collected at a sampling frequency of 100 Hz.

Figure 1 near here

A force platform was used to record the following kinetics data at a sampling frequency of 1000 Hz: vertical ground reaction force (*Fz*), shear force (*Fx* and *Fy*) in the anteroposterior (AP) and mediolateral (ML) directions, and moment (*Mx* and *My*) around the AP and ML axes. The COP positions in the AP direction (COPx) and in the ML direction (COPy) were calculated using following formulas (Winter, Prine, Frank, Powell, & Zabjek, 1996):

$$COPx = -(My + Fx * d) / Fz$$

$$COPy = (Mx + Fy * d) / Fz,$$

where d is the distance from the origin of the force platform to the surface. Both COP positions were calculated from the kinetics data using the above formulas by PowerLab (ADInstruments, Castle Hill, Australia). Additionally, these positions were shown on the monitor of a personal computer in real time and checked by an investigator to confirm the initial static standing position during the experiment.

Subjects were instructed in how to selectively activate each muscle to determine the surface electrode placements (Kendall, McCreary, Provance, Rodgers, & Romani, 2005). Before pasting the surface electrodes, their skin was subjected to abrasive cleaning and alcohol cleaning to maintain a condition of low skin impedance. If necessary, only the area of skin of the patients that was covered by the electrode was shaved. Interelectrode impedance was less than 5 kΩ. Surface electromyographic (EMG) data were collected bilaterally using disposable self-adhesive electrodes (Ambu Corporation, Copenhagen, Denmark) from the following muscles: tibialis anterior (TA), gastrocnemius (GAS), rectus femoris (RF), and biceps femoris (BF). The surface electrodes were placed over each muscle belly with their centers 3 cm apart (Cram, Kasman, & Holtz, 1998). In addition, a reference electrode was attached to the lateral aspect of the fibula. To maintain consistent placement across the different training days, the electrode placements over each muscle were photographed using a digital camera on the first training day. All analog signals were digitized at a sampling frequency of 1000 Hz with 16-bit resolution.

2.4 Data analysis

Kinematics data were digitally low-pass filtered using a dual-pass Butterworth filter with a cut-off frequency of 8 Hz. To determine the onset of the reaching movement, the velocity of the right hand movement was obtained by differentiating the position of the marker attached to the third metacarpal bone. Definitions of the reaching parameters using data from a representative trial of a single subject are shown in Figure 1A. The onset of the reaching movement (time zero, t_0) was defined as the time when the velocity of right hand movement exceeded 5 cm/s. Reaction time was defined as the time from the start of the beep signal to t_0 (Figure 1A). The termination time of the reaching movement was defined as the time when the subjects touched the force sensor attached to the target. The total reaching movement time was obtained from t_0 to the termination time. The amplitude of force was determined by the force sensor to quantify the accuracy of the reaching movement. The position of the whole-body COM was calculated using the 14-segment COM model described by Winter (1990). The COM velocity was obtained by differentiating its position.

APAs were defined as postural responses preceding the onset of a focal movement (Aruin & Latash, 1995; Kaminski & Simpkins, 2001). In this study, the onset of postural muscle activity and the COP displacement preceding the onset of the reaching movement (t_0), integrated EMG (IEMG) from -100 to 0 ms with respect to t_0, and the amplitude of anticipatory backward COP displacement at t_0 were defined as parameters of the APAs.

EMG signals were rectified and band-pass filtered from 20 to 500 Hz using a fourth-order zero-lag Butterworth filter. EMG onset times were calculated in relation to the right hand movement (t_0). The mean and standard deviation (SD) of baseline muscle activity were calculated from -500 to -300 ms prior to t_0 in individual trials. EMG onset was defined as the time when the EMG amplitude was more than 3 SD from the mean baseline level (Aruin, Shiratori, & Latash, 2001). In addition, the event was required to last for at least 50 ms. The IEMG during the reaching movements was calculated for the anticipatory phase (Figure 1A; gray area). The time window for this phase extended from -100 ms to t_0 ($\int EMG_{100}$). This data was further corrected by subtracting the baseline activity, defined as the integral from -500 to -300 ms ($\int EMG_{200}$) with respect to t_0 in the following manner:

$IEMG = \int EMG_{100} - 1/2 \int EMG_{200}$

To compare the activity level of muscle responses across reaching training sessions and across subjects, the IEMG was normalized across subjects. The maximum value of the IEMG was identified across all trials performed on each day for each subject and each muscle, and all other values of the IEMG were normalized with respect to the maximal value. Normalization was performed separately on each day (Aruinet al., 2001; Fautrelle, Berret, Chiovetto, Pozzo, & Bonnetblanc, 2010).

Similarly, the onset of the COP displacement was calculated in relation to the right hand movement (t_0). The mean and standard deviation (SD) of the baseline level were calculated from -500 to -300 ms prior to t_0 in individual trials. The onset of the COP displacement was defined as the time at which the COP amplitude was less than 3 SD from the mean baseline level. The amplitude of anticipatory backward COP displacement was defined as the distance from the mean baseline level to the COP position at t_0.

Each parameter was plotted against the number of reaching trials for each subject.

For each plot, an exponential rise or decay function was fitted as a trial function to assess adaptation on the first training day. The time constant from these exponential functions, referred to as the adaptation coefficient (AC) by Martin, Keating, Goodkin, Bastian, and Thach (1996), represents the number of trials in which approximately 63.2% of total adaptation would change. This fitting technique is widely used to examine the rate of adaptation (Falvo, Horak, & Earhart, 2008; Lang & Bastian, 1999; Morton, Lang, & Bastian, 2001).

Because postural response during the reaching movement is influenced by posture before the start of movement, after the experiment, we confirmed whether the reaching movement was performed from an identical static standing posture across training sessions by examining the anterior-posterior position and mediolateral position of the pelvis, trunk flexion angle, and the anterior-posterior and mediolateral position of the COP. The anterior-posterior position of the pelvis was defined as the distance from the midpoint of the left and right anterior superior iliac spine (ASIS) to the line connecting the left with right heel. The mediolateral position of the pelvis was defined as the distance from the midpoint to the left and right ASIS till the midline of the left and right heel. The trunk flexion angle was defined by the position of the acromion process, greater trochanter, and ankle marker. The anterior-posterior position of the COP was defined as distance between 45% of the foot length from the heel and the position of the COP. The mediolateral position of the COP was defined as the distance from the midline of the left and right heel to the position of the COP. The mean values of these parameters during the 200-ms epoch before the beep signal were computed across training sessions.

