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## How a new behavioral pattern is stabilized with learning determines its persistence and flexibility in memory

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**Abstract** Memory organization should be at times persistent and at others flexible in the face of environmental perturbations. Unlike conceptualizations that bear on the reduction of the mismatch between the memory trace and the model, it is assumed here that changes in the memory system are governed by stability principles. Results of a bimanual coordination learning task indicated that (1) persistent memories are created and stabilized, when the competition between the preexisting (0 and 180° of relative phase) and the to-be-learned (90°) patterns leads to a qualitative change in the memory layout; (2) transient memories arise without stabilization, when the competition is weaker, leading to a temporary shift of an initially stable pattern (90°) toward the required value (135°). These findings call for further examination of the relationship between stability and memory persistence, which might give a new thrust to understanding its neural correlates.

**Keywords** Motor coordination · Self-organization · Dynamical pattern theory · Forgetting

### Introduction

The relationship between *stability* and memory *persistence* may appear to be quite trivial and straightforward. Persistence is a property of the memory system to remain within specific boundaries over time. The concept of stability, however, is far from being univocal or unitary (Grimm and Wissel 1997): it may refer to different notions such as inertia, temporal dependency, or asymptotic stability (Haken 1983), leading thus to different predictions about memory persistence.

Inertia refers to the amount of perturbation that can be withstood before a change occurs. An inert system is not necessarily persistent, since the initial state is forgotten once the system has been perturbed. Temporal dependency concerns auto-correlation between successive samples (Newell and Slifkin 1998). Counterintuitively, a system characterized by long-term dependencies does not forget its initial state, but does not persist in time (Haken 1983). Finally, asymptotic stability corresponds to the capacity of the system to return to its initial state after a small perturbation. Such an asymptotically stable system will therefore persist over time. The latter proposal is put under scrutiny in the present work.

We shall investigate the issue from the perspective of dynamical pattern theory (Kelso 1995), through the window of learning a bimanual (motor) task (Zanone and Kelso 1994). Our tenet is that the commonsensically obvious, if actually elusive link between performance, learning, and memory is behavioral stability, as defined by underlying coordination dynamics. Thus, the stabilization incurred by a coordination pattern during practice predicts its long-term persistence in memory, whatever its accuracy may be at the end of learning. Reduction of error, a characteristic feature of learning, may go with the stabilization of a new coordination pattern, corresponding to the *creation* of a new stable, hence persistent memory state within the memory layout (Schöner et al. 1992; Zanone and Kelso 1992). An increase in accuracy, notwithstanding, may also occur without stabilization, based on the *shift* of pre-existing stable memory state toward the to-be-learned pattern (Schöner 1989; Zanone and Kelso 1997). This process, ensuring the *flexibility* of motor output, leads to but a transient adaptation to the task requirement, and thus to forgetting.

Regarding bimanual coordination, only a small number of coordination patterns proved to be spontaneously accurate and stable, prior to any change due to practice (Kelso 1984). As for all periodic motion, a relevant variable capturing the current coordinative state is

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*relative phase* (RP), a measure of the temporal delay between the end-effectors, expressed in degrees. Operationally, the within-trial mean of RP reflects the accuracy of the performed pattern, while, given the inverse relationship between asymptotic stability and variability (Schöner et al. 1986; Schöner and Kelso 1988), the associated within-trial SD assesses its stability (Zanone and Kelso 1992; Smethurst and Carson 2001). Therefore, the decrease in SD of RP observed with learning (Zanone and Kelso 1992) is an experimental sign of the pattern stabilization in memory (Kostrubiec and Zanone 2002).

