Robust retention of individual sensorimotor skill after self-guided practice

Se-Woong Park1 and Dagmar Sternad1,2,3,4

1Department of Biology, Northeastern University, Boston, Massachusetts; 2Department of Electrical and Computer Engineering, Northeastern University, Boston, Massachusetts; 3Department of Physics, Northeastern University, Boston, Massachusetts; and 4Center for the Interdisciplinary Research of Complex Systems, Northeastern University, Boston, Massachusetts

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Park SW, Sternad D. Robust retention of individual sensorimotor skill after self-guided practice. J Neurophysiol 113: 2635–2645, 2015. First published February 4, 2015; doi:10.1152/jn.00884.2014.—Long-term retention of a motor skill has received relatively little systematic study, even though lasting neuroplasticity is the holy grail of any clinical intervention. This study examined the acquisition and retention of a novel bimanual polyrhythmic skill, practiced with sparse explicit feedback mimicking real-life scenarios. Self-paced and metronome-paced practice conditions were compared in their effect on long-term retention. Two groups of subjects first underwent extensive practice of 20 practice sessions over 2 mo, then followed up with three retention sessions after 3 mo. Results showed that subjects developed robust spatiotemporal patterns, despite the lack of reward and little quantitative error feedback about their performance (Hypothesis 1). These movement patterns were reproduced after a 3-mo interval, frequently even in the first trial, with no intermediate practice (Hypothesis 2). Self-paced training of movement patterns led to slightly less variability in the retention test (Hypothesis 3). These results document the specificity and stability of kinematic patterns and their underlying neuroplastic changes and underscore the effectiveness of self-guided practice. The findings are discussed in the context of current neuroimaging results and their clinical implications.

IT IS WIDELY AGREED UPON THAT learning, or changes in the central nervous system, have only occurred when practice-induced performance changes show long-term persistence (Schmidt and Lee 2005). Hence, to study the underlying mechanisms of learning and neuroplasticity, it is not sufficient to only trace learning curves, but it is necessary to also examine long-term stability and forgetting after some interval of no practice (Adams 1987; Dayan and Cohen 2011). Although some strides have been made toward understanding motor memory, both behavioral and neural data of long-term retention of sensorimotor skills are still only few and far between (Kandel 2009; Rohrer and Pashler 2010; Squire and Zola 1996). Attention to this topic is even more necessary, as long-term stability of a practiced motor behavior is the holy grail for any therapeutic intervention.

Several functional imaging studies on human motor learning and long-term retention have identified structural changes in cortical and subcortical structures, both in white and gray matter (Dayan and Cohen 2011; Draganiski et al. 2004; Landi et al. 2011; Scholz et al. 2009). An electrophysiological study on primates showed persistent changes in M1 after 1 yr that was correlated with properties of the task (Matsuzaka et al. 2007). Neuroimaging of rodents revealed the continuous formation and loss of dendritic spines during practice and in long-term retention tests (Xu et al. 2009; Yang et al. 2009). While revealing where and how neural plasticity occurs, practice-induced changes in anatomically specified locations are mute about what is learned and which conditions of practice ensure such plastic processes in the brain. The present study examined acquisition and long-term retention of a novel skill with extensive practice under two practice conditions. Fine-grained analyses of kinematic data aimed to reveal the specificity and stability of the sensorimotor patterns.

Retention is also recognized as an important indicator of learning in many studies on motor adaptation (Huang et al. 2011; Scheidt et al. 2000). The target “skill” of numerous studies has been adaptation of a reaching movement to a visual rotation or an unusual force field (Lackner and Dizio 1994; Osu et al. 2004; Shadmehr and Mussa-Ivaldi 1994). However, these studies have focused on savings, the accelerated relearning of a target skill, as a probe to shed light on the type of internal model of the dynamic environment established through practice or as the behavioral indicator for the memory of previous errors (Herzfeld et al. 2014). In such adaptations, the learned behavior vanishes relatively fast after the perturbation is removed. This differs from the real-life scenario where a new skill is learned in unperturbed practice conditions, such as playing the piano or skateboarding, where the acquired competence persists for a long time. It remains an open question whether such learning of a new skill and adaptation of a known behavior lead to the same neuroplastic changes. The present study examines practice and retention of a novel bimanual skill that has not been part of the behavioral repertoire.

