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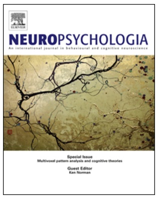

Sensory-guided motor tasks benefit from mental training based on serial prediction

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ABSTRACT

Mental strategies have been suggested to constitute a promising approach to improve motor abilities in both healthy subjects and patients. This behavioural effect has been shown to be associated with changes of neural activity in premotor areas, not only during movement execution, but also while performing motor imagery or action observation. However, how well such mental tasks are performed is often difficult to assess, especially in patients. We here used a novel mental training paradigm based on the serial prediction task (SPT) in order to activate premotor circuits in the absence of a motor task. We then tested whether this intervention improves motor-related performance such as sensorimotor transformation.

Two groups of healthy young participants underwent a single-blinded five-day cognitive training schedule and were tested in four different motor tests on the day before and after training. One group ($N=22$) received the SPT-training and the other one ($N=21$) received a control training based on a serial match-to-sample task.

The results revealed significant improvements of the SPT-group in a sensorimotor timing task, i.e. synchronization of finger tapping to a visually presented rhythm, as well as improved visuomotor coordination in a sensory-guided pointing task compared to the group that received the control training. However, mental training did not show transfer effects on motor abilities in healthy subjects beyond the trained modalities as evident by non-significant changes in the Jebsen–Taylor handfunctiontest.

In summary, the data suggest that mental training based on the serial prediction task effectively engages sensorimotor circuits and thereby improves motor behaviour.

1. Introduction

When aiming to show the perfect jump off a high board, a diver prepares the successive movements over and over again by imagining herself/himself performing every step, breath, rotation and dive into the water as vividly and exactly as she/he would do in the real situation. Mental strategies such as motor imagery, i.e. the mental rehearsal of movements without overt execution, are long known in the field of sports and exercise psychology to improve motor performance (Holmes & Calmels, 2008; Rushall & Lippman, 1998). The effect of active imagination of a movement upon overt motor performance is most commonly attributed to the observation that the imagination and execution of an action recruit overlapping neural circuits, among others in premotor areas (Dietrich, 2008; Jeannerod, 1994, 2001; Stephan et al., 1995). This holds also true for other types of mental representations of actions like action intention or action observation (Jeannerod, 2001). Mental training has thus been considered to be promising in conditions where neural networks have to be reorganized, i.e. after brain lesions (Decety, 1993; Jackson, Lafleur, Malouin, Richards, & Doyon, 2001; Warner & McNeill, 1988). Previous studies have already demonstrated that mental practice through motor imagery can indeed improve motor recovery in stroke patients (cf. Johnson-Frey, 2004; Malouin & Richards, 2010 for reviews on that topic).

Nevertheless, a number of problems exist with respect to this type of mental practice. First, to date it remains controversial whether the concept of “shared neural networks” for overt

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execution and mental rehearsals also applies to complex every-day life movement sequences like getting up from a chair or brewing a coffee. Unfortunately, such complex motor tasks cannot be investigated with functional imaging due to technical and methodological constraints. However, the most important limitation of motor imagery (and any type of mental training in general) is that it is difficult to asses how well the task at hand is performed by the subject apart from indirect measures of performance like self-ratings, mental chronometry or the maintenance of Fitt's law (which predicts that the time required to rapidly move to a target area is a function of the distance to the target and the size of the target).

In order to overcome some of the shortcomings mentioned above, we employed a novel mental training paradigm based on the “serial prediction task” (SPT, (Schubotz, 1999)). As a perceptual counterpart to the serial reaction time task (Nissen & Bullemer, 1987), the SPT involves sequential processing on an explicit and purely perceptual level but under non-motor requirements. Using the same visually presented stimulus material, the subjects` attention can be directed to different properties of the stimulus, for instance to the spatial, object or temporal properties of the sequence (i.e. a grouped series of events). The sequence is structured according to one of the stimulus properties and repeated within the trial various times, which allows subjects to set up an expectation about how the sequence will evolve. That enables a detection of deviants in the stimulus train, i.e. the violation of the sequential order. In contrast to motor imagery tasks, SPT performance can be directly tested, e.g., by asking subjects to detect such sequential violations in a forced-choice paradigm. In a series of functional magnetic resonance imaging (fMRI) studies, this experimental paradigm was shown to result in robust activations of the premotor cortex and interconnected parietal areas (Schubotz, 2007; Schubotz & von Cramon, 2003, 2004). Therefore, the SPT has the great potential to activate components of the sensorimotor system in a behaviourally well-controlled way. It has been suggested that premotor activity observed during serial prediction may reflect activity of visuomotor or audiomotor neurons tuned to the to-be-predicted stimulus (Schubotz, 2007). From that perspective, SPT-based training might alter the tuning of premotor neurons that subserve sensory-guided movement.

Therefore, in the present study, we aimed at investigating whether motor skills in a population of young healthy participants can be modulated by a mental training based on the SPT paradigm. To test this hypothesis, we employed a between-subjects design in which we trained one group of participants over five days in two conditions of the SPT (spatial and timing). In order to control for putative non-specific effects of being engaged in a five-day cognitive training schedule, a second group of subjects underwent a “dummy training”, i.e. a serial match-to-sample task with identical stimulus material. Due to the working memory property of the task prefrontal rather than premotor activation and hence no motor improvement was expected (Cohen et al., 1997; D’Esposito, 2001). In order to evaluate training-specific changes in motor performance, four different motor tasks addressing different aspects of motor performance were used.

2. Material and methods

2.1. Participants

A total of 43 healthy volunteers without any history of neurological, psychiatric or orthopaedic diseases participated in the study in exchange of course credit. They all were right-handed according to the Edinburgh Inventory of Manual Preference (Oldfield, 1971). Twenty-two subjects (13 male, mean age 25.8 years, range 19–32 years) attended the SPT-training and 21 subjects (10 male, mean age 25.6 years, range 21–30 years) were allocated to the “dummy-training”. All subjects were naive concerning the stimulus material and blinded with respect to the training group. Three participants were excluded from the analysis due to poor SPT-training performance (defined as stagnation at the first training level) and one additional participant (SPT-group) because of extreme worsening in motor performance, thereby representing a statistical outlier (cf. Section 3).

