Exp Brain Res (2007) 178:499–508
DOI 10.1007/s00221-006-0757-3

RESEARCH ARTICLE

When practice does not make perfect: well-practiced handwriting interferes with the consolidation phase gains in learning a movement sequence

Meirav Balas · Neta Roitenberg · Nir Giladi · Avi Karni

Received: 31 July 2006 / Accepted: 8 October 2006 / Published online: 8 November 2006

Abstract Practice on a novel sequence of movements can lead to two expressions of procedural memory consolidation: delayed performance gains evolving hours after training, and a decrease in the susceptibility of the training-related gains to interference by subsequent experience. It has been assumed that behavioral interference occurs only if a critical overlap between the representations of the two tasks exists, and that such overlap is more likely when the two tasks are novel, competing for general resources for their execution. We investigated whether the delayed gains in the simple finger-opposition sequence (FOS) learning task are more prone to interference by well practiced than by less practiced complex hand movements. Participants were trained on the FOS task in a baseline (no interference) and an interference training condition. In the Interference condition, after FOS practice, participants wrote Hebrew common words in Hebrew (native script) or a Latin script (Heblatin). Native script writing but not the less practiced Heblatin, interfered with FOS learning, with significantly reduced delayed gains. Our results show that interference can occur even when two tasks share little or no kinematic or dynamic features and indicate that the representation of complex but well-practiced movement sequences may overlap with the representation of simpler ones. This result is in line with the notion that well-practiced complex movement sequences come to be represented as simpler ones in long-term motor memory.

Keywords Motor learning · Motor memory · Interference · Motor representation · Memory consolidation · Handwriting

M. Balas · A. Karni
The Brain Behavior Research Center,
University of Haifa, Haifa, Israel

M. Balas (✉) · N. Roitenberg · N. Giladi
Movement Disorders Unit, Department of Neurology,
Tel-Aviv Sourasky Medical Center, 6 Weiznamm St,
Tel-Aviv, 64239, Israel
e-mail: mbalas@study.haifa.ac.il

N. Giladi
Sackler School of Medicine, Tel-Aviv University,
Tel-Aviv, Israel

Introduction

Several studies have recently shown that in addition to the gains in performance that emerge concurrently with practice on a novel sequence of movements (within session gains), robust gains in the speed and accuracy of performance can evolve after the practice experience has ended, i.e., between sessions, delayed gains (e.g., Fischer et al. 2002; Karni et al. 1998a, b; Walker et al. 2002). These delayed gains in performance presumably reflect procedural memory consolidation processes (Karni et al. 1998a, b; Ungerleider et al. 2002; Walker et al. 2002, 2003; Korman et al. 2003; Maquet et al. 2003). There is, however, another measure for memory consolidation, established in both human (e.g., Brashers-Krug et al. 1996; Krakauer et al. 2005) and animal (McGaugh 2000) models of memory formation. The latter measure relates to the notion that during the post-acquisition phase, newly acquired experience-dependent neural changes are transformed from tenuous, interference susceptible, into more stable forms (McGaugh 2000). Hence, within the first few hours after the termination of a training experience, subsequent experience may result in the loss of the expected training related gains in the initial task (Brashers-Krug et al. 1996; Shadmehr and Brashers-Krug 1997; Walker et al. 2003; but see Goedert and Willingham 2002).

It is not clear however, what types of experience constitute effective interference for a given task. Effective interference is often caused by a variation on the initial task (Adams 1987; Miall et al. 2004; Krakauer et al. 2005) suggesting that tasks that depend on similar performance parameters and neural resources would be more likely to interfere with each other. Thus, interference occurs if there is a critical overlap between the representations of the two tasks experienced during the consolidation time-window (Tong et al. 2002). Such an overlap may result in the weakening or even the taking over of ongoing neuronal consolidation processes, triggered by the initial training experience, by the subsequent experience (Fonseca et al. 2004).

Previous studies have suggested that the level of experience with the to-be-interfered (initial) task may constitute a critical factor in determining the amount of interference between two tasks, with novice performers more susceptible to interference than expert ones (Shea and Morgan 1979; Del Rey et al. 1982; Shea et al. 1990; Guadagnoli and Lee 2004). Others have argued that major shifts occur between brain representations of motor performance, as a function of experience (e.g., Shadmehr and Holcomb 1997; Korman et al. 2003; Sosnik et al. 2004; Ungerleider et al. 2002; Jueptner et al. 1997). We tested the notion that different motor representations subserve the performance of well and less well-trained handwriting sequences, and therefore determine its interference potential with a given non-writing task. Our results suggest that rather than the task per-se, the level of experience with, and the type of motor sequences performed in the subsequent task, constitute a critical factor in determining its interference potential, even when the resemblance of the movements of the interfering task to the movements of the initial task is minimal.

Materials and methods

Experiment 1

Participants

Forty-three young university students (mean 25.13, SD 3.21), 14 men and 29 women, were paid to train on the FOG learning task. All were right handed, native Hebrew speakers, highly familiar with the Latin alphabet through mainly English script. Participants had no medical conditions that could impair fine motor performance and had no known learning disability. The study was approved by the ethics committee of the Tel-Aviv Souraski Medical Center.

Design and procedure

Each participant took part in two study phases, 1 week apart (Fig. 1b). Each study phase consisted of a training session and a test session a day later. In all sessions, the participants performed the tasks while lying supine with their arm supported on their hip and the palm facing up, in direct view of a video camera. In the training session, participants were instructed to oppose the fingers of their dominant hand to the thumb in one of three possible sequences (43124, 42314, 41324) (Fig. 1a). Visual feedback was not afforded. In the initial session, each participant underwent a pre-training performance test (*test* 1), a training interval and an immediate post-training performance test (*test* 2). The next day, a delayed performance test (*test* 3) was administered. Each training interval consisted of 160 repetitions of the sequence divided into 20 training blocks. During training, following preparatory and "start" auditory signals for each block, the initiation of each sequence was cued by an auditory signal at a rate of 0.4 Hz (2.5 s per sequence). Each training block terminated in a "stop" signal. The three performance tests were composed of four, 30 s blocks, each initiated by an auditory "start" signal, during which participants were instructed to tap the sequence repeatedly and continuously as fast and accurately as possible, until given a stop signal. The intervals between test blocks were kept constant (30 s). No feedback was provided. The participants' performance during the test blocks was video recorded and two measures of performance were determined from the recordings: a. speed-number of correctly completed sequences in a block and b. Accuracy-number of errors made in a block (incorrect sequences). One experimenter scored the video recordings by playback at reduced speed.

Twenty-two participants first completed the baseline condition and then the interference condition and 21 were run in the reversed order. Both conditions were identical except that in the latter condition, participants were required to perform a handwriting (interference) task immediately after *test2* (Fig. 1b). The two conditions were run on separate sessions, 1 week apart. The order of the conditions (phases) was pseudo-randomized across participants.

In the interference task, participants wrote two, randomly ordered, auditory dictated Hebrew words, using either the Hebrew alphabet or the Latin (Heblatin). [The two words were "closet" and "pillar" ("ארון" and

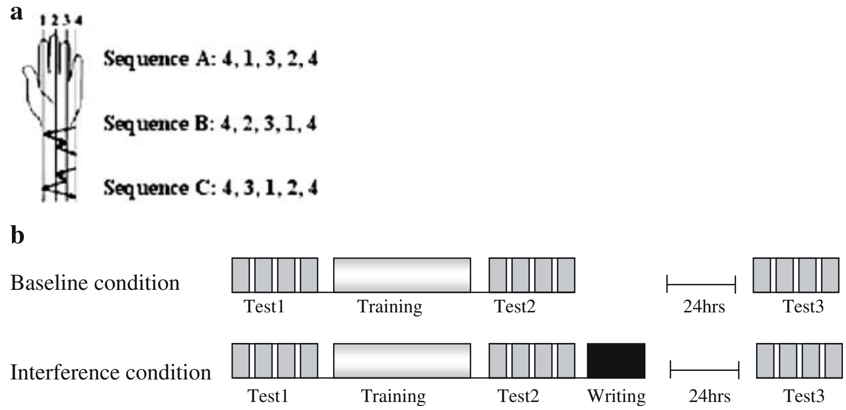

Fig. 1 **a** The finger-to-thumb opposition task. The three sequences were similarly constructed and contain identical component movements. **b** The design of the baseline and the interference conditions, in Experiment 1 and Experiment 2. Note that the conditions are identical except for the writing (interference) phase added in the latter condition

"עמוד"—"aron" and "amud", in Hebrew and Latin alphabets, respectively)]. Participants were randomised into two groups; one group of 21 subjects was instructed to write in Hebrew (familiar writing condition), and the other group, with 22 subjects, in Heblatin (unfamiliar writing condition). Writing was done with a non-inking pen on A4 paper laid upon a digitizing tablet (WACOM, Intuos 2, 17.5″ × 17.1″ × 1.5″, active area 12″ × 12″, sampling rate of 100 Hz, spatial accuracy ± 0.025 cm, spatial resolution 0.05 cm) mounted perpendicular to the bed in a custom holding device. A double mirror system was used to enable participants get a clear view of their hand movements only during writing. The workspace for the handwriting task was composed of four horizontally parallel lines (each 8 cm long, and spaced 1.3 cm apart) on the lower right side of the paper (since writing in Hebrew progresses from right to left). Each participant chose (based on comfort) one line that was then used throughout the session. Participants were instructed to rest the pen tip on a cross, placed to the right of each line, and return to this point after writing each word. Overall, the task consisted of 16 repetitions of each of the two target words in a random order (total of 32 words) divided into 8 blocks of writing (4 words in each block) separated by 30 s of rest. Each trial (word) was cued by an auditory signal with 3.5 s afforded for its completion. The words were presented amplified through loudspeakers.

Experiment 2

To further explore the loss of performance gains after Hebrew interference (including the negative delayed gains), at 24 h post-training relative to the performance at the end of the practice session, 12 additional participants (2 men, 10 women; mean age 25.37, SD 1.4) were trained in the FOS and wrote in Hebrew immediately after *test* 2 (that followed the termination of the training session). The design and procedures of Experiment 2 were identical to those used in the Hebrew condition of Experiment 1. Each participant completed two study phases, baseline and Hebrew interference 1 week apart. Half the participants first completed the baseline condition and then the Hebrew interference condition and the rest were run in the reversed order. This design allowed for a full, within-subjects repeated measures comparison.