With the interest in long-term neuroplasticity, not only the task itself, but also the specific practice process may play a significant role. What practice conditions facilitate long-term retention? In almost all motor learning studies, the importance of controlled quantitative feedback about error has been unchallenged (Salmoni et al. 1984). For example, in adaptation to visuomotor rotations, the online display of the cursor relative to the target and quantitative error feedback were shown to be essential, and the quality of performance and rate of improvement deteriorated in its absence (Shabbott and Sainburg 2010). This highly controlled scenario contrasts with real-life scenarios, where exact quantitative feedback is typically absent. For example, children frequently practice in an exploratory, self-guided manner when they learn to ride a skateboard, only guided by a mental image of their desired skill from observation of peers and role models. Nevertheless, this self-guided training is also successful. A recent longitudinal case study on
the acquisition of a polyrhythmic bimanual task first demonstrated that practice without any quantitative feedback could lead to stable retention not only after 6 mo, but also after 8 yr (Park et al. 2013). The present study uses a larger cohort of subjects that practices a slightly modified task to corroborate the observed kinematic specificity of retention. We hypothesize that self-guided practice leads to stable sensorimotor patterns that are retained over a long time.

To further probe into conditions of practice on forming sustainable individual coordination patterns, the present study examined the role of extrinsic timing. Therefore, one of the two conditions included auditory metronome pacing, with which subjects synchronized. The frequency was close to the preferred pace to ensure comparable conditions to the self-paced group. One conjecture was that such auditory pacing facilitates learning as the extrinsic timer provided a perceptual “anchor” (Fink et al. 2000). Alternatively, the extrinsic timer may require additional attention and corrective adjustments to meet the target period (Repp and Keller 2004). The absence of extrinsic guidance may also afford more exploration and facilitate that subjects acquire their individually preferred solutions. We therefore hypothesized that self-guided practice with few task constraints will lead to an individual-specific movement pattern that has long-term stability.

The absence of stringent task constraints and exact quantitative error information gives individuals ample opportunity to develop their own realization. The target task is to produce an average frequency ratio without any amplitude prescriptions. While the temporal features defined the task, spatial aspects were free to vary. As such, the task contained task-relevant and task-irrelevant dimensions. This was expected to lead to significant interindividual variations in the spatial patterns.

In overview, the study tested the following three hypotheses. 1) When participants practice a novel skill in self-guided fashion, i.e., with only sparse extrinsic feedback, they acquire their preferred sensorimotor pattern with idiosyncratic, but stable variations. 2) This spatiotemporal pattern has long-term stability and can be reproduced after 3 mo. 3) Self-guided practice with few task constraints leads to more robust retention than practice with extrinsic guidance. To test these hypotheses, subjects performed a novel polyrhythmic bimanual task with the two arms coordinating in a 3:2 frequency ratio than practice with extrinsic guidance. To test these hypotheses, subjects performed a novel polyrhythmic bimanual task with the two arms coordinating in a 3:2 frequency ratio.

Procedure and Task Instruction

Participants were asked to first familiarize themselves with the equipment and perform unimanual movements with each forearm, followed by bimanual symmetric movements for 2 min. Then the experimenter gave the following instructions: “Move your right arm three cycles, while your left arm moves two cycles; move as continuously and consistently as possible.” Following this verbal instruction, participants watched a simulation of a computer-generated 3:2 performance on the projection screen: the two rotating bars moved with sinusoidal movements in a 3:2 frequency ratio with the right bar moving three times as fast as the left bar. The frequency, amplitude, and center of the oscillations was matched to the participants’ performance obtained from a pilot study; the frequency of the right fast

Experimental Apparatus

The participant sat on a chair placing his/her forearms on two custom-made manipulanda that were mounted on a tripod each and facilitated rotation of the forearms in the horizontal plane (Fig. 1A). The length of the aluminum support arm was 40 cm, and its weight was 150 g. This light weight kept the inertia low and had therefore very little influence on the movement frequency. A wooden sphere was affixed on the distal tip of the manipulandum, and participants grasped the sphere in a half-supinated hand orientation similar to holding a cup. Each elbow joint was aligned with the pivot of the support arm, enabling measurement of single-joint elbow flexions and extensions. The tripods with the two manipulanda on each side of the participant were adjusted to each individual’s body size to afford a comfortable arm position when rotating their forearms. Once determined, the position of the manipulanda was fixed throughout all experimental sessions.