2.2. Study design

The experimental protocol was conducted on eight consecutive days (Fig. 1). It consisted of (i) task familiarization (day 1), (ii) evaluation of motor performance (days 2 and 8), and (iii) mental training (days 3 to 7). Training difficulty increased based on the subject's individual performance. Each training session lasted for 1 h and was interrupted by a short break of at most five minutes after about thirty minutes. The SPT-training consisted of two tasks (SPT-rhythm and SPT-position, see below). Task order was counterbalanced over days and participants. The dummy training consisted of one task only. Apart from that, the dummy- and SPT-trainings followed identical procedures. On the days directly before and after the SPT-/dummy-training (i.e. days 2 and 8) a motor status evaluation (status-pre and status-post) in four different motor tasks (see below) was performed. The motor

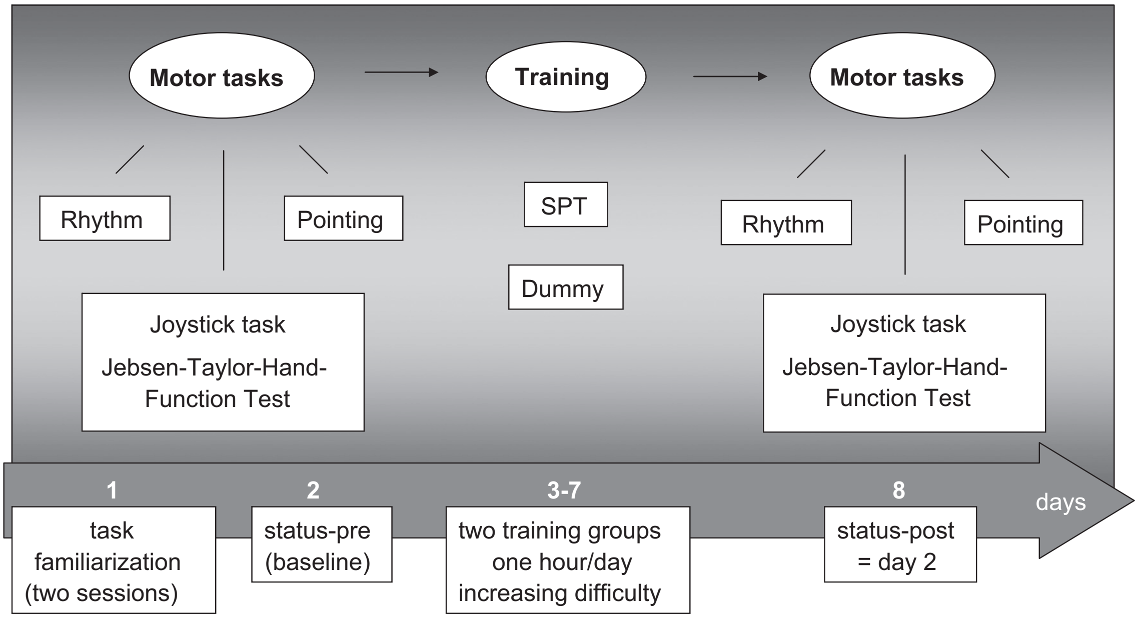

Fig. 1. Study design. The entire protocol took eight consecutive days. For motor status evaluation, four different motor tasks had to be executed before and after training. One group of participants was trained with the SPT; the other one received a control training (“dummy”).

scores achieved were used to test (i) whether motor performance improved after the SPT-/dummy-training, and (ii) whether the groups showed differential improvements.

2.3. *Stimuli and tasks*

Both conditions of the SPT-training (rhythm and position) as well as the dummy-training were presented on a laptop screen (Lenovo ThinkPad X200 Tablet) and relied on identical visual stimuli (Fig. 2): An array of twelve, sixteen or twenty transparent small circles was shown on a grey background arranged in one large circle (4.9 cm radius, corresponding 5° visual angle). The numbers of circles varied as a function of task difficulty. The centre of the large circle was indicated by a transparent square of 3 mm side length and an edge of 0.5 mm. Each of the small circles had a diameter of 1 cm with an edge of 1 mm. Their locations were as follows: 20°, 50°, 80°, 110°, 140°, 170°, 200°, 230°, 260°, 290°, 320° and 350° (twelve circles); 5°, 27.5°, 50°, 72.5°, 95°, 117.5°, 140°, 162.5°, 185°, 207.5°, 230°, 252.5°, 275°, 297.5°, 320° and 342.5° (sixteen circles); 14°, 32°, 50°, 68°, 86°, 104°, 122°, 140°, 158°, 176°, 194°, 212°; 230°, 248°, 266°, 284°, 302°, 320°, 338° and 356° (twenty circles). The software "Presentation" (Version 12.0, Neurobehavioral Systems, USA,