Data from failed trials, which comprised 21.1% of all trials, were excluded from the analysis. In addition, trials in which the onset of TA activity began less than 50 ms after the beep signal were also eliminated from the analysis, since it is possible that the subjects anticipated the beep signal rather than reaching in reaction to the actual auditory stimulus. Trials eliminated as anticipatory responses comprised 3.1% of all trials. Furthermore, to exclude the possible strategy for participants to take more time to develop the APAs, trials with a reaction time greater than 500 ms were also eliminated from the analysis. Such trials comprised 1.4% of all trials. The remaining trials (74.4%) were defined as successful trials. The success rate was calculated for each of the 10 trials. All signals were processed off-line using MATLAB 7.7 software (Mathworks, Natick, MA, USA).

2.5 Statistics

Only data from successful trials were statistically analyzed, except for success rate and force. The means of each parameter in consecutive sets of 10 trials were used for statistical analysis. To assess immediate adaptation, the mean Baseline value was compared with those of Early, Middle, and Late (Figure 1B). In addition, to assess learning effects, the mean Baseline value was also compared with those of Short learning and Long learning. To assess generalization, the mean pretest value was compared with that of posttest. A one-way repeated measures ANOVA was used to examine the effect of repetitive reaching movements. A Bonferroni post-hoc test was also conducted to compare the means of each set of 10 trials. To examine the relationship between improvements in reaching performance and changes in postural control, Pearson correlation coefficients were calculated, and two-tailed Student's t-tests were used. To assess generalization, mean values of the reaching parameters for the left arm on the first training day (pretest) were compared with those of the first 10 trials with the left arm on the fifth training day (posttest). Two-tailed paired Student's t-tests were used for comparisons. All statistical analyses were performed using SPSS 18.0J for Windows (SPSS Japan Inc., Tokyo, Japan). The significance level was set at $p < 0.05$.

3. Results

3.1 Initial standing posture before the start of reaching movement

Initial positions of the pelvis and the COP and the trunk flexion angle before the start of the reaching movement are shown in Figure 2. The anterior-posterior and mediolateral position of the pelvis, trunk flexion angle, and anterior-posterior and mediolateral positions of the COP did not significantly change within the training session on the first day or across the training sessions on different days [anterior-posterior position of the pelvis: $F(5, 75) = 0.610$, $p = 0.692$; mediolateral position of the pelvis: $F(5, 75) = 0.281$, $p = 0.922$; trunk flexion: $F(5, 75) = 0.275$, $p = 0.925$; anterior-posterior position of the COP: $F(5, 75) = 0.504$, $p = 0.773$; mediolateral position of the COP: $F(5, 75) = 0.376$, $p = 0.864$]. These results indicate that repeated reaching movements were performed from an identical static standing posture across training sessions.

Figure 2 near here

3.2 Adaptation during reaching training

The mean values for the first (gray line, Baseline) and last (black line, Late) 10 trials of a representative subject during reaching movement with the right arm on the first training day are shown in Figure 3. The peak velocity of the right hand and the COM of this subject increased across the 100 trials on the first training day [hand velocity: 2.82 ± 0.14 m/s (mean

± SD) in Baseline, 3.31 ± 0.12 m/s in Late; COM velocity: 0.16 ± 0.02 m/s in Baseline, 0.19 ± 0.01 m/s in Late]. These performance parameters also increased significantly across each subject (Figure 4) [hand velocity: 2.79 ± 0.61 m/s in Baseline, 2.82 ± 0.60 m/s in Early, 3.20 ± 0.42 m/s in Middle, 3.43 ± 0.40 m/s in Late, $F(3, 45) = 24.288$, $p < 0.001$; COM velocity: 0.18 ± 0.05 m/s in Baseline, 0.19 ± 0.04 m/s in Early, 0.20 ± 0.04 m/s in Middle, 0.21 ± 0.03 m/s in Late, $F(3, 45) = 7.958$, $p < 0.001$]. During the training session on the first day, the onset of bilateral TA and RF activities occurred earlier than the onset of the reaching movement (Figure 3). Thus, anticipatory muscle responses were observed in all subjects. In particular, the onset of the right TA muscle activity and the COP in the Early, Middle, and Late periods significantly preceded that in Baseline (Figure 4) [right TA: -112.5 ± 41.0 ms in Baseline, -112.5 ± 41.0 ms in Early, -134.7 ± 52.3 ms in Middle, -144.6 ± 43.7 ms in Late, $F(3, 45) = 14.796$, $p < 0.001$; COP: -90.6 ± 39.8 ms in Baseline, -113.1 ± 39.3 ms in Early, -122.6 ± 41.8 ms in Middle, 125.3 ± 35.5 ms in Late, $F(3, 45) = 13.728$, $p < 0.001$]. However, anticipatory muscle activity of the left BF, as shown in Figure 3, was only observed in less than half the subjects. Muscle response of the left BF in other subjects was late for the onset of the reaching movement (18.7 ± 87.0 ms across all subjects over the training session on the first day).

Anticipatory muscle activities in the right lower limb changed prominently during repeated reaching movements. However, those in the left lower limb demonstrated few changes (Figure 3). The activity of the GAS was inhibited in the anticipatory phase and did not significantly change during repeated reaching movements across each subject [$F(3, 45) = 0.781$, $p = 0.48$]. Different muscle activity patterns were observed in the right and left homonymous muscles, as shown in the BF, because the reaching movement in this study was asymmetric (Figure 3).

Figure 3 and 4 near here

On the first training day, the success rate of the reaching movement in the first 10 trials with the right hand was approximately 56.2 ± 12.0% (mean ± SD) across all subjects (Figure 4). After 100 trials, this rate significantly improved to 81.3 ± 15.9% [$F(3, 45) = 13.497$, $p < 0.001$]. In addition, movement time decreased from 1005 ± 157 ms to 894 ± 151 ms [$F(3, 45) = 25.259$, $p < 0.001$], and force decreased from 2.36 ± 1.12 N to 1.68 ± 0.84 N [$F(3, 45) = 8.326$, $p < 0.001$]. By contrast, reaction time was not improved across training sessions on the first day [283.0 ± 65.8 ms in Baseline, 287.9 ± 92.0 ms in Early, 272.8 ± 67.8 ms in Middle, 265.1 ± 72.8 ms in Late; $F(3, 45) = 1.084$, $p = 0.366$]. Thus, the repeated reaching training allowed subjects to acquire accurate and fast movements and to change anticipatory postural responses. However, improvements in reaching performance and muscle response changes gradually decreased and reached a plateau after approximately 30–50 trials, as shown in Figure 5.