The rotations of the manipulanda were recorded by an optical encoder at a sampling frequency of 120 Hz (model A2, US Digital, Vancouver, WA). The digital signals were acquired by custom-made software written in MATLAB (The Mathworks, Natick, MA). The data were instantaneously transformed and displayed on a projector screen located in front of the participant at a distance of 2.0 m (Fig. 1B). The forearm rotations were displayed as bars on the screen (length 30 cm), rotating around a point of rotation.

Fig. 1. Apparatus and practice schedule. A: the participant (P) was seated on a chair and rotated his/her forearms in the horizontal plane, while each arm rested on a single-joint manipulandum. B: the angular displacements of the two manipulanda were projected online onto a back projection screen in front of the subject. C: practice schedule with 20 practice (PS) and 3 retention sessions (RS) after a 3-mo interval; each session consisted of 15 trials of 45-s duration each. [Photograph reprinted with permission from J. Ebert and N. Kuznetsov].
were asked to match every fast right-arm cycle with the beats. The P16), participants listened to metronome beats played at 0.75 Hz and group (MP). In the SP group (P1 to P8), the participant was encour-
comparable: the self-paced (SP) group, and the metronome-paced fast. This score may also have provided some motivational effect. Neverthe-
less, a ratio of 2.0 indicated that overall the right arm was moving too fast. This score may also have provided some motivational effect.

The 16 participants were randomly assigned to one of two experiment-
groups, keeping age, sex, handedness, and musical experience comparable: the self-paced (SP) group, and the metronome-paced group (MP). In the SP group (P1 to P8), the participant was encour-
aged to find his/her own comfortable pace; in the MP group (P9 to P16), participants listened to metronome beats played at 0.75 Hz and were asked to match every fast right-arm cycle with the beats. The metronome pacing was present in all practice, including the retention sessions.

All participants performed 20 practice sessions (PS-1 to PS-20) followed by 3 retention sessions (RS-1, RS-2, RS-3) after a 3-mo-long pause (Fig. 1C). Each session consisted of 15 trials, with each trial 45 s long, leading to a total duration of 3 h and 45 min of continuous movements. Participants came to the laboratory three to five times per week based on their availability, such that the 20 practice sessions extended over 37.4 ± 4.1 days, on average. Participants returned for a retention test after an interval of 97.4 ± 5.8 days. Occasionally, participants could not maintain their regular schedule, but post hoc analyses assured that slightly longer intervals between practice ses-
sions did not affect performance measures. Experimental parameters, such as total duration of the experiment, intersession intervals, and retention intervals, were not significantly different between the SP and MP group.

Data Analysis and Dependent Measures

The kinematic data were filtered and analyzed, and the following dependent measures were calculated.

Frequency ratio. To obtain the continuous movement frequencies of the two hands and their ratio, the two arms’ position data were transformed into instantaneous phase using the Hilbert transform (Park et al. 2013; Pikovsky et al. 2003). Figure 2, A and B, shows two trial segments early and late in practice with different degrees of regularity in period, amplitude, and relative phase. The Hilbert transform turned the original periodic signal into a time series of phase and amplitude in the complex plane. For the duration of one continuous trial, the instantaneous phase is continuously increasing (Fig. 2, C and D); the first derivative of this phase renders the instantaneous phase velocity or frequency, which is approximately constant across cycles, but shows considerable fluctuations (Fig. 2, E and F). This phase