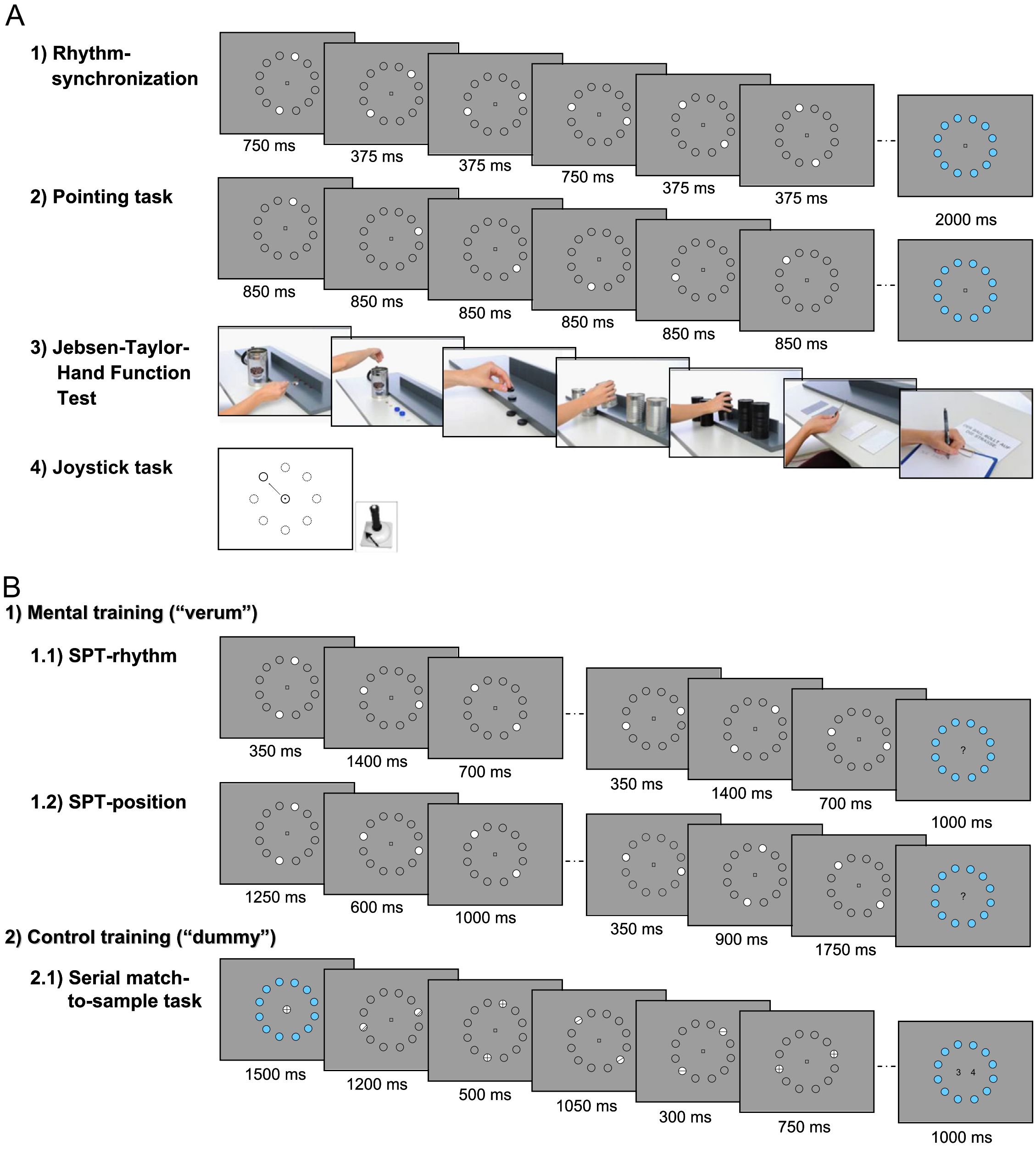

Fig. 2. Experimental paradigm. Motor performance was evaluated in four different motor tasks (A) before and after (mental) training (B). Rhythm-synchronization (A1) required synchronized finger tapping to a visually given rhythm: The white circles changed positions in a certain inter-onset-interval (IOI) as exemplarily depicted. In the pointing task (A2) the highlighted target positions should be directly tapped on a touch screen. The Jebsen–Taylor handfunctiontest (A3) evaluated several aspects of major hand functions and should be performed as fast as possible. In the joystick task (A4) subjects used a joystick to move a cursor from the central circle into one of eight possible peripheral circle positions. One group of participants received a mental training based on the serial prediction task (SPT, B1). The other group was allocated to a control training (Dummy, B2). The SPT-training had two conditions, a temporal (SPT-rhythm, B1.1) and a spatial one (SPT-position, B1.2). In the SPT-rhythm task opposing circle positions were highlighted randomly for certain IOIs, visually implementing the rhythm. Three consecutive pictures formed a unit, subjects should attend to. Subjects were required to indicate in a forced-choice mode, whether the last triplet presentation deviated from the first one(s), i.e. the predicted sequential evolvement. In the SPT-position task the temporal progression was irrelevant, whereas the spatial sequence of the highlighted positions was crucial. In the depicted example the first two pictures of the last triplet are interchanged, indicating a deviation of the sequential order. The dummy-training (B2.1) was designed as a serial-match-to-sample task. The white circle positions had 1 of 24 possible inlays consisting of 1 or 2 lines that could be crossed and varied in terms of their orientations. After an initial presentation of the sample-inlay, subjects were required to count the number of matching inlays in a series of following presentations containing the sample and distractor-inlays. IOIs were identical to the ones of the SPT-training without serving any rhythmical information. At the end of each trial, the correct number of matching inlays out of two given possibilities was supposed to be indicated via button press.

http://www.neurobs.com) was used for stimulus presentation and data recording during training and the computer-based motor-tasks (rhythm-synchronisation, pointing and joystick task, see below).

2.4. Mental training

2.4.1. SPT-training

The SPT-training was based on the serial prediction task paradigm (Schubotz, 1999) and therefore required the perception of a series of events that were visually presented and structured in a sequential order. These sequences of events were grouped into triplets, i.e. three events formed a unit to which subjects should attend (compare Fig. 2B1.1 and B1.2). A triplet was repeated in always the same manner or presented in a changed sequential order (sequence violation). At the end of each trial, participants had to judge in a forced-choice paradigm whether the sequence had been violated. Responses were given via a computer mouse by button presses with the right index or middle finger. Subjects were trained in two conditions of the task, addressing either temporal ("SPT-rhythm") or spatial ("SPT-position") task properties. For presenting a temporal or spatial sequence, two circles in opposite position within the array of circles changed their colour from grey to white for a given duration (range 250–2100 ms). The white circles changed positions in the array with a pre-defined inter-onset-interval (IOI). Since there were no gaps between events, the IOIs were equal to the stimulus duration.

In the *SPT-rhythm training condition* participants were instructed to attend to the stimulus duration of the first three events (e.g., 300–900–1200 ms), representing a rhythmical sequence (triplet). This sequence was either repeated or violated (50% of trials). For instance, the timing of the first two events of the triplet could be interchanged (e.g., 900–300–1200 ms). Depending on the training difficulty, the initial triplet could be presented once, twice or three times until the final sequence was shown in the original or deviant way. Participants were unaware of the respective trial length, i.e. the number of repetitions. They were informed about the training purpose of the task beforehand. In the SPT-rhythm training condition, the position of the opposing white circles was random in each sequence.

In the *SPT-position training condition*, the positions of the first three stimuli determined the respective sequence (e.g., 20°/200°–50°/230°–110°/290°) that could be repeated or violated (thus 50°/230°–20°/200°–110°/290°) in the last triplet presentation. The presentation duration of the white circles was random in each sequence.

Based on previous versions of the paradigm (among others Schubotz & von Cramon, 2001, 2002a, 2002b) and on the results of a pilot study, we generated a number of training levels varying in difficulty depending on (i) the number of triplet repetitions before a violation occurred (trial length), (ii) the variability and combination of temporal structures (rhythm training condition) or the distance between successive white circle pairs (position training condition) within triplets, (iii) the total number of circles displayed in the main array, and (iv) the duration of presenting the stimuli (cf. Supplementary material). The inter-trial-interval was 3 s and consisted of a response period (1 s), feedback presentation (1 s), and a short rest period (1 s) before the next trial started. The next higher level of training was reached when at least 90% correct responses were given. A visual feedback on the overall individual performance was presented at the end of each training level (5 s) followed by a rest period (10 s) before the next training level of the same or higher difficulty began.