To identify the spontaneously accurate and stable states, Zanone and Kelso (1992) introduced an operational method coined as *scan* (see [Methods](#) below for details). Participants were required to perform a wide range of bimanual patterns between 0 and 180° of RP. An analysis of performance accuracy and variability reflected the presence of stable patterns, so-called attractors of the underlying coordination dynamics. Participants who spontaneously exhibited accurate and stable 0° RP (in-phase) and 180° RP (anti-phase) were coined as *bistable*; The (fewer) participants endowed with three accurate and stable patterns, 0, 180, and 90°, were coined as *tristable* (Zanone and Kelso 1994). Typically, the 0° RP pattern turned out to be more stable than 180 and 90° states (Kelso 1984). Such an analysis of the behavioral repertoire prior to learning ensures, on the one hand, that the to-be-learned pattern did not belong to the set of spontaneously accurate and stable patterns in the first place. Typically, bistable and tristable participants would then learn a 90 or 135° RP, respectively (Zanone and Kelso 1997; Kelso and Zanone 2002). On the other, such an analysis also provides a snapshot of the initial memory layout (Kostrubiec and Zanone 2002).

After practice, bistable participants did stabilize a new pattern close to to-be-learned 90°, thereby increasing the number of stable states shown in the scan, hence in the behavioral repertoire: this is a typical sign of learning. In contrast, tristable participants lost 90° in the favor of newly acquired 135°, leaving thus the number of the stable states unchanged (Zanone and Kelso 1997; Kelso and Zanone 2002). This suggests that the bistable–tristable distinction represents a non-trivial inter-individual difference, since it corresponds to two qualitatively distinct alterations of the initial behavioral repertoire, hence of the memory layout, with practice.

From a theoretical perspective, the creation of a new pattern or the shift of an initially stable pattern depends on the level of *competition* between the preexisting stable states and the task to be learned. Schöner (1989) suggested that when competition arises and is weak, the system can annihilate it by shifting an initially stable state toward the state to be learned. On the longer run, however, any novel perturbation occurring close to the just-learned pattern would shift it again, leading to a form of forgetting. Now, when the competition is stronger, the shift toward the pattern to be learned may

be unpractical, so that competition would remain unresolved (Zanone and Kostrubiec 2004). Therefore, in order to escape the pressure of competition, the system must *bifurcate*, creating an entirely new stable and persistent state at the to-be-learned value. The competition level is related, among other features, to the distance ( $\Delta$ ) between the initially stable patterns and the task requirement (Fontaine et al. 1997; Lee et al. 1995; Wenderoth et al. 2002; Levin et al. 2004; Kostrubiec and Zanone 2002).

The creation of a new stable pattern should be manifested by (1) a large variability of the to-be-learned pattern at the beginning of practice, reflecting the high level of competition; (2) a decrease in variability with learning, related to the new pattern stabilization; (3) the emergence of a distinct, additional stable pattern within the behavioral repertoire/memory layout; and (4) the long-term persistence of the newly created pattern across repeated recalls. The shift of an initially stable state toward the task requirement should be accompanied by opposite features: (1) a low variability at the beginning of practice, due to the weak competition; (2) no decrease in variability, because of the displacement of already stable state, (3) no change in the number of stable states, but a broad, non specific improvement in accuracy; and (4) a noticeable forgetting of the just produced coordination pattern.

To date, the first three features have been demonstrated empirically (Zanone and Kelso 1992, 1997; Lee et al. 1995; Wenderoth and Bock 2001). The present study addresses the still open issue of long-term retention. Two hypotheses will be examined: (a) learning a 90° RP pattern by bistable participants ( $\Delta = 90^\circ$ ) leads to the acquisition of an accurate, stabilized, and persisting coordination pattern on the long run; and (b) learning a 135° RP by tristable participants ( $\Delta = 45^\circ$ ) leads to an accurate but marginally stabilized, and thus less persistent pattern.

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## Method

### Participants

Seven males and nine females (18–32 years), student at the Faculty of Sport Sciences in Toulouse, volunteered for this experiment. All were naïve to the purpose of the experiment and none presented any impairment impeding the perception of the visual signal or the production of the required RP. They were not paid for their services and they signed an informed consent form, in agreement with the University guidelines and the ethical standards laid down in the declaration of Helsinki.

### Apparatus

The apparatus consisted of a pair of joysticks fixed on a table 10 cm apart restricting two-dimensional

movements to the left-right direction with maximal amplitude of  $\pm 40^\circ$ . Each joystick was connected to a linear potentiometer whose output was continuously sampled at 200 HZ and stored into a PC for further treatment. Participants were comfortably seated with their elbows on the table and grasped the joystick at the distal end.