Fig. 2. Frequency ratio. A and B: angular displacement profiles of an exemplary participant (P12) in early and late practice (PS-8 and PS-18, respectively). While both trial segments were close to the desired 3:2 frequency ratio, the amplitude was considerably more variable early in practice. The vertical lines demarcate global cycles, which define the repetition of the bimanual 3:2 pattern. C and D: unwrapped phase profiles calculated from the same trial segments shown in A and B, respectively. For better visualization, the actual phase profiles were shifted such that, at the 15-s mark, relative phase was zero. E and F: first time derivative of the instantaneous phase yields instantaneous phase velocity or frequency. The instantaneous frequency ratio was obtained by dividing the fast arm frequency by the slow arm frequency at every time point. G and H: average profiles of instantaneous frequency ratio across one global cycle early and late in practice, respectively. The global cycles of one trial were normalized, and means (solid line) and SDs (shading) per time bin were obtained. The integral of the SDs across the cycle quantified intercycle variability.
derivative was obtained by applying the Savitzky-Golay filter of order 4 and length 0.5 s (Press et al. 2007). The movement frequency of each hand was defined as the average over the duration of a trial.

**Frequency modulation and intertrial variability.** The instantaneous frequency ratio was calculated as the ratio of the frequency of the fast (right) arm over the slow (left) arm at each time point. Figure 2, G and H, shows the continuous frequency ratio across one global cycle for one trial. Perfect sinusoids in a 3:2 frequency ratio would produce a straight horizontal line. However, the individual participants differed in their realizations. To quantify these individual patterns, the time series was parsed into global cycles, i.e., segments delimited by every third peak in the fast arm’s angular displacement (vertical lines in Fig. 2, A and B). The peak in the fast arm was chosen as demarcation because the right arm generally showed less variability, and in the MP group the right peak was synchronized with the metronome sound. Each trial comprised an average of 10 global cycles, depending on the preferred movement frequency. The frequency ratio profiles of all global cycle segments were then normalized to unit time and divided by 250 time points. For each time point, a mean and SDs of the frequency ratio were determined (shown as solid line and shaded bands in Fig. 2, G and H).

**Variability of frequency ratio.** The SDs around the mean profile represented how consistent this modulation was across cycles. The example traces in Fig. 2, G and H, show that the shaded area was markedly wider in early practice (PS-8) compared with late practice (PS-18). To quantify this intracycle variability in a single measure, the SDs at each of the 250 time points were averaged.

**Acquisition time.** During the first trials most participants showed highly fluctuating behavior and did not achieve the 1.5 frequency ratio, but then “locked into” the target ratio. Hence, the mean frequency ratio served as a measure to determine the time when participants had “found” the 3:2 pattern. The time of task acquisition (AQ) was defined as the session when the desired frequency ratio was maintained continuously until the end of practice. The criterion deviation from the target frequency ratio was 0.05.

**Lissajous orbits.** To compare the individual realizations of the 3:2 task across practice and retention and also between participants, the angular displacements of the two arms were plotted against each other, i.e., in a Lissajous representation. To this end, the angular displacement of one trial was first parsed into global cycles that were then time-normalized and binned (100 time points). The means across cycles at each time bin rendered a representation of an averaged global cycle that were then plotted against each other for the Lissajous representation.

**Statistical Analyses**

Two separate sets of analyses were conducted to evaluate learning across practice and to assess retention. To test Hypothesis 1 and quantify learning between AQ and PS-20, performance variables were submitted to a 2 (AQ, PS-20) × 2 (SP, MP) mixed-design ANOVA with participants as random effect. Each session had 15 trials, and session was regarded as a factor with repeated measures. To test Hypothesis 2 and assess retention, we submitted performance variables to a 4 (PS-20, RS-1, RS-2, RS-3) × 2 (MP, SP) mixed-design ANOVA with participants as random effect. Tukey post hoc analyses were performed to test Hypothesis 3 and assess group effect. Values that exceed 3 SDs were eliminated when the analyses were run. All analyses were performed in IBM SPSS Statistics version 21 (IBM, Armonk, NY).

**RESULTS**

**Frequency Ratio**

To examine how well participants achieved the explicit task goal, a first test examined the frequency ratio in each trial over practice. Figure 3 shows the mean frequency ratios of all 15 individuals. SP and MP to the self-paced group (SP), and P9 to P16 of the metronome-paced group (MP). The vertical lines mark the acquisition time (AQ), defined when the mean of the 15 trials entered and stayed within the frequency band of [1.45, 1.55] (horizontal lines) until the end of practice.
trials across the 20 practice and 3 retention sessions for all 16 participants in the 2 practice groups (P1 to P8 are in the SP group, P9 to P16 are in the MP group). The two horizontal lines denote the range of [1.45, 1.55], which was the resolution of the feedback that subjects received. All participants showed highly variable performance in the beginning of practice, potentially speaking to the exploration of different coordination patterns. However, once they had entered the band, the frequency ratio remained close to the 1.5 ratio and was rarely lost again.