The SPT-trained participants were informed about the nature of increasing training difficulties without knowing the total number of training levels. Accordingly, a consistent attention and motivation to the mental training throughout training sessions and conditions should be reached.

2.4.2. Control (Dummy)-training

This training served as control providing equal task affordances but lacking sequence processing. The underlying paradigm, a serial-match-to-sample task, does not rely on serial prediction but on working memory strategies known to activate prefrontal rather than premotor regions (Cohen et al., 1997; D'Esposito, 2001, compare discussion). We used the identical set up of circles (Fig. 2B2) which, however, were presented in a randomized rather than sequential order. Trial length (6, 9 or 12 events), response monitoring, feedback-presentation and task duration were identical to the SPT-training. The difference to the SPT task was the absence of a sequential structure of stimuli and the presentation of a sample (see below) at the beginning of each trial that should be recognized in a series of targets and distractors. The control task, hence, required subjects to distinguish little details presented within the circles. These inlays consisted of either one or two black lines (parallel or crossbred, thickness 1 mm) and were equally presented within a pair of white circles presented in opposite directions. At the beginning of each trial, one of overall 24 different inlays was presented in the centre of the screen for 1.5 s. Subjects were requested to count how often this target inlay appeared among a variety of distractors which – depending on the difficulty level – more or less resembled the target inlay. At the end of each trial, two numbers were presented side by side, one reflecting the actual target number that should be indicated by left or right button presses (mouse device). Task difficulty was varied with respect to (i) percentage of targets, (ii) similarity of samples and distractors, and (iii) stimulus duration. The increasing difficulty levels were trained for 1 h with a short break in between at each of the five consecutive training days. For a detailed explanation of training levels and inlays please confer to the Supplementary material.

2.5. Motor tasks

Four different motor tasks were used to evaluate changes in motor performance after SPT-training (Fig. 2A). Two of the tasks, i.e. (i) the rhythm-synchronization task and (ii) the pointing task, were especially designed to test for putative specific transfer effects from the two conditions of the SPT-training (rhythm and position prediction) on visuomotor performance. These two visually guided motor tasks made use of the same main display (12 circles), which hence served as an identical reference frame where the performance was tested in temporal as well as spatial motor dimensions. The other two tasks (i.e. the Jebsen-Taylor handfunctiontest and a visuomotor joystick task) were used to test for general transfer of training effects on motor performance. Due to practical reasons, the testing battery always started with the Jebsen–Taylor handfunctiontest, the order of the three remaining computer-based tasks was counterbalanced across subjects and days. The time needed to assess the whole battery was about an hour.

2.5.1. Rhythm-synchronization task

Participants were required to tap with their right index finger on the left button of a mouse device. The instruction was to synchronize tapping to the visually presented rhythm as close as possible. For practical reasons we chose a regular computer mouse for response recording. Even if this set-up may have facilitated a slight blurring of the exact response times, this would also apply to the "dummy training" condition and also for the pre-post comparisons, making it more difficult for differences to become statistically significant (due to an increase in variance). For visualization of the rhythm, two opposed white circle positions "moved" clockwise around the same array of circles as used in the training sessions (compare Fig. 2A1). The respective IOIs could be presented in isochronous (regularly every 300, 700 or 1000 ms) or non-isochronous patterns. The non-isochronous patterns could consist of two to four intervals (750–250 ms, 850–150 ms, 750–375–375 ms, 900–450–450 ms, 999–333–333–333 ms or 1332–666–666–666 ms). This set of rhythms considers the fact that the optimal IOI range enabling 1:1 in-phase tapping has been shown to be between 200 and 1800 ms (see Repp, 2005 for an overview on that topic). Subjects had to perform 12 taps per trial synchronized with the respective IOIs. The inter-trial-interval was 2 s with a total trial number of 90 and a total task duration of 15 min.

2.5.2. Pointing task

Subjects were instructed to tap on a touch screen of the laptop with their right index finger. For this task, the laptop monitor was turned down and laid slightly inclined (13°) on a table in front of them. The identical main display with 12 circles as in the previous tasks was used (Fig. 2A2). However, only one circle (instead of two) was highlighted and changed its position in a clockwise manner. The distances between the labelled positions could be equidistant (one after another, every second or every third circle) or non-equidistant (alternately the proximate and second one, the proximate and the third one or the second and third position). All pointing frequencies were isochronous with inter-stimulus-intervals ranging from 350 to 1000 ms. Subjects should tap as accurately and quickly as possible onto the centre of the target circle. This task requires spatial transformation for eye-hand coordination (cf. Crawford, Medendorp, & Marotta, 2004 for an overview). Identical to the rhythm-synchronization task, 12 taps per trial were required, 90 trials in total. The x and y coordinates as well as the times of the taps were recorded at a rate of 60 Hz for further data analyses. The completion of the task required 18 min on average.

2.5.3. Joystick task

Identical to previous studies (Grefkes, Wang, Eickhoff, & Fink, 2010; Wang, Fink, Dafotakis, & Grefkes, 2009) subjects were seated in front of a computer screen and handled a joystick with their right hand in order to move a cursor from a central circle to a peripheral one (Fig. 2A4). The peripheral circle could randomly appear at eight possible locations (0°, 45°, 90°, 135°, 180°, 225°, 270°, 315°) at a distance of 3.0° visual angle relative to the central circle. In each of the 105 trials, participants were required to move the cursor as accurately and quickly as possible from the central circle to the middle of the appearing peripheral circle and to hold it there until it disappeared (2 s after stimulus onset). Subjects were then allowed to move the cursor back to the centre and after an inter-trial-interval of 2 s the next trial started. This task particularly relies on visuomotor coordination and online-control of precision movements (Grefkes, Ritzl, Zilles, & Fink, 2004). The x and y coordinates of the cursor as well as the movement times were recorded at a rate of 60 Hz for subsequent data analyses. The total task duration was about 12 min.

2.5.4. Jebsen–Taylor handfunctiontest

This test evaluates several major aspects of hand function and comprises a series of seven standardized subtests: (i) writing a sentence, (ii) turning over cards, (iii) picking up small objects, (iv) simulated feeding, (v) stacking checkers, (vi) lifting up large light objects, and (vii) lifting up large heavy objects (Jebsen, Taylor, Trieschmann, Trotter, & Howard, 1969; Fig. 2A3). The subtests should be performed as rapidly and accurately as possible, alternately with the left or the right hand while subjects were sitting in front of a table. The variable of interest was the time to complete each subtest as assessed using a stop watch. Measurements always started with the non-dominant (left) hand. For task familiarization, each subtest was trained before the actual measurement began. The timings of all subtests were summed up for both hands. The whole task including training lasted about five minutes for each hand. For the Jebsen–Taylor handfunctiontest, reference data are available for males and females of different age groups (Hackel, Wolfe, Bang, & Canfield, 1992; Jebsen et al., 1969).