A visual metronome, composed of two light-emitting diodes (LEDs) set 8 cm apart, was standing on a 33x24 cm<sup>2</sup> black screen placed 80 cm in front of the participants. The onsets of the right and left LEDs were controlled via a microcomputer so that various RPs were displayed at a constant frequency of 1.25 Hz. A 15" monitor provided a visual KR in the form of a plot displaying the cycle-by-cycle produced RP as a function of time, as well as its within-trial mean and SD.

### Task and procedure

The task was to produce cyclical 1:1 frequency-locked oscillations of both arms in synchrony with the pacing signal from the visual metronome. The right and left LEDs paced the right and left arm motion, respectively. Each participant was seen five times over a 24-day periods. Figure 1 exposes the experimental design, presenting how the various sessions were distributed (row 1) and when the various tasks were administered (framed in row 2), and highlighting some their features (rows 3–5).

In first day, the experiment started with a *familiarization* (F), in which participants were instructed to perform 0, 180, and 30° patterns, in accordance with the LEDs. This task ensured that participants could perform accurately and stably 0 and 180° patterns. Immediately next, the initial individual memory layout was probed by a pre-learning *scan* (S1). Participants tried to perform 13 consecutive RP plateaus from 0 to 180° increasing by 15° steps. No KR was returned during or after the scan in order to prevent any uncontrolled learning. On the basis of S1, participants were classified as bistable or tristable: participants who spontaneously produced 90° RP with both AE < 15° and SD < 25° were classified as tristable; the remaining participants were classified as bistable. As a result, ten bistable and six tristable participants were allocated to the 90 and 135° learning task, respectively.

Right after S1, 50 *practice* trials of the required pattern (90 or 135°) were administered, with KR provided after each trial. All trials lasted 20 s (viz. 25 cycles) and were grouped into 5 *blocks* (B1–B5) separated by 1-min

intervals. Next, a post-learning scan (S2) checked whether and how the patterns eventually learned altered the memory layout.

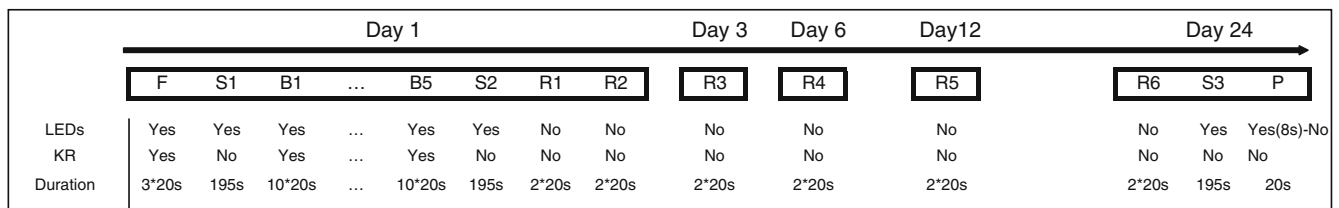
Each *recall* consisted in two consecutive 20 s trials in which the required coordination pattern was performed from memory (i.e., without the LEDs). A first recall (R1) was administered immediately after S2, in order to test the direct effect of the model withdrawal on the practiced pattern. Further recalls (R2–R6) were carried out 3 min, 3, 6, 12, and 24 days after R1, in order to test the persistence of the eventually learnt pattern.

A 24 days scan (S3) probed the persistence of the learning-induced alterations in the memory layout. It was immediately followed by a so-called *prompting* (P), which tested a potential reactivation of memory. The visual metronome displayed the to-be-learnt pattern for 8 s without actual practice. As soon as it was turned off, participants reproduced it from memory for 20 s.

### Data reduction and analysis

The RP between the moving limbs was assessed by means of a cycle-by-cycle point-estimate method (Zanone and Kelso 1992), which represents the ratio of the time difference between peak pronation of the right hand and the period of the cycle of the left hand that contained it. For each trial, three variables were studied: mean RP, absolute error (AE) between the mean produced and required RP, and the associated SD. RP characterizes the produced pattern, AE assesses its accuracy and SD its variability, hence stability. AE and SD were considered for analyzing practice and scan, while RP and SD were relevant for recalls and prompting tasks, in order to capture the direction of the shift of the memorized pattern.