AQ was defined as the session, when the mean frequency ratio entered and stayed in the target range of [1.45, 1.55]. The vertical lines in Fig. 3 mark AQ for each participant, showing variations between sessions 1–11 across individuals. An independent t-test comparing AQ in the two groups did not reveal a significant difference in the number of sessions they required to find the 1.5 ratio. To examine whether further learning occurred after AQ, the frequency ratios at AQ were compared with those at practice session PS-20 in a 2 (AQ, PS-20) × 2 (SP, MP) ANOVA. None of the effects was significant, showing that there were no further changes after AQ, and no difference between the two groups: session main effect, F(1,476) = 0.01, P = 0.922; group main effect, F(1,476) = 0.824, P = 0.364; interaction, F(1,476) = 0.711, P = 0.399.

To test whether participants retained the acquired performance after 3 mo, a 4 (session) × 2 (SP, MP) ANOVA compared the frequency ratio of PS-20 with the retention sessions RS-1, RS-2, and RS-3 in the two groups. None of the effects was significant. Hence, participants did not show significant decrements in their acquired skill, neither in the SP, nor in the MP condition: session main effect, F(3,951) = 1.182, P = 0.315; group main effect, F(1,951) = 0.160, P = 0.689; interaction, F(3,951) = 0.100, P = 0.960.

Given the extensive practice with consolidation time between sessions, we also tested whether there was offline learning or warm-up decrements at the beginning of each session. Paired sample t-tests found neither an improvement at the beginning of the sessions, nor a decrement compared with the previous session. We also inspected whether the two participants with musical training (P8 and P15) performed differently than the other participants. Here and in other dependent measures, the two participants performed better than the group average, but they were not the best performers, as can be seen in the figures.

**Movement Frequency**

Did participants in the MP group achieve the instructed synchronization with the metronome, and how did their frequency compare to the self-selected frequencies of the SP participants? To address these two questions, each individual’s fast right-arm frequency was evaluated. Figure 4 shows absolute frequency of both arms during practice and retention sessions for all 16 participants. Participants in the MP group indeed performed the right-arm oscillation at 0.75 Hz and the left-arm oscillation at 0.5 Hz throughout practice and retention.

In contrast, the corresponding frequencies in the right arm of the SP participants at AQ spanned from 0.59 to 1.16 Hz, showing that the skill was performed with a wide range of frequencies. This range bracketed the fixed frequency of 0.75 Hz of the MP group and remained relatively stable across sessions. From AQ to PS-20, participants increased or decreased their movement frequency, but reached an asymptote

![Fig. 4. Absolute frequencies of the fast and slow arms across 20 PS and 3 RS. The vertical lines mark the AQ as in Fig. 3. Following initial variations, all participants in the MP group learned to synchronize their right fast arm movements with the frequency of 0.75 Hz of the metronome.](http://jn.physiology.org/doi/10.1152/jn.00884.2014)
at PS-20 that was between 0.50 and 1.05 Hz. A one-sample $t$-test comparing the mean frequencies between the SP and MP group in PS-20 did not reveal a significant difference ($P = 0.27$).

To assess whether inertial properties may have determined the chosen frequencies in the SP group, we compared the frequencies of male and female participants, on the assumption that female arms were generally smaller than those of males. Their individual frequencies at PS-20 were as follows: male (P1, P2, P3, P5): 0.93, 0.66, 0.50, 1.05 Hz; and female (P4, P6, P7, P8): 0.88, 0.80, 0.90, 0.86 Hz, respectively. A $t$-test did not identify a significant difference, $t(6) = -0.59$, $P = 0.58$.