2.6. *Data analysis*

2.6.1. *Mental training*

Performance accuracy and reaction times were recorded for the two conditions of the SPT-training (rhythm and position) as well as for the dummy-training. The next higher level of difficulty was achieved upon reaching at least 90% correct responses in a given trial.

2.6.2. *Motor tasks*

For all computer-based tasks we analysed reaction times and error rates.

(a) Rhythm-synchronization task

Due to the anticipatory task property of given rhythm perception, a response (finger tap) could either classically follow or even precede the stimulus (highlighted circle positions) by some tens of milliseconds. To allow for a clear attribution of stimulus and tap, we pre-defined an interval before and after the stimulus onset, for which responses were accepted (stimulus onset ± of 40% of the respective inter-stimulus-intervals). Additional taps exceeding the first response within that predefined "response-interval" as well as taps outside that interval were considered to be erroneous. Error rate thus was calculated as the sum of these temporally unrelated and surplus tapping-events divided by the number of answered events (total events minus missings). Only correct responses were taken for calculating mean reaction times. To account for the anticipatory task property and therefore possible negative mean reaction times we used the absolute value for all further calculations. For a more detailed explanation of synchronized tapping variables please compare Fig. 3 and Repp (2005).

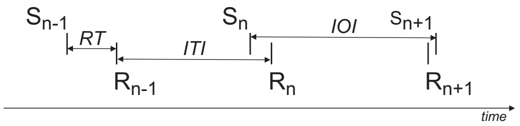

Fig. 3. Schematic example of stimulus presentation and finger tapping in the rhythm-synchronization task. Note that responses (R) can either follow or precede the stimuli (S) in case of sensorimotor synchronization. Reaction time (RT) reflects the time between stimulus onset and its related tap. A stimulus is followed by the other in a certain inter-onsetinterval (IOI). The period between two responses represents the individual inter-tap-interval (ITI).

(b) Pointing task

Mean reaction times of (correct) responses were calculated as the delay between stimulus presentation (white circle) and finger-tap on the touch screen monitor (in ms). Reaction times were corrected for outliers (median ± 1.5 × interquartile range). Taps were not allowed to exceed a distance from the target circle centre of more than half the distance between two neighboured circle centres (1.3 cm). Only the first response was accepted for calculation, whereas additional taps were considered to be erroneous. Thus, error rates were calculated as the sum of spatially unrelated and surplus responses divided by the number of answered events (total events minus missings).

(c) Joystick task

Reaction times (in ms) and error rates were calculated after 5 Hz filtering of the data with a dual low-pass Butterworth digital filter (Winter, 1990). The reaction time (of correct responses) was defined as the interval between stimulus onset (appearance of peripheral target circle) and onset of the joystick movement (Teasdale, Bard, Fleury, Young, & Proteau, 1993). A movement error was defined as a subject being unable to finish a trial within the target circle, i.e. error rate reflects the number of erroneous joystick movements per total trial number.

(d) Jebsen–Taylor handfunctiontest

The time (in s) needed to perform all seven subtests of the task with the left and right hand was summed up.

2.7. *Statistical analysis*

All statistical analyses were conducted using the software SPSS Statistics (version 21, IBM SPSS Inc., USA). To reveal significant effects of the mental training on the variables tested in the motor tasks, we computed univariate repeated measures analysis of variance (ANOVA) on the within-subject factor "time" (two conditions: status-pre and status-post) and the between-subject factor "training" (two conditions: SPT-training and dummy-training). *p*-Values were adjusted to the number of comparisons. Corrected *p*-values passing the statistical threshold of $p < .05$ were considered to be significant. The group data of each motor task as well as the task specific ANOVA are summarized in Table 1. Post-hoc *t*-tests (Bonferroni-corrected for multiple comparisons) were calculated in case of significant interactions of the factors "time" and "training".

To account for non-linear effects, we additionally computed unpaired Mann–Whitney-*U*-tests on the normalized improvement (in percent) of task performance. Improvements were defined as the normalized difference between the motor performance before and after training ([(status-pre−status-post)/status-pre] × 100). Such an approach also accounts for fluctuations in daily performance and for unspecific training effects. Again *p*-values were adjusted to the number of comparisons. Changes in motor performance (improvement or worsening) of more than ± 1.5 × interquartile range of the median were considered to indicate single outliers within the data. One participant showed such peculiarities in two variables of two different status motor tasks (rhythm-synchronisation and pointing) and was

Table 1

Group data and statistics. Means, standard deviations and results of ANOVAs are shown.

	Dummy		**SPT**		**Time**			**Training**			**Time × training**		
Rhythm-synchronization	***Pre***	***Post***	***Pre***	***Post***	***F*(2,35)**	p^{a}	p^{b}	***F*(2,35)**	p^{a}	p^{b}	***F*(2,35)**	p^{a}	p^{b}
***Reaction time* (ms)**	51 29.67	54.39 33.14	42.86 26.49	37.70 23.47	0.112	0.740		1.828	0.185		5.463	0.025	0.050
***Error rate* (%)**	22.70 5.04	21.91 4.86	21.58 7.83	18.24 6.92	17.704	0.000	0.000	1.545	0.222		6.718	0.014	0.028
Pointing task	***Pre***	***Post***	***Pre***	***Post***	***F*(2,33)**	p^{a}	p^{b}	***F*(2,33)**	p^{a}	p^{b}	***F*(2,33)**	p^{a}	p^{b}
***Reaction time* (ms)**	315.44 56.16	315.63 48.59	314.03 55.06	305.67 56.93	1.467	0.234		0.111	0.741		1.610	0.212	
***Error rate* (%)**	16.42 6.90	15.66 6.64	15.25 9.06	12.09 6.06	3.946	0.054		1.275	0.266		1.475	0.232	
Joystick task	***Pre***	***Post***	***Pre***	***Post***	***F*(2,35)**	p^{a}	p^{b}	***F*(2,35)**	p^{a}	p^{b}	***F*(2,35)**	p^{a}	p^{b}
***Reaction time* (ms)**	155.37 43.69	166.08 40.44	157.88 35.22	166.86 34.72	5.986	0.019	0.038	0.019	0.890		0.046	0.831	
***Error rate* (%)**	15.75 2.83	15.68 3.56	15.67 2.48	15.43 1.92	0.091	0.765		0.051	0.823		0.031	0.862	
Jebsen–Taylor test	***Pre***	***Post***	***Pre***	***Post***	***F*(1,37)**	p^{a}	p^{b}	***F*(1,37)**	p^{a}	p^{b}	***F*(1,37)**	p^{a}	p^{b}
***Total time* (s)**	85.00 9.90	82.16 8.17	83.04 10.97	80.56 9.93	9.476	0.004	0.004	0.349	0.558		0.043	0.836	

[a] Uncorrected.