Figure 5 near here

3.3 Relationship between reaching performance and APAs

Correlation coefficients between reaching performance improvements and APA changes are reported in Table 1. The anticipatory responses of TA activity and COP displacement were strongly correlated with reaching performance. For example, the earlier the onset of the TA activity is (that is, the longer the APA duration is), the shorter the movement time and the faster the reaching movement. In Table 1, the correlation between COP onset and peak hand velocity was negative. This negative relationship indicated that the earlier the COP onset, the larger the peak hand velocity. Because the COP onset was defined as the time relative to the onset of the focal arm movement (t_0), the earlier the COP onset, the more negative its value (see the COP trace in Figure 1 and the panel showing of the onset of the COP displacement in Figure 4). However, the IEMG of the RF was moderately correlated with reaching performance. In addition, the onset of COP displacement was strongly correlated with the onset of TA activity ($r = 0.96$, $p < 0.01$). By contrast, reaction time was not correlated significantly with most APA parameters.

The adaptation coefficient (AC: the number of trials required for adaptation) is shown in Table 2. Reaching performance variables reached 63.2% of the total change after approximately 30 trials. By contrast, changes in APA parameters reached the same ratio after approximately 20 trials and occurred significantly earlier than those in reaching performance ($p < 0.01$). Similarly, APA parameters, such as the right lower limb muscle responses, were significantly changed in Early (11–20 trials) compared to Baseline (trials 1–10). However, reaching performances were not significantly improved in the Early period, but were improved in the Middle period (trials 51–60) compared to Baseline.

Table 1 and 2 near here

3.4 Learning effects

Subjects discontinued the reaching training for one day after three consecutive days of training. Data on the fifth day (Short learning) are plotted in the open circles in Figure 5. Most parameters over the first 10 trials on the fifth training day were nearly equivalent to those in the last 10 trials on the first training day. When the mean values in Baseline were compared with those in Short learning, learning effects were clearly retained for all analyzed performance parameters except reaction time (Baseline and Short learning success rate: 56.2 ± 12.0% and 74.4 ± 13.6%, respectively, $p < 0.01$; force: 2.36 ± 1.12 N and 1.85 ± 0.68 N, respectively, $p < 0.01$; movement time: 1005 ± 157 ms and 924 ± 122 ms, respectively, $p < 0.05$; peak hand velocity: 2.79 ± 0.61 m/s and 3.25 ± 0.53 m/s, respectively, $p < 0.01$; peak COM velocity: 0.18 ± 0.05 m/s and 0.21 ± 0.06 m/s, respectively, $p < 0.01$; Figure 4). In addition, learning effects on success rate, movement time, and peak hand velocity were retained even after three months (Long learning; success rate: 73.1 ± 11.9%, $p < 0.01$; movement time: 933 ± 126 ms, $p < 0.05$; peak hand velocity: 3.23 ± 0.44 m/s, $p < 0.05$). Learning effects of right TA activity and COP displacement on the anticipatory phase were also retained in Short and Long learning compared to that in the Baseline period, but no learning effect was found in the right RF (right TA onset: -112.4 ± 41.0 ms in Baseline, -149.0 ± 38.2 ms in Short learning, $p < 0.05$, -145.8 ± 35.7 ms in Long learning, $p < 0.05$; right TA IEMG: 0.43 ± 0.13 in Baseline, 0.58 ± 0.16 in Short learning, $p < 0.01$; COP onset: -90.6 ± 39.8 ms in Baseline, -125.1 ± 31.4 ms in Short learning, $p < 0.05$, -124.0 ± 40.6 ms in Long learning, $p < 0.05$; anticipatory COP displacement: 2.2 ± 0.81 cm in Baseline, 3.0 ± 0.90 cm in Short learning, $p < 0.01$).

3.5 Effects on the contralateral arm and limb

To examine training effects on the contralateral arm and limb, left arm reaching movements were evaluated on the first (pretest) and fifth (posttest) days (Figures 1B and 6). The success rate (54.0 ± 19.0% in pretest, 74.0 ± 15.8% in posttest, $p < 0.05$), force (2.7 ± 0.64 N in pretest, 1.62 ± 0.48 N in posttest, $p < 0.01$), movement time (1164 ± 99 ms in pretest, 991 ± 88 ms in posttest, $p < 0.01$), and peak velocity of the left hand (2.2 ± 0.56 m/s in pretest, 2.8 ± 0.61 m/s in posttest, $p < 0.05$) were significantly improved in the posttest evaluation. In addition, the onset of the left TA (-92.2 ± 31.9 ms in pretest, -134.1 ± 33.3 ms in posttest, $p < 0.01$), the onset of the COP displacement (-81.6 ± 35.3 ms in pretest, -114.1 ± 33.2 ms in posttest, $p < 0.01$), and anticipatory COP displacement (-1.7 ± 0.70 cm in pretest, -2.7 ± 0.61 cm in posttest, $p < 0.01$) were also significantly changed in the posttest evaluation. However, the onset of the left RF showed no change ($p = 0.52$).

Figure 6 near here

4. Discussion

We found that repeated whole-body reaching training induced not only improvements in motor performance but also changes in APAs. Interestingly, the APA changes occurred earlier than reaching performance improvements. Even when subjects discontinued training, the APA learning effects were retained and were generalized to the untrained arm and limb. The results of this study support our hypothesis and suggest that changes in anticipatory postural responses by repetitive standing movements are an important factor in improving the performance of arm movement.

The spatiotemporal change of APAs in various situations has been reported. For example, Yiou, Hussein, and Larue (2012) tested the duration and amplitude of APAs during rapid leg flexion in a reaction time condition (as soon as possible in response to an auditory signal) and in a self-initiated condition. The APA duration was shorter in the reaction time condition than in the self-initiated condition, but the APA amplitude increased, suggesting that the CNS was able to modulate the spatiotemporal features of APAs in such a manner as to both hasten the initiation of the voluntary movement and maintain optimal conditions of dynamic stability. Moreover, during a bimanual load-lifting task, anticipatory activity on the brachioradialis and triceps pair of antagonist muscles showed a co-contraction pattern in younger children, but changed to a reciprocal pattern with development from childhood into adulthood, suggesting that experience and development contribute to the acquisition of APAs (Schmitz et al., 2002). In the present study, we found that APA changes were evoked by experience to improve motor skills. Interestingly, even if a commonly performed movement is repeated, the APAs appear to be changed by the repetitive training. We also found that the changes in APAs occurred earlier than improvements in performance. Previous investigations on the relationships between motor performance and postural control reported that the CNS was able to modulate APAs based on the prediction of forthcoming motor performance (Ito, Azuma, & Yamashita, 2004; Le Pellec & Maton, 2000) and the complex sequential movement of several tasks (Yiou & Do, 2001), suggesting the involvement of APAs in motor performance improvement (Azuma, Ito, & Yamashita, 2007; Yiou & Do, 2001; Yiou, Hamaoui, & Le Bozec, 2007). The results of this study are in line with these findings and suggest that APA change induced by repetitive arm movement training in a standing posture must provide postural stability and a forward driving force for improving motor performance.