A one-way ANOVA compared the frequencies of the SP participants from the last practice session PS-20 to the three retention sessions, RS-1, RS-2 and RS-3. There were no significant differences, indicating that the frequency neither changed from PS-20 to RS-1, nor across the retention sessions, $F(3,476) = 2.46$, $P = 0.062$. Hence, the participants developed their own preferred frequencies, different from 0.75 Hz, that were remarkably stable across retention.

**Frequency Ratio Modulation**

While the trial means of the absolute frequency and the frequency ratio assessed task performance, the averaging process over the entire trial duration rendered only a coarse-grained picture. Given that the acquisition process was self-guided with only sparse feedback, subjects developed very different realizations of the 3:2 task. This individual modulation was best captured by the continuous frequency ratio within a global cycle.

Figure 5 shows the average frequency ratio profiles over a global cycle across all sessions starting at AQ for four select participants. Each profile was calculated within a single trial, trial 8, from the respective sessions. The shaded bands show 1 SD around the mean; the practice sessions are shown in black and retention sessions in red for four selected participants (P2, P8, P10, P13). The four panels illustrate that each of the individuals developed his/her own temporal accentuation of the two arms to achieve the mean frequency ratio of 1.5. Note that...
a perfect frequency ratio with two sinusoidal profiles would lead to a straight line. Importantly, the three retention sessions displayed a very similar profile, highlighting that the same subtle pattern was reproduced after the 3-mo-long dormant period.

To further probe into the immediate retention performance after the 3 mo, the frequency ratio profiles of the last trial 15 in PS-20 were compared with the first trial 1 in RS-1. Figure 6 graphs both trial profiles for all 16 participants. The two profiles are offset to avoid overlap. This juxtaposition illustrates the robustness of this modulated profile after this long dormant period. Note that subjects were not aware of this subtle modulation.

Variability of Frequency Ratio

The SDs around the mean profile express how variable or robust the modulation was over successive cycles. Integrating the SDs over the global cycle gave a measure of intercycle variability. Figure 7 overviews the values across the practice sessions for all participants. In contrast to the discontinuous acquisition of the 3:2 frequency ratio, this measure showed an approximately exponential decline across all 20 practice sessions. This measure was submitted to a 2 (AQ, PS-20) × 2 (SM, MP) ANOVA that assessed the variability during the acquisition process between AQ and PS-20 in both groups. The main effect for session documented that, as to be expected, the variability dropped significantly across practice, $F(1,473) = 15.65, P < 0.001$. In addition, the two groups differed significantly, $F(1,473) = 6.92, P < 0.01$, and a significant interaction was found, $F(1,473) = 5.78, P = 0.017$. Post hoc tests revealed that, at AQ, the MP group showed more variability than the SP group ($P = 0.01$), while performance at PS-20 no longer differed ($P = 0.47$).

To assess how robust the modulation was across the retention interval, the same integrated variability was submitted to a 4 (session) × 2 (group) ANOVA comparing PS-20 with RS-1, RS-2, and RS-3 in both groups. Results showed an interaction, $F(3,951) = 3.17, P < 0.05$, and a main effect for session, $F(3,951) = 11.90, P < 0.001$, but no main effect for group, $F(1,951) = 1.12, P = 0.29$. Post hoc analyses revealed that the variability in the MP group increased significantly from PS-20 to RS-1, while the SP group remained unchanged. Except for a small increase in the SP group from RS-2 to RS-3, no other pairwise comparison was significant. Within-individual comparisons with paired-sample t-tests showed that this increase in variability in the MP group was seen in six of the eight individuals, compared with only two individuals in the SP group (Fig. 8).

Continuous Kinematic Realizations

To further inspect the retention of the individual realizations, the continuous displacements of the right and left arm were visualized in angle-angle or Lissajous plots. Figure 9 shows the Lissajous orbits of all 16 participants; the black lines depict the orbit in trial 15 of PS-20, and the red lines depict trial 1 in RS-1. First, individuals showed remarkably different shapes caused by differences not only in movement amplitude, but also in relative phase between the two movements. This visualization underscores the robustness of the individual kinematic profile from the last practice trial across the 3-mo interval until measured again in the retention trial.
DISCUSSION