[b] Corrected for number of comparisons, only significant results are shown.

therefore excluded from further analysis. Additionally, single extreme outliers of more than ±3 × interquartile range of the median were removed from the data. This criterion led to a removal of 3.1% of the data. For improvements of all subjects please confer to the table provided as Supplementary material.

3. Results

3.1. Mental training

A learning effect during the SPT-/dummy-training was assumed when participants showed behavioural improvements over time as reflected by achieving higher training levels, i.e. levels of task difficulty. Three participants of the SPT-group had to be excluded from the study because they stagnated on the first training level during the entire five training days in at least one of the two task conditions. During the dummy-training all subjects successfully passed the first level. In general the participants trained with the SPT had more difficulties with the rhythmic than with the positional condition of the task. This is reflected in a higher number of level repetitions in the SPT-rhythm than in the SPT-position training condition: In 69.2% a level was repeated during SPT-rhythm, whereas on average 24.4% level repetitions occurred during the SPT-position training. During dummy-training 16.9% of levels were repeated.

3.2. Motor tasks

3.2.1. Rhythm-synchronization task

The repeated measures ANOVA of the two factors “time” (status-pre, status-post) and “training” (SPT-training, dummy-training) revealed a significant interaction effect (time × training) for the dependent variable “error rate” ($p=.028$, corrected) as well as a significant main effect of “time” for error rate ($p<.001$, corrected, cf. Table 1). The interaction effect of the dependent variable “reaction time” met the statistical threshold ($p=.05$, corrected). Post-hoc t-tests showed that error rates in the SPT-group significantly decreased ($t(17)=3.843$, $p=.002$, Bonferroni corrected), which was not the case when subjects had received the dummy-training ($t(20)=1.517$, $p=.290$, Bonferroni corrected). Likewise, the SPT-trained group showed significantly greater improvement in error rates compared to the dummy-training group (Mann-Whitney, $z=-2.423$, $p=.015$, corrected, cf. Fig. 4a), i.e. the decrease of error rates was significantly greater for SPT-trained participants. With respect to reaction times, the post-hoc t-test revealed a trend for shorter times after the SPT-training compared to the status-pre measurement ($t(16)=2.258$, $p=.074$, Bonferroni corrected), whereas reaction times after the dummy-training showed no significant difference ($t(19)=-1.294$, $p=.420$, Bonferroni corrected). Accordingly, we found a trend toward a

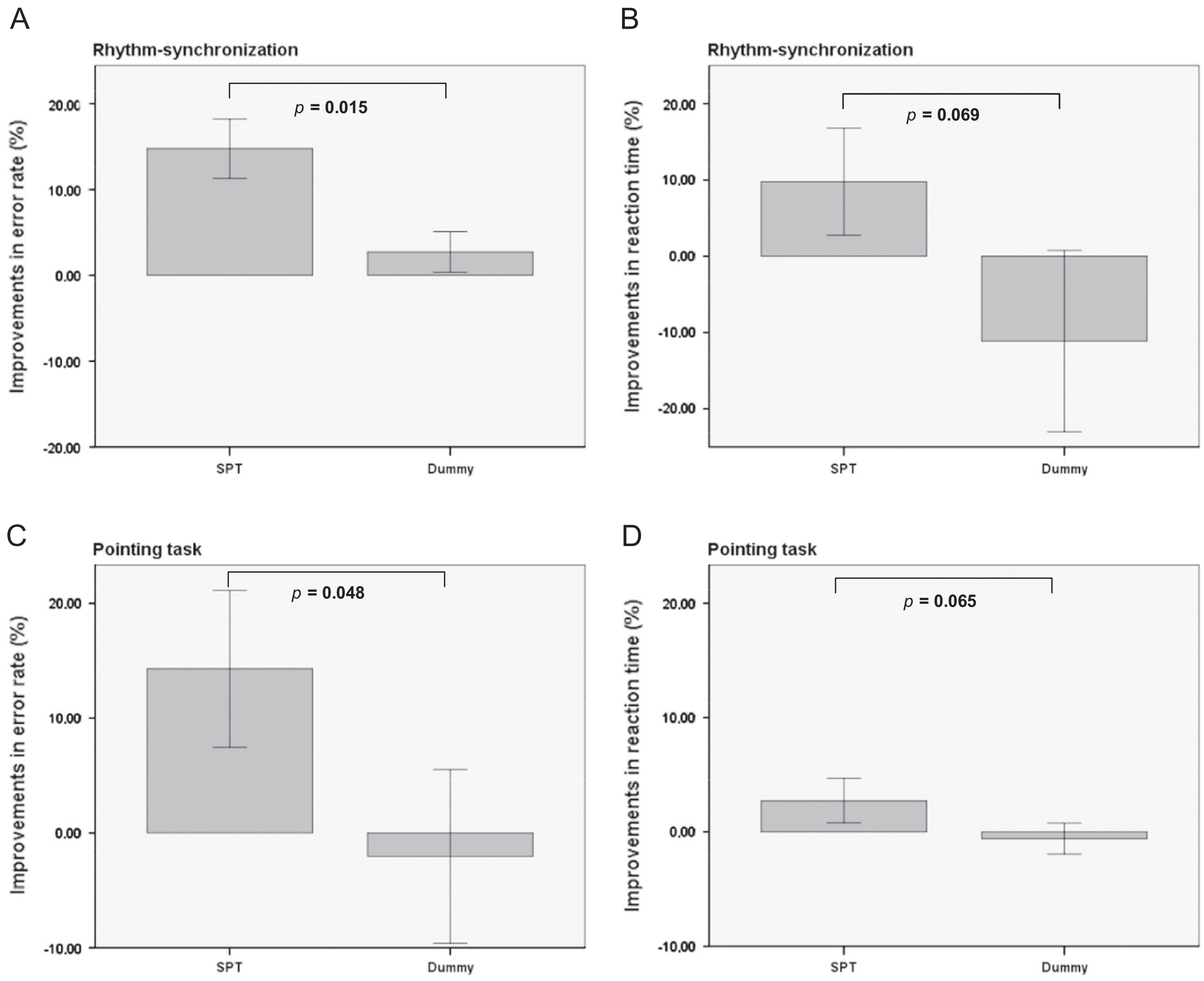

Fig. 4. Improvements in motor performance after mental training; p corrected for number of comparisons; error bars show standard error ±1. (a) Improvements in error rate of rhythm-synchronization in %. (b) Improvements in reaction time of rhythm-synchronization in %. (c) Improvements in error rate of pointing task in %. (d) Improvements in reaction time of pointing task in %.