Muscle activity is decreased by repetition of expected perturbation and movement becoming more skilled (Horak et al., 1989; Nashner, 1979; Thoroughman & Shadmehr, 1999).

However, the results of the current study indicate that postural muscle activity in the lower limbs increased during repetitive reaching movements (Figures 3 and 4). The difference between the current study and previous studies was in the instruction to subjects. Our subjects were asked to perform the reaching movement as quickly as possible. Consequently, movement time decreased and peak COM velocity increased during repetitive reaching movements (i.e., the postural muscles may strongly activate to provide more powerful driving force for initiating the whole-body forward movement).

Although a trade-off between speed and accuracy is observed in various movements (Fitts, 1966), we found that both the movement velocity and accuracy improved after repeated reaching training. These findings may indicate that motor skill was enhanced through motor training. Moreover, the motor and postural changes were retained even after discontinuation of training (Figure 4 and 5), and the anticipatory muscle responses were generalized to the untrained limb (Figure 6). These improvements in motor and postural components seem to be unexplained by temporary adaptations resulting from the enhanced excitability of muscles and motor neurons in the spinal cord. However, it has been suggested that the CNS enables interlimb generalization of neurological responses in lower limbs through motor training (Earhart et al., 2002; van Hedel, Biedermann, Erni, & Dietz, 2002). The results of the current study might therefore indicate learning effects associated with the CNS. The fact that APAs as well as movement were generalized may have clinical importance. The APAs in this study result from stored information about the dynamics of the whole-body reaching movement through repetitive training to generate the corrected postural response. The CNS allows such developed APAs to generalize. The developed APAs are controlled by the CNS in a feed forward manner and utilized effectively for the stabilization of postural disturbance and initiation of movement following APA onset. The APAs are available for an untrained limb, which has applications to the design of rehabilitation protocols for individuals with balance impairments or those at risk of falling. In this regard, however, the possibility of APA involvement in the generalization of motor skills remains to be determined (Morton, Lang, & Bastian, 2001).

The brainstem reticular formation (Takakusaki, Saitoh, Harada, & Kashiwayanagi, 2004), cerebellum (Coffman, Dum, & Strick, 2011; Diedrichsen, Verstynen, Lehman, & Ivry, 2005; Diener, Dichgans, Guschlbauer, Bacher, & Langenbach, 1989; Yamaura, Hirai, & Yanagihara, 2013), basal ganglia (Latash, Aruin, Neyman, & Nicholas, 1995), cerebral cortex (Slijper, Latash, Rao, & Aruin, 2002), primary motor cortex, and supplementary motor area (Viallet, Massion, Massarino, & Khalil, 1992) have been described as neural regions responsible for dynamic postural balance control. Severe lack of anticipatory EMG change was observed in parkinsonian patients, indicating the significance of the basal ganglia for generating APAs (Viallet, Massion, Massarino, & Khalil, 1987). Similar impairments of anticipatory postural response have been reported in patients with lesions of the primary motor cortex and supplementary motor area (Viallet et al., 1992). These brain sites are also involved in the generation of APAs (Kazennikov, Solopova, Talis, & Ioffe, 2008). Although Timmann and Horak (1998) indicated that predictive postural responses in cerebellar patients were relatively preserved during stepping perturbed by support surface translation and that the cerebellum does not seem to be critical for the early postural responses associated with centrally intended movement. However, they also demonstrated that cerebellar patients have a long latency and inability to scale the size of anticipatory muscle activity compared to control subjects. Moreover, some researches have reported dysfunction associated with the generation or modulation of APAs in patients and animals with cerebellar lesions (Babin-Ratte, Sirigu, Gilles, & Wing, 1999; Coffman et al., 2011; Diedrichsen et al., 2005; Diener et al., 1989; Yamaura et al., 2013). The cerebellum is activated significantly during motor tasks and plays an essential role in motor learning (Gross et al., 2002; Jerbi et al., 2007). Overall, the integration of the sensory and motor systems are indispensable in motor learning, and we found that reaching performance was improved and correlated strongly with changes in APAs, suggesting a potential contribution of the cerebellum to both the focal and postural components.

5. Conclusions

We found that changes in APAs induced by repetitive reaching training occurred earlier than improvements in reaching performance, and that the training effects were retained after subjects discontinued training. These findings suggest that the CNS may be able to adapt APAs for improvement in motor performance. Importantly, appropriate postural control allows for a functional arm movement in a standing posture. Therefore, a better understanding of postural control mechanisms in patients with postural instability may be useful for physical therapy practices. Future research should address the contribution of the CNS to changes in postural control during repetitive movement.

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Figure Legends

Figure 1. Experimental reaching movement setup. (A): A representative trial of a single subject is shown. The first and second vertical dashed lines represent the onset and termination of the reaching movement, respectively. The gray shaded area for the right TA trace represents the period of calculated IEMG. Excitatory activity in the bilateral TA began before the onset of the reaching movement in all subjects. Almost simultaneously, the COP displacement began toward the posterior direction. (B): The reaching training days and the number of trials. On the first training day, reaching movements with the left arm were repeated 10 times, and then those with the right arm were repeated 100 times. R and L represent the reaching training with the right and left arm, respectively.

Figure 2. Initial standing posture before the start of reaching movement. The mean ± standard error is plotted. No parameters significantly changed across training sessions between the first and subsequent days. COP: center of pressure.

Figure 3. The mean values for the first (gray line) and last (black line) 10 trials of a representative subject during reaching movement with the right arm on the first training day. A vertical dashed line represents the onset of the reaching movement. The peak velocity of the reaching hand and the COM increased through repetitive trials. In all subjects, the onsets of the right TA activity and COP displacement were advanced by repetition, as indicated by the arrows. COM: center of mass, COP: center of pressure, TA: tibialis anterior, GAS: gastrocnemius, RF: rectus femoris, BF: biceps femoris.

Figure 4. Adaptation and learning with repetitive reaching training. The mean ± standard error during the reaching movement with the right arm is plotted. *Significantly different from baseline ($p < 0.05$). COM: center of mass, COP: center of pressure, TA: tibialis anterior, RF: rectus femoris.

Figure 5. The mean reaching parameter values in each trial for all subjects. Data from the first and fifth training day are indicated by open and filled circles, respectively. An exponential decay function (black curved line) was fitted to the data on the first training day. AC: adaptation coefficient, COM: center of mass, TA: tibialis anterior, RF: rectus femoris.

Figure 6. Generalization to the untrained (left) arm and limb by repeated reaching training. The mean ± standard deviation during the reaching movement with the left arm is plotted. **Significant difference between pretest (the first training day) and posttest (the fifth training day; $p < 0.01$). *Significant difference between pretest and posttest; $p < 0.05$). COP: center of pressure, TA: tibialis anterior, RF: rectus femoris.