Aside from isolated studies that reported relatively gross behavioral measures, usually on very few subjects, there have been only few studies that assessed retention after more than a few days or weeks (Adams 1987; Dayan and Cohen 2011; Nourrit-Lucass et al. 2013; Park et al. 2013; Romano et al. 2010; Swift 1910). Even less attention has been given to practice conditions that may facilitate robust long-term retention and, thereby, ensure stable neural changes. Despite the evidently time-consuming nature of these experiments, more insight is needed as long-term stability is the goal of all practice and therapy interventions. A recent meta-analysis of neuroimaging results on skill learning underscored that long-term retention (defined as 1 day to 5 wk) requires separate analysis as different neural substrates are engaged at short- and long-term stabilization (Lohse et al. 2014). With increasing practice duration, they reported a shift from the cortico-cerebellar system, engaged in short-term learning, to the cortico-striatal system in long-term learning. The present study addressed this need for long-term data and obtained fine-grained behavioral data documenting the acquisition and stability of a novel skill after 3 mo.

Participants practiced a novel bimanual task in a self-guided fashion without explicit feedback of the error. We hypothesized that subjects do not need such controlled feedback and can learn in a self-guided manner, relying on their own proprioceptive feedback and an intrinsic model of the target performance (Hypothesis 1). Evidently, this may lead to individual realizations within the task constraints. Motivated by a prior case study, we expected that this preferred pattern is stably reproduced after 3 mo of no practice (Hypothesis 2). To examine practice conditions, two groups trained the same task, but one group synchronized their movement frequency to a metronome. We hypothesized that the paced group would retain less well, as their pattern was temporally constrained and anchored to an external timer (Hypothesis 3). The results were consistent with the three hypotheses.

Hypothesis 1: Self-guided Learning with and without Metronome

Two groups of participants underwent extensive practice, a total of 3 h 45 min of movement time separated into 20 practice sessions, which was distributed over 2 mo. Compared with most other studies, this study presented a relatively long training schedule that provided ample opportunity for consolidation between the practice sessions, including sleep, which was expected to support learning (Stickgold 2005). It was possible that there was offline learning between sessions (Abe et al. 2011), but there was no significant improvement at the first trial of the session. However, there was also no warm-up decrement (Adams 1961; Ajemian et al. 2010). It should also be noted that the mere acquisition of the relatively complex and demanding task required up to 11 practice sessions.

Counter to common experimental practice, where the learner received knowledge of results or reward after every trial or intermittent trials (Salmoni et al. 1984), we provided only extremely sparse feedback after each trial: the mean frequency ratio averaged over about 10 repetitions of the movement pattern in each trial. There was neither an explicit reward for good performance, nor a penalty for deviations from the 1.5 ratio. While the sparse feedback may have served as motivation, it contained very little error information. While receiving the “score” of 1.5 does not necessarily satisfy 3:2 coordination task, scores of, for example, 2.0 would signal that the right arm was moving too fast. Hence, subjects had to rely on their intrinsic error information through proprioception and match it to an intrinsic model, provided by the first display and instruction. It may be possible that rhythmic movements particularly lent themselves for such self-guided learning, as deviations from the frequency ratio will result in phase wrapping that introduces variability across cycles. Nevertheless, this result highlights subjects’ ability to rely on and learn based on intrinsic information.

All 16 subjects of both groups acquired the target pattern under these conditions. Initially, the mean frequency ratio varied greatly, probably evidence for exploration, but, once participants “discovered” the 3:2 movement pattern, they never deviated from this performance again. Subjects in the MP group synchronized with the metronome frequency, and subjects in the SP group settled on a frequency that became stable throughout practice. Strikingly, while satisfying the temporal task requirements, the spatial aspects varied greatly, showing that spatiotemporal coupling emerged from a purely temporal task. Interindividual variations were seen in those aspects of the task that did not affect the required performance. The variability of the instantaneous frequency within each cycle was also not essential to the achievement of the task. These observations are consistent with findings in complex tasks that have redundancy, where variability is found in those dimensions that “do not matter” for task achievement (Cohen and Sternad 2009; Scholz and Schöner 1999; Sternad et al. 2011; Todorov and Jordan 2002).