significant improvement of reaction times after the SPT-training compared to the dummy-training (Mann–Whitney, $z=-1.829$, $p=.069$, corrected, cf. Fig. 4b). In the SPT-group, improvements in reaction times and error rates were not correlated ($p=.531$), and the number of temporally correctly delivered taps did not change significantly after training ($p=.186$). In contrast, the SPT-trained participants made significantly less surplus taps ($p=.001$), and significantly less responses were omitted ($p=.011$), indicating to different mechanisms that might have resulted in reduced error rates and reaction times in the SPT-group.

3.2.2. *Pointing task*

The data of two participants (one SPT-, one dummy-training) showed an incorrect recording of responses and were excluded from analysis in this task (SPT-training: $N=17$, dummy-training: $N=20$).

The repeated measures ANOVA on "time" and "training" showed no significant interaction effect for the dependent variables "reaction time" ($p=.212$, uncorrected) and "error rate" ($p=.232$, uncorrected), indicating that the SPT-training had no differential effect on the two tested motor variables compared to the dummy-training. Likewise, no significant main effects of "time" and "training" (cf. Table 1) were found, thus the training groups did not differ and no changes in the pointing performance had occurred over time. However, Mann–Whitney-*U*-tests on improvements revealed a significantly greater improvement of error rates (Mann–Whitney, $z=-1.981$, $p=.048$, corrected) in the group trained with the SPT compared to the dummy-training-group as well as a strong trend towards significance with respect to improvements in reaction times (Mann–Whitney, $z=-1.859$, $p=.065$, corrected), cf. Fig. 4c and d. The improvements in reaction times and error rates were not correlated ($p=.826$) in the SPT-group.

3.2.3. *Joystick task*

As for the aforementioned task, the repeated measures ANOVA neither revealed a significant interaction effect between the factors "time" and "training" for "reaction time" ($p=.831$, uncorrected) and "error rate" ($p=.862$, uncorrected) nor a significant main effect of "training" for the dependent variables. Therefore, the SPT-training effect did not transfer onto more general visuomotor motor functions as tested by the joystick task.

3.2.4. *Jebsen–Taylor handfunctiontest*

The repeated measures ANOVA for the dependent variable "total time" revealed a significant main effect of "time" ($p=.004$), indicating changes in reaction times in both training groups. However, there was no interaction effect between "training" and "time" ($p=.836$). Therefore, general motor abilities as tested by the JTT did not improve in the SPT-training group compared to the dummy-training group.

4. Discussion

The aim of the present study was to investigate whether motor skills in a population of young healthy adults can be improved through a novel mental training paradigm based on the serial prediction task (Schubotz, 1999).

To address this question, two groups of participants underwent a single-blinded five-day cognitive training schedule and were tested in four different motor tasks on the day before and after training. One group received the SPT-training and the other one a "dummy-training" consisting of a serial match to sample task that engaged working memory rather than serial prediction. The results showed significant improvements in error rates in subjects who underwent the SPT-training compared to those who underwent the dummy-training in a visuomotor timing as well as a visuomotor coordination task, indicating a specific transfer effect of the mental SPT-training on motor-related performance, i.e. sensorimotor transformations. Moreover, there were statistical trends towards SPT-training-specific improvements in reaction times in both these tasks. In contrast, more complex motor abilities remained unaffected by the training procedure in this group of healthy subjects.

4.1. *Rhythm-synchronization task*

As hypothesized, we found an improvement of finger-tapping synchronized to a visually specified rhythm in the subject group trained with the SPT compared to the control group.

SPT-training led to a significant improvement in error rates and a trend towards significantly improved reaction times, i.e. reduced mean asynchrony in the case of cued finger-tapping, (Aschersleben, 2002; Jäncke, Loose, Lutz, Specht, & Shah, 2000; Lutz, Specht, Shah, & Jäncke, 2000; Pollok, Krause, Butz, & Schnitzler, 2009; Repp, 2005). As mentioned above, the improvements in mean asynchrony and error rates were not correlated and the number of temporally correct delivered taps did not change significantly. In contrast, significantly less surplus taps were made as well as significantly less responses were omitted, reflecting less uncertainty in rhythm production, probably owing to the availability of more accurate forward models gained during the SPT-training (Large, Fink, & Kelso, 2002; Wolpert & Flanagan, 2001). Given the assumption that a close temporal coupling of stimulus and response reflects how well an event is anticipated and therefore how well a given rhythm has been internalized, SPT-training seems to improve visuomotor coupling in the context of rhythm-synchronization. This result goes in line with the notion of a common neural substrate of pure attentional perception and overt production of rhythmical sequences within lateral premotor cortex. In the context of computational forward models (Wolpert & Flanagan, 2001), the perceptual training with the SPT encourages the generation of sensorimotor simulations for predicting the future perceptual rhythm identical to the ones generated for the overt rhythm production of a predictive rhythm (Grush, 2004). Note that different rhythmical structures were used for SPT-training and motor status evaluation. The better the internal forward model predicts the perceived and tapped rhythm, the closer the timing between stimulus and response as reflected in a shorter ("more negative") mean asynchrony. Accordingly, Ramnani and Passingham (2001) showed that rhythmic learning behaviourally came along with shorter reaction times as well as a shifted distribution of reaction times towards stimulus onset since subjects became increasingly more accurate in predicting the onset of the stimuli. On a neural level this is accompanied by learning-related increases in areas of a neocortical-cerebellar loop, among others including the lateral premotor cortex (Ramnani & Passingham, 2001). Further neuroimaging studies also showed an involvement of the motor system in both the perception and the production of rhythmical events (Bengtsson et al., 2009; Coull, Vidal, Nazarian, & Macar, 2004; Grahn & Brett, 2007; Jäncke et al., 2000; Lutz et al., 2000; Pollok et al., 2009). Interestingly, whereas the inferior-most portion of the ventral premotor cortex is supposed to be crucial for the perception of rhythmical sequences (Schubotz, 2007), the "effector" needed for response in our task (index finger of right hand) is supposed to be represented more superior in the ventral premotor cortex (Chaminade, Meary, Orliaguet, & Decety, 2001) indicating an effector-independent transfer effect, which extends beyond pure direct matching of perception and action (Jeannerod, 2001).