For each participant, mean RP, AE, and SD were averaged over the five blocks of practice. The effect of practice was evaluated by an analysis of variance (ANOVA) with repeated measures on Block (5) for the AE and SD of each pattern to be learnt. The effect of withdrawing the model between the last practice block (B5) and the first recall (R1) was assessed by an ANOVA with repeated measures on LED (2) carried out on RP and SD. The six recalls were analyzed with an ANOVA with repeated measure on recall (6) on RP and SD. The effect of the prompting comparing the last practice block (B5) to Prompting (P) was investigated through an ANOVA with repeated measures on prompting (2).



**Fig. 1** Experimental design. *F* Familiarization; *S* Scan; *B* Block of practice; *R* Recall; *P* Prompting (details in the text)

With regard to the scans, in order to overcome a well-known hysteresis effect, that is, a tendency of the system to stay in the most stable state  $0^\circ$  without switching to the less stable  $180^\circ$  irrespective to the task requirements (Tuller et al. 1994; Zanone and Kelso 1997), only patterns most susceptible to change with learning were scrutinized.

For bistable participants, two repeated measures ANOVAs Scan (2)  $\times$  Pattern (4) were carried out on AE and SD of 0, 75, 90 and  $105^\circ$  patterns. The first analysis compared the pre- and the post-learning scans, the second, the pre-learning and the 24-day scans. For tristable participants, the same repeated measures ANOVAs Scan (2)  $\times$  Pattern (5) were carried out on AE and SD of 0, 90, 105, 120 and  $135^\circ$  patterns. Bonferonni-Dunn contrasts have been conducted if necessary. For all analyses, the threshold of significance was fixed at  $P < 0.05$ .

## Results

### Learning

The evolution of performance with practice is illustrated in Fig. 2. For bistable participants (Panel A of Fig. 2), mean AE and SD underwent a monotonic decrease as a function of practice, an evolution quite similar to a classical learning curve. From B1 to B5, mean AE decreased on average by 50% (from 24 to  $13^\circ$ ) and mean SD by 25% (from 24 to  $18^\circ$ ). Statistical analyses revealed a significant main effect of Block on AE [ $F(4,36) = 4.841$ ;  $P < 0.0005$ ] and SD [ $F(4,36) = 4.707$ ;  $P < 0.005$ ].

For tristable participants (Panel B of Fig. 2), AE revealed a substantial decrease by 70%, while SD exhibited only a 15% reduction. Statistical analyses revealed a significant Block effect for AE [ $F(4,20) = 9.552$ ;  $P < 0.001$ ], but not for SD [ $F(4,20) = 2.217$ ; *ns*]. Note that a comparison of accuracy and variability of both practiced patterns ( $90^\circ$  for bistable and  $135^\circ$  for tristable participants) at the end of learning revealed no significant

difference [ $F(1,14) = 0.809$ ; *ns*, and  $F(1,14) = 0.184$ ; *ns*, for AE and SD, respectively].

### Recall and reactivation

A main interest of our study was whether changes in performance eventually induced by learning persisted over time (Fig. 3). Panel A of Fig. 3 indicates that for bistable participants practicing  $90^\circ$ , mean RP remained quite similar to the required RP ( $90^\circ$ ) all over the retention period. Likewise, the mean SD exhibited no apparent change between the first and the last recall, except for the day 3, where an increase of SD ( $23^\circ$ ) was observed. This effect was due to a sudden increase in SD for one participant only. Analyses revealed no significant effect of LED either on mean RP or on SD [ $F(1,9) = 0.286$ ; *ns*, and  $F(1,9) = 0.087$ ; *ns*, respectively], and no significant effect of Recall on both mean RP and SD [ $F(5,45) = 1.115$ ; *ns* and  $F(5,45) = 1.486$ ; *ns*, respectively].