Table 1. A correlation coefficient was calculated from the mean values of the ten trials on the first training day.

APAs	**Performance**					
	Success rate	**Force**	**Reaction time**	**Movement time**	**Peak hand velocity**	**Peak COM velocity**
Right TA onset	–0.910*	0.831*	0.494	0.894*	–0.881*	–0.928*
Right TA IEMG	0.921*	–0.940*	–0.618**	–0.914*	0.938*	0.978*
Right RF onset	–0.858*	–0.719*	–0.422	0.806*	–0.824*	–0.851*
Right RF IEMG	0.806*	–0.726*	–0.586	–0.770*	0.705*	0.614**
COP onset	–0.911*	0.875*	0.600	0.866*	–0.909*	–0.954*
COP displacement	–0.892*	0.75*	0.437	0.869*	–0.807*	–0.836*

* Values indicate a significant correlation at $p < 0.01$.

** Values indicate a significant correlation at $p < 0.05$.

COM: center of mass, COP: center of pressure, IEMG: integrated electromyography, RF: rectus femoris, TA: tibialis anterior.

Table 2. The number of trials required for adaptation

Reaching performance			
Success rate	31.4	±	13.6
Force	25.3	±	11.3
Reaction time	47.5	±	17.2
Movement time	32.3	±	14.1
Peak hand velocity	32.8	±	13.7
Peak COM velocity	29.6	±	12.8
Anticipatory postural adjustments			
Right TA onset	19.5	±	13.2
Right TA IEMG	19.8	±	11.5
Right RF onset	21.2	±	15.3
COP onset	18.8	±	14.6
COP displacement	16.9	±	13.8

The number of trials required to reach 63.2% of the total change across 100 trials on the first training day (see the data analysis).
The mean ± standard deviation during the reaching movement with the right arm is represented.
COM: center of mass, COP: center of pressure, IEMG: integrated electromyography,
RF: rectus femoris, TA: tibialis anterior

Fig.1

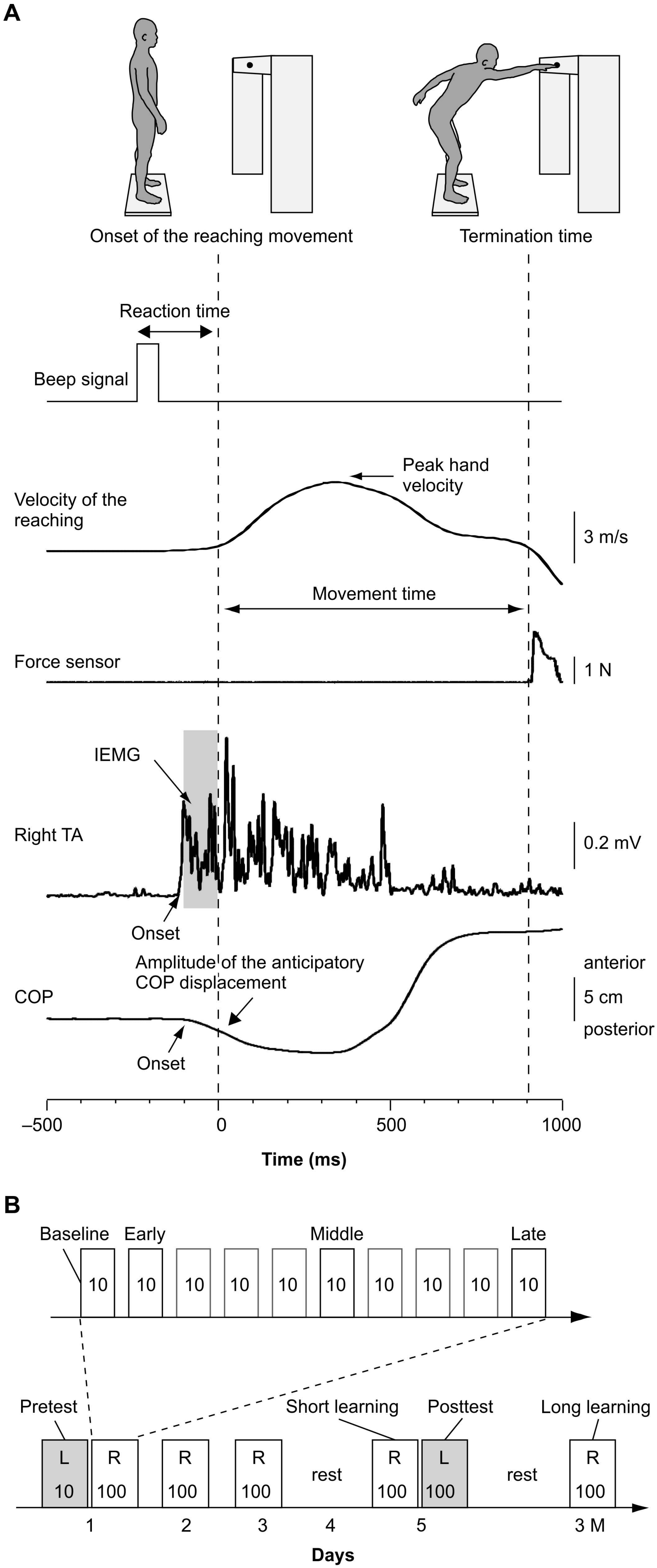
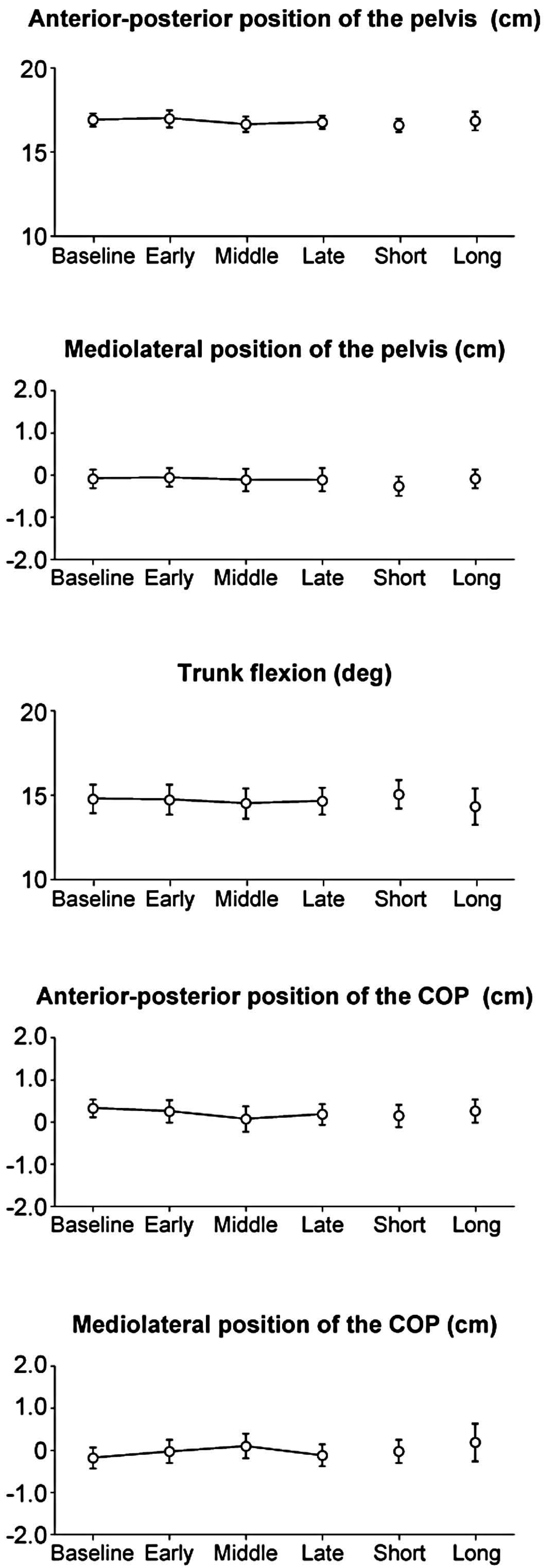
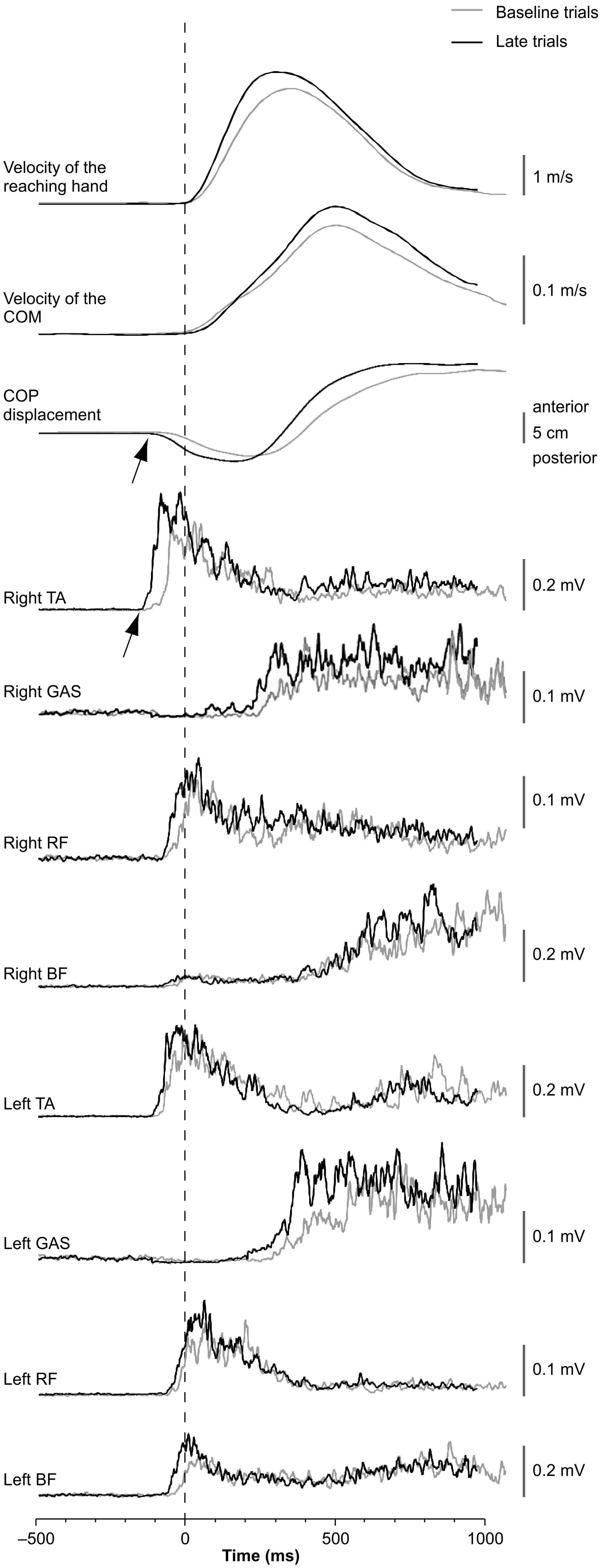