Both the changes in mean asynchrony as well as the improvement in error rate refer to qualitatively distinct effects on rhythm-synchronization: (i) more effective phase error correction (i.e. asynchrony) resulting in a stronger visuomotor coupling and (ii) higher certainty in rhythm anticipation and production (Grush, 2004; Ramnani & Passingham, 2001; Repp, 2005; Wolpert & Flanagan, 2001). These effects cannot be ascribed to an unspecific practice effect due to task repetition itself, but have to be taken as a specific SPT-training effect, because similar changes would not be observed in the dummy-group performing the motor-status-evaluation in exactly the same manner.

4.2. *Pointing task*

In contrast to the aforementioned task, we did not find a significant interaction effect "time" by "training" in the ANOVA. However, with respect to the normalized improvements of task performance, significant changes in error rates could be observed, i.e. significantly fewer pointing errors were made after the SPT-training compared to the dummy-trained group. Additionally a trend towards significantly improved reaction times was found. Visuomotor coordination is a complex process that requires the synergistic function of different systems, for example the visual, proprioceptive and motor control system as well as cognitive aspects like attention and memory (cf. Battaglia-Mayer, Caminiti, Lacquaniti, & Zago, 2003; Crawford et al., 2004 for detailed reviews on that topic). Here the (dorsal) premotor cortex plays a prominent role, for example, when encoding information about target location, movement direction and amplitude in combination with eye-signals (Boussaoud, Jouffrais, & Bremmer, 1998; Fu, Flament, Coltz, & Ebner, 1995; Fu, Suarez, & Ebner, 1993). The (posterior) parietal cortex on the other hand is supposed to house higher-order spatial representations based on sensory information (Lacquaniti, Guigon, Bianchi, Ferraina, & Caminiti, 1995) and is especially responsible for reference framed transformations (Andersen & Buneo, 2002; Xing & Andersen, 2000). Analogous to the computational models mentioned above in the context of sensorimotor synchronization, we expected the SPT-position-training task to specifically generate spatial visuomotor simulations via internal forward models through dorsal premotor cortex activation. In the context of motor control, a combination of feedforward and feedback processes is supposed to be crucial for adequate visuomotor coordination (Crawford et al., 2004; Seidler, Noll, & Thiers, 2004). The tendency of shortened reaction times and significantly decreased error rates in visuomotor performance after SPT-training might reflect enhanced feed-forward computations facilitated by the SPT. Nevertheless, due to the over trained character of visuomotor coordination in our every-day life, especially healthy young adults might need a more intense training and/or more complex motor task to yield broader effects.

4.3. *Joystick task and Jebsen–Taylor handfunctiontest*

The other two motor tasks (i.e. the joystick task and Jebsen–Taylor handfunctiontest) were chosen to evaluate putative general transfer effects on motor performance. Our data did not show an SPT-specific training effect on performance in these two motor tasks. The reasons for the missing training effect might be identical to the one of the pointing-task mentioned above. An additional attenuation of transfer could have occurred due to the less similar operations (with respect to task properties) offered between the SPT-position and pointing task, and the SPT-position and the joystick task, respectively, according to the transfer-appropriate processing view (Kolers & Roediger, 1984; Shanks & Cameron, 2000).

4.4. *Conclusion and further implications*

Our results indicate a specific transfer effect of a mental SPT-training on sensory-guided motor performance, particularly with respect to error rates in sensorimotor synchronization and visuomotor coordination. These two visually guided motor tasks served as an identical reference frame for the mental SPT-training and tested motor performance in temporal as well as spatial dimensions. No general transfer of training effects on motor performance could be observed, here tested by using the Jebsen–Taylor handfunctiontest and a visuomotor joystick task. In conclusion, our data clearly show that the cognitive training by means of the SPT led to a significant improvement of motor performance in tasks resembling the trained dimensions. This finding is remarkable as it shows that cognitive training other than motor imagery can indeed influence active motor performance.

Motor learning without motor training, especially in a temporal dimension, has been shown before, where an auditory perception of temporal intervals transferred to the overt production of these intervals (Meegan, Aslin, & Jacobs, 2000). Here we found a transfer effect of visually perceived rhythmical stimuli to a more complex task, where combinations of different inter-stimulus-intervals had to be produced in rhythmical structures, thereby confirming and extending previous results.

We trained a population of young healthy participants without any motor impairment 1 h per day over five consecutive days and thereby improved motor performance in training-related tasks. The fact that we observed training effects specific to the kind of task (i.e. improvements in pointing abilities and rhythm/temporal aspects of movements) confirms our initial hypothesis that mental training based on the serial prediction task effectively improves motor behaviour, probably by co-activation of sensorimotor circuits (Schubotz, 2007). The question arises whether the SPT has the potential to influence general motor performance in a cohort with much more room to improve, i.e. patients with motor impairments. In such a population mental strategies especially in combination with classical motor rehabilitation methods like physical therapy, occupational therapy and logopaedics may offer a favourable therapeutic approach (Allami, Paulignan, Brovelli, & Boussaoud, 2008; Avanzino et al., 2009; Braun, Beurskens, Borm, Schack, & Wade, 2006; Braun et al., 2008; Malouin, Richards, Doyon, Desrosiers, & Belleville, 2004; Munzert, Lorey, & Zentgraf, 2009; Page, Levine, & Khoury, 2009; Zimmermann-Schlatter, Schuster, Puhan, Siekierka, & Steurer, 2008). Other than previous approaches (Dijkerman, Ietswaart, Johnston, & MacWalter, 2004; Gentili, Han, Schweighofer, & Papaxanthis, 2010; Jackson, Lafleur, Malouin, Richards, & Doyon, 2003; Gentili, Papaxanthis, & Pozzo, 2006; Hewett, Ford, Levine, & Page, 2007; Katiuscia et al., 2009; Nyberg, Eriksson, Larsson, & Marklund, 2006; Olsson, Jonsson, Larsson, & Nyberg, 2008; Wohldmann, Healy, & Bourne, 2007), the SPT-training accounts for the individual accuracy in task performance in a feedback-based manner. Furthermore, task difficulty, complexity and duration can be modified stepwise and can be monitored online. Therefore, studies are now needed that test the potential of the SPT in a neurorehabilitative setting.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version at http://dx.doi.org/10.1016/j.neuropsychologia.2013.11.018.

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