This result corroborates the previous case study, where subjects acquired a 3:1 pattern without any feedback (Park et al. 2013). This previous experiment also highlighted the presence of several time scales in different variables, which was again seen in the present study. While variability showed an exponential decline with continued improvement until the 20th practice session, the frequency ratio underwent a discontinuous transition from a highly variable phase before AQ, to the robust repetition of the correct temporal pattern across sessions. Such different time scales may reflect different underlying learning mechanisms (Huang et al. 2011). While the initial part may reflect trial-and-error learning or model-free learning, the steady repetition of the pattern is likely to be use-dependent learning. This type of learning is defined as neural or behav-
ioral changes that are induced through the simple repetition of movements in the absence of systematic errors (Bütefisch et al. 2000; Diedrichsen et al. 2010).

Hypothesis 2: Robust Retention of Spatiotemporal Patterns

Compared with most other related research, this study tested retention after a relatively long interval: 3 mo (Adams 1987; Dayan and Cohen 2011; Schmidt and Lee 2005). Hence, the retention sessions tested the subjects at exactly the same task that they practiced. One common alternative design in learning experiments is to test performance of different training groups in one common task. However, this design would assess the differential effectiveness of two training schedules and the generalization of skill, rather than the persistence of the exact task that was practiced. It was also not appropriate to include a pretest, as the initial movement patterns were similarly variable, and none of the subjects could perform the target pattern. Given that in our study subjects developed their own

Fig. 9. Continuous kinematics in Lissajous representation of each individual. Each plot shows the averaged trajectory of trial 15 in PS-20 (black) and trial 1 in RS-1 (red). There was no practice before the first recorded retention trial. The differences in orbit shapes were due to differences in amplitudes and relative phase between the two arms. Before this representation, the raw displacement profiles were mean-subtracted to center the trajectories at zero.
Hypothesis 3: Role of Task Constraints

While all participants practiced without quantitative error feedback, one group synchronized their fast oscillations with a metronome that provided temporal error feedback. While the metronome could also be regarded as additional extrinsic learning aid, it turned out that behavioral measures did not differ significantly during the acquisition process. All participants acquired the skill after a similar number of practice sessions, and the variability measure did not show significant differences between the two groups in the last practice session, suggesting that the metronome neither helped nor hindered the skill acquisition. The only difference was seen in retention tests: those who performed with extrinsic pacing retained the pattern less stably than participants who practiced in self-paced fashion. The differential persistence of the pattern could be due to the fact that self-guided practice may afford more offline learning, thereby stabilizing the pattern. This interpretation is partially consistent with an argument by Abe and colleagues (2011) that reward-based learning led to better consolidation than neutral or penalty-based learning.

This different stability may also be ascribed to the fact that indeed practice with extrinsic pacing involves different areas of the supplementary cortex (Deiber et al. 1999). While this functional MRI study employed the simple task of sequential finger movements, the focused imaging of four areas of the supplementary motor area highlighted that self-paced and visually triggered movements evoked differential engagement of subareas of the supplementary motor area. The distinction between intrinsic and extrinsic timing is not as subtle as it appears at first sight.

Conclusion and Implications

The study presents relatively unique longitudinal data that highlight that skill acquisition can proceed with relatively little guidance or feedback. Even more, such self-reliance may present advantages; the results showed that there was a small but significant benefit in practicing without extrinsic pacing. Given the emphasis on controlled reward-based and error-based learning, it is valuable to highlight that subjects are also able to self-guide their skill acquisition process. This result has implications for clinical studies where extrinsic guidance is common. Given the ubiquity of self-guided practice in real life, studying the processes underlying such learning is important.

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DISCLAIMER

Any opinions, findings, and conclusions or recommendations expressed in this material are those of the authors and do not necessarily reflect the views of the funding organizations.

DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the author(s).

AUTHOR CONTRIBUTIONS

Author contributions: S.-W.P. and D.S. conception and design of research; S.-W.P. performed experiments; S.-W.P. analyzed data; S.-W.P. and D.S. interpreted results of experiments; S.-W.P. prepared figures; S.-W.P. and D.S. drafted manuscript; S.-W.P. and D.S. edited and revised manuscript; S.-W.P. and D.S. approved final version of manuscript.
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