Another picture emerges for the  $135^\circ$  recall in tristable participants. Panel B of Fig. 3 suggests a decrease in mean RP ( $131$  vs.  $113^\circ$ , respectively) associated to a decrease in mean SD (from 17 to  $13^\circ$ ) from B5 to R1. For R1 to R6, mean RP eventually diminished between R1 and R6, from 113 to  $102^\circ$ , while mean SD increased from 13 to  $18^\circ$ . Statistical analyses revealed a significant effect of LED on mean RP [ $F(1,5) = 8.506$ ,  $P < 0.05$ ] but not on mean SD [ $F(1,5) = 1.558$ ; *ns*]. Notwithstanding, there was no significant effect of Recall on mean RP [ $F(5,25) = 0.805$ ; *ns*], but a significant effect on SD [ $F(5,25) = 2.818$ ;  $P < 0.05$ ]. Inspection of individual data showed that, on the sixth day, two participants shifted toward the preexisting stable  $180^\circ$  pattern (RP =  $161^\circ$  and SD =  $21^\circ$ ), whereas the remaining four participants shifted toward the other stable  $90^\circ$  pattern (RP =  $106^\circ$  and SD =  $21^\circ$ ) with an increase of SD. After the sixth day, individual performance scattered, as reflected by the high inter-individual SD.

With regard to the prompting task, analyses revealed no significant Prompting effect for either bistable

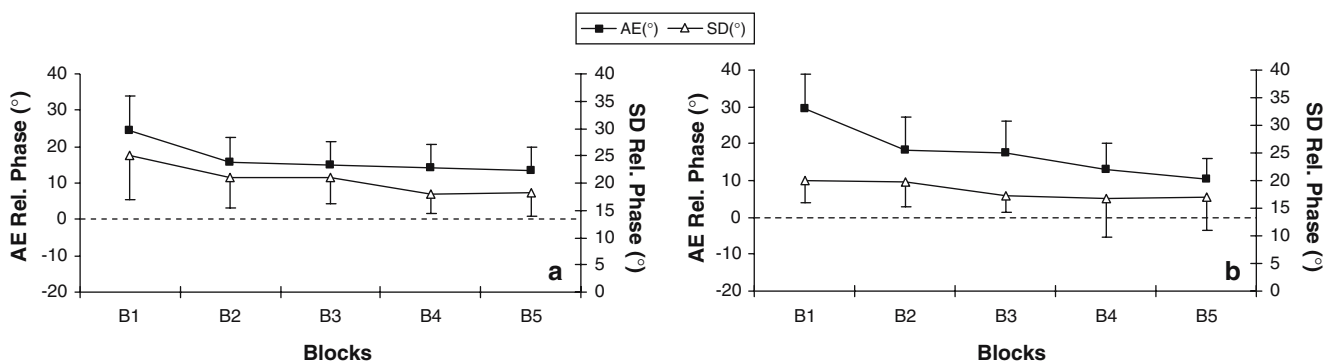
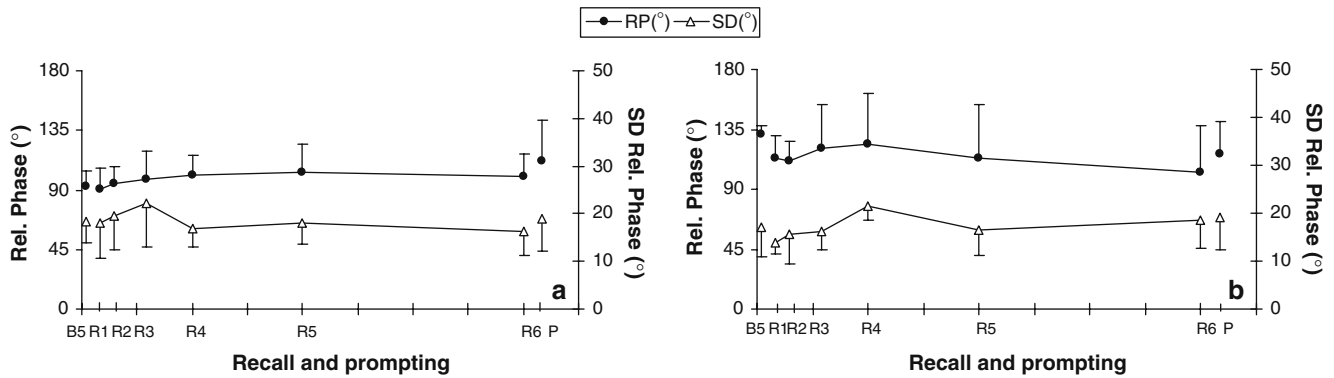