A
Onset of the reaching movement
Termination time
Reaction time
Beep signal
Peak hand velocity
Velocity of the reaching
3 m/s
Movement time
Force sensor
1 N
IEMG
Right TA
0.2 mV
Onset
Amplitude of the anticipatory COP displacement
COP
anterior
5 cm
posterior
Onset
–500
0
500
1000
Time (ms)
B
Baseline
Early
Middle
Late
10
10
10
10
10
10
10
10
10
10
Pretest
Short learning
Posttest
Long learning
L 10
R 100
R 100
R 100
rest
R 100
L 100
rest
R 100
1
2
3
4
5
3 M
Days

Fig.2



Anterior-posterior position of the pelvis (cm)
20
15
10
Baseline
Early
Middle
Late
Short
Long
Mediolateral position of the pelvis (cm)
2.0
1.0
0
-1.0
-2.0
Baseline
Early
Middle
Late
Short
Long
Trunk flexion (deg)
20
15
10
Baseline
Early
Middle
Late
Short
Long
Anterior-posterior position of the COP (cm)
2.0
1.0
0
-1.0
-2.0
Baseline
Early
Middle
Late
Short
Long
Mediolateral position of the COP (cm)
2.0
1.0
0
-1.0
-2.0
Baseline
Early
Middle
Late
Short
Long

Fig.3



Baseline trials
Late trials
Velocity of the reaching hand
1 m/s
Velocity of the COM
0.1 m/s
COP displacement
anterior
5 cm
posterior
Right TA
0.2 mV
Right GAS
0.1 mV
Right RF
0.1 mV
Right BF
0.2 mV
Left TA
0.2 mV
Left GAS
0.1 mV
Left RF
0.1 mV
Left BF
0.2 mV
−500
0
500
1000
Time (ms)

Fig.4

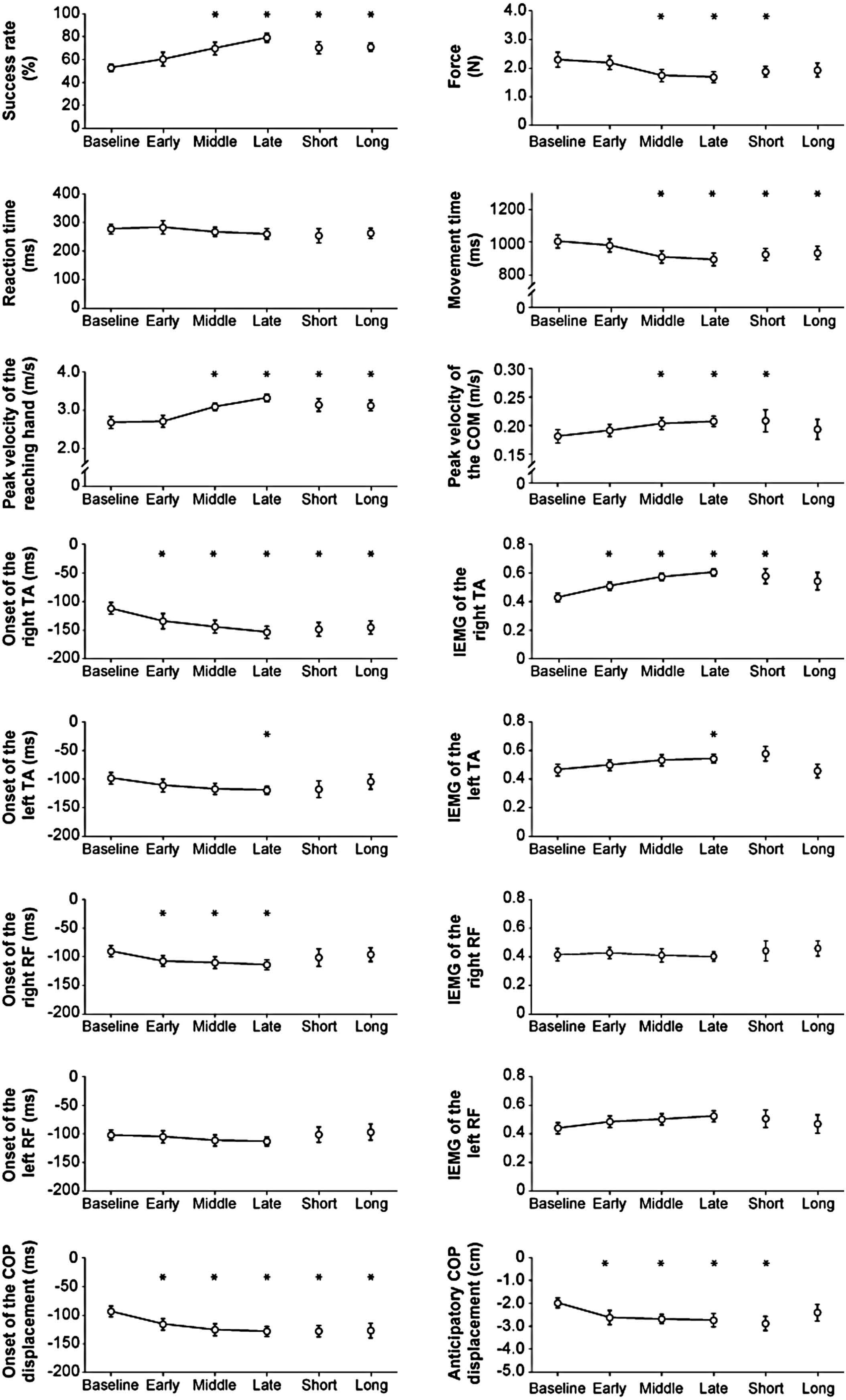
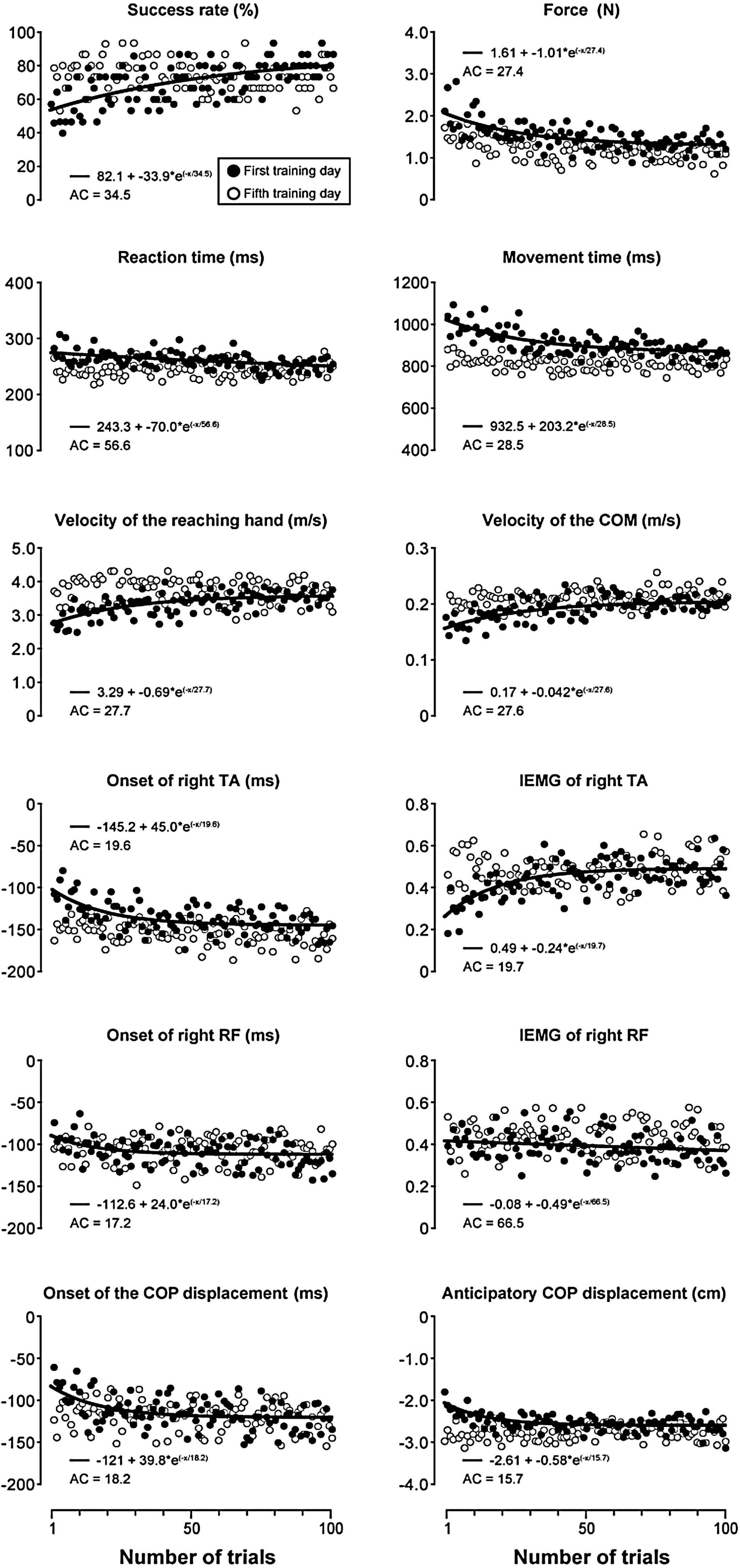
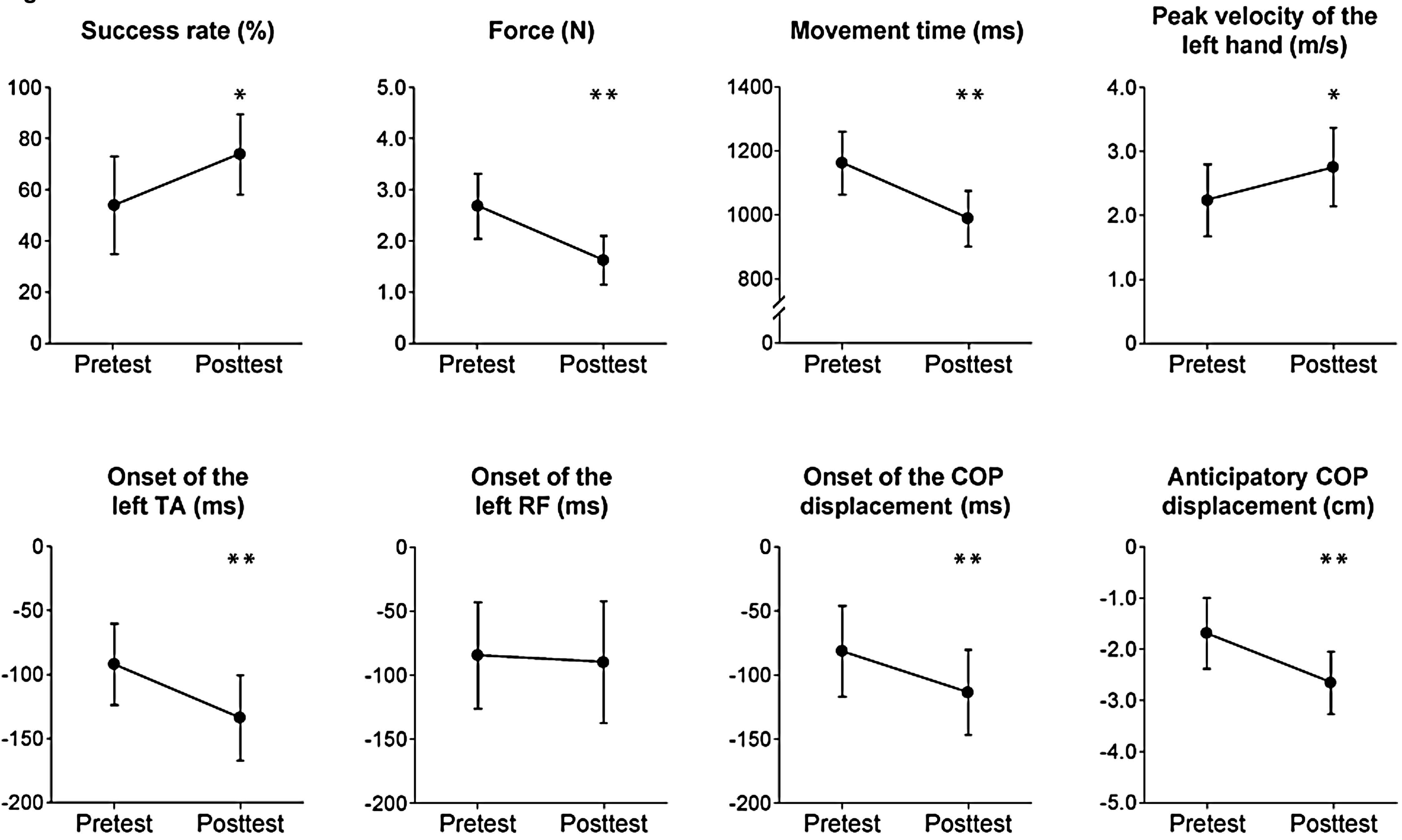

Success rate (%)
Force (N)
Reaction time (ms)
Movement time (ms)
Peak velocity of the reaching hand (m/s)
Peak velocity of the COM (m/s)
Onset of the right TA (ms)
IEMG of the right TA
Onset of the left TA (ms)
IEMG of the left TA
Onset of the right RF (ms)
IEMG of the right RF
Onset of the left RF (ms)
IEMG of the left RF
Onset of the COP displacement (ms)
Anticipatory COP displacement (cm)
Baseline
Early
Middle
Late
Short
Long

Fig.5



Success rate (%)
82.1 + -33.9*e^(-x/34.5)
AC = 34.5
First training day
Fifth training day
Force (N)
1.61 + -1.01*e^(-x/27.4)
AC = 27.4
Reaction time (ms)
243.3 + -70.0*e^(-x/56.6)
AC = 56.6
Movement time (ms)
932.5 + 203.2*e^(-x/28.5)
AC = 28.5
Velocity of the reaching hand (m/s)
3.29 + -0.69*e^(-x/27.7)
AC = 27.7
Velocity of the COM (m/s)
0.17 + -0.042*e^(-x/27.6)
AC = 27.6
Onset of right TA (ms)
-145.2 + 45.0*e^(-x/19.6)
AC = 19.6
IEMG of right TA
0.49 + -0.24*e^(-x/19.7)
AC = 19.7
Onset of right RF (ms)
-112.6 + 24.0*e^(-x/17.2)
AC = 17.2
IEMG of right RF
-0.08 + -0.49*e^(-x/66.5)
AC = 66.5
Onset of the COP displacement (ms)
-121 + 39.8*e^(-x/18.2)
AC = 18.2
Anticipatory COP displacement (cm)
-2.61 + -0.58*e^(-x/15.7)
AC = 15.7
Number of trials
Number of trials

Fig.6


Success rate (%)
100
80
60
40
20
0
*
Pretest
Posttest
Force (N)
5.0
4.0
3.0
2.0
1.0
0
**
Pretest
Posttest
Movement time (ms)
1400
1200
1000
800
0
**
Pretest
Posttest
Peak velocity of the left hand (m/s)
4.0
3.0
2.0
1.0
0
*
Pretest
Posttest
Onset of the left TA (ms)
0
-50
-100
-150
-200
**
Pretest
Posttest
Onset of the left RF (ms)
0
-50
-100
-150
-200
Pretest
Posttest
Onset of the COP displacement (ms)
0
-50
-100
-150
-200
**
Pretest
Posttest
Anticipatory COP displacement (cm)
0
-1.0
-2.0
-3.0
-4.0
-5.0
**
Pretest
Posttest