Fig. 2 Mean AE (upper curve) and associated SD of RP (lower curve) during five blocks of practice of  $90^\circ$  by bistable participants and of  $135^\circ$  by tristable participants (a and b, respectively). Vertical bars encompass  $\pm 1$  between-participant SD



**Fig. 3** Mean RP (*upper curve*) and associated SD of RP (*lower curve*) for the last practice block (*B5*), the six recalls (*R1–R6*) and the prompting (*P*) of 90° by bistable participants and 135° by

tristable participants (**a** and **b**, respectively). *Vertical bars* encompass  $\pm 1$  between-participants SD

[ $F(1,9) < 2.963$ ; *ns*] or tristable, [ $F(1,5) < 3.664$ ; *ns*] participants.

## Scans

In order to assess the long-term evolution of the memory layout deemed to be altered by learning a new pattern, we compared the pre-learning (*S1*), the post-learning (*S2*), and the 24-day scans (*S3*), which are presented in the left, middle, and right parts of Fig. 4, respectively.

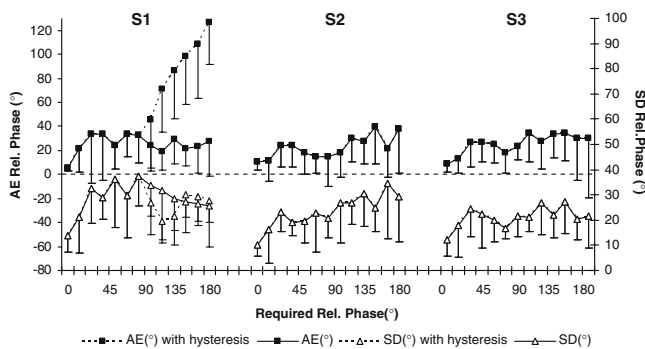
For bistable participants, *S1* (left part) exhibited the lowest mean AE (4°) and SD (16°) for the 0° pattern. Note that in *S1*, the procedure did not make the 180° pattern appear in three participants: these participants remained in the most stable 0° pattern during the entire scan, although they could produce accurately and stably 180° in the familiarization. In all bistable participants, individual mean AE and SD for the required 90° and its adjacent 75 and 105° patterns did not reach our criterion for stability (e.g., 33° of EA and 37° of SD, for 90°), suggesting that 90° was a truly unstable pattern initially.

After practice, results of *S2* (middle part of Fig. 4) showed that mean AE and SD of the 90° pattern (14 and 14°, respectively) and its adjacent 75 and 105° patterns came close to the mean AE and SD of the baseline 0° pattern (10 and 10°, respectively). In *S3* (right part of Fig. 4) performed 24 days after the practice, mean AE and SD of these patterns remained low.

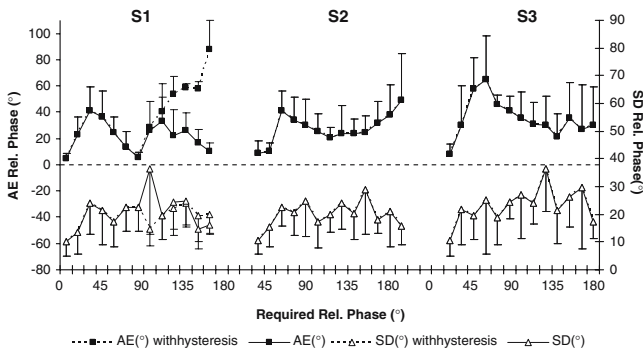
Statistical analyses revealed significant a Pattern effect for all scans ( $P < 0.05$ ). Comparison of *S1* and *S2* showed a significant effect of Scan on AE [ $F(1,9) = 6.386$ ,  $P < 0.04$ ] and on SD [ $F(1,9) = 6.945$ ,  $P < 0.03$ ], indicating that accuracy and stability for 0, 75, 90, and 105° increased with practice. Comparison of *S1* and *S3* revealed a significant Scan  $\times$  Pattern interaction on AE [ $F(3,27) = 4.138$ ,  $P < 0.02$ ] and a significant Scan effect on SD [ $F(1,9) = 19.177$ ,  $P < 0.002$ ], suggesting that the stabilization of the 0, 75, 90 and 105° patterns persisted for 24 days after practice.

Figure 5 presents the three scans, *S1*, *S2* and *S3*, for tristable participants. *S1* (left part of Fig. 5) showed lowest mean AE (4°) and SD (10°) for the 0° pattern, while the 90° pattern also exhibited a fairly low AE (5°) and SD (22°). Inspection of individual data revealed that before practice (*S1*) 180° did not appear as stable a pattern for two participants, as these subjects stayed in the more stable 90° pattern and never switched to 180°. After practice of 135° (*S2*) all patterns between 75 and 135° exhibited a low AE. Finally, after the recalls (*S3*) revealed that mean AE and SD remained low for 120 and 135°, but increased for 90 and 105° (from 20 to 35° and from 19 to 27°, respectively). The SD curve, notwithstanding, did not change from the pre-learning to the 24-day scan.

The effect of Pattern was significant in all analyses of the scans ( $P < 0.05$ ). Comparison of *S1* and *S2* revealed a significant Scan  $\times$  Pattern interaction on AE [ $F(4,20) = 3.118$ ;  $P < 0.04$ ], but not on SD [ $F(4,20) = 0.64$ ; *n*], as did a comparison of *S1* and *S3* [ $F(4,20) = 3.009$ ;  $P < 0.05$ , and  $F(4,20) = 1.987$ ; *ns*, respectively]. Posthoc contrasts showed that for *S1*, 120 and 135° were significantly less accurate than 0° (Diff = -31.048 and -27.927, respectively) and than 90° (Diff = -30.366 and -27.245,



**Fig. 4** Mean AE (*upper curve*) and associated SD of RP (*lower curve*), as a function of the 13 required RPs, stepped by 15°, during the scans administered before (*S1*), after practice (*S2*), and 24 days (*S3*) after practice of 90° by bistable participants. *Dashed curves* represent mean AE and associated SD of RP of three participants displaying hysteresis (see text for details). *Vertical bars* encompass  $\pm 1$  between-participants SD



**Fig. 5** Mean AE (*upper curve*) and associated SD of RP (*lower curve*), as a function of the 13 required RP, stepped by 15°, during the scans administered before (*S1*), after practice (*S2*), and 24 days (*S3*) after practice of 135° by tristable participants. *Dashed curves* represent mean AE and associated SD of RP of two participants displaying hysteresis (see text for details). *Vertical bars* encompass  $\pm 1$  between-participants SD

respectively). For *S2*, no difference was significant, whereas for *S3*, 90° was significantly less accurate than 0° (Diff = -27.221).

## Discussion

The present study addresses the deep issue of the relationship between learning and memory through a fresh angle assuming that these are two facets of the same process that could be unified through the concept of asymptotic stability. Our tenet was that “true” learning involves stabilization of the behavioral pattern and thereby persistence in memory. In contrast, a transient adaptation to the task requirement, without stabilization, would result in forgetting. Strictly speaking, what matters is not which stability level is eventually attained with learning, but how it is reached, that is, which route the evolution of stability takes. To test this prediction, we scrutinized how persistent learning was for two coordination patterns, 90 and 135° of RP, following from the differential levels of competition arising for bistable versus tristable pre-learning behavioral/memory layouts.

In accordance with our hypothesis, the 90° pattern that was actually stabilized by practice persisted in memory without change in accuracy or variability over 3 weeks of retention. In contrast, the 135° pattern exhibited a low variability level at the beginning of practice, so that there was no room left for further decrease with practice. Thus, the 135° pattern only improved in accuracy with practice and underwent distortion and forgetting during the retention interval. Again, as the level of variability attained at the end of learning was comparable for the two learning tasks, the critical predictor for learning to follow a route to successful retention or to forgetting is whether there is an increase in stability and not in accuracy. Converging evidence for the dissociation of accuracy and stability

may be found in a study by Giraud and Pailhous (1999) on the temporal dependencies between successive reproductions of spatial configurations of dots. These authors showed that an independent evolution of these two processes led to memory distortion. In line with dynamical theory of learning (Zanone and Kelso 1992; Zanone and Kostrubiec 2004) stability is a critical property of behavior. Accuracy may well reflect the goal achievement during practice, but only stability provides a full rendition of the constraints imposed to behavior at the end of practice, in particular, the possible evolution of accuracy during recall: accuracy cannot evolve outside the boundaries allowed by pattern variability.

The interplay between the creation/stabilization of a new pattern and a transient shift of an existing one enables the memory system to cope with incoming perturbations. On the one hand, the shift-based process ensures the system’s fast adaptation. On the other hand, by breaking down the memory layout, the stabilization of a new pattern limits the scope of such adaptation: it forbids the process to operate outside the limits defined by pattern variability and thereby restricts the impact of forgetting. In this light, some features of the performance portrayed by Parkinson patients (Verschueren et al. 1997) might pertain to a specific deficiency in the creation/stabilization of a new coordination pattern, while the shift-based adaptation is preserved. Parkinsonians may be successful in adopting a different bimanual pattern, reflected by an improvement in accuracy (shift), but not in learning a new stable pattern (creation). Therefore, when perceptual information is withdrawn, performance drops, resulting in a fast forgetting. Then, few subjects migrated toward 180°, whereas the majority stayed at 90°. Since both 90° and 180°, which were stable prior to practice, are equidistant from 135° required pattern, they developed an equivalent attractive force when the 135° memory waned. However, this memory did not completely break down. The increase in variability observed on the sixth day could be ascribed to a process of reminiscence, which actually failed in recovering the required pattern. Further support to this idea is brought by the prompting and the last scan, which led to a fast reactivation of 135° due to the exposure of the visual model. This highlights a key feature of the shift-based learning process, namely, its flexibility and its swift adaptation to environmental or task constraints. It is then likely that if tristable participants were allowed to practice the 135° and 90° patterns concurrently, they would be temporarily able to produce both of them, through the alternate shift of the attractor from a RP value to another. Nevertheless, as performance would not be grounded on two distinct states in the memory layout, the less stable pattern, probably 135°, would be forgotten after the practice.

The prompting task also indicates that recall by reactivation of the forgotten pattern can be successful after the interval retention, since the stable 135° pattern was retrieved 24 days after practice, both in the prompting and scans, and not in the previous recalls.

Note that all the patterns between 90° and 135° became accurate in the post-learning scan, whereas only 105°, 120°, and 135° stayed accurate after 24 days and 90° was lost altogether. These results suggest that the memory layout is reorganized during the entire retention interval in favor of 135° and in detriment of 90°. This reorganization is reminiscent of a consolidation phenomenon (see Paller 1997, for a review). Consolidation confers coherence to the dispersed neocortical memory traces, in the absence of further practice. Thus, memory traces become more compact and resistant to interference, probably due to the interplay between hippocampal and several neocortical zones (Squire and Zola 1997). This consolidation effect proved to be particularly strong in motor memory (Brashers-Krug et al. 1996; Shadmehr and Brashers-Krug 1997).

The level of coherence may be tentatively captured by within-trial variability. Such variability proves to pertain to the extent of the associated brain activation. Bimanual coordination engages a wide network distributed cortically and sub-cortically (Debaere et al. 2001). Coordination is deemed to come about by dynamically assembled and disassembled linkages, in response to different task demands that benefit from the tendencies of neuronal populations toward apartness and togetherness (Cardoso de Oliveira 2002). Less stable patterns result in broader network activation (Jantzen et al. 2002). Regarding learning the short-term practice of a less stable pattern leads accordingly to a decrease in the number of active regions (Jantzen et al. 2001, 2002). In the view of the present study, a next step is to investigate whether the newly learned 90° pattern engages a narrower neuronal population than 135° and whether the 135° neural assembly evolves over the retention interval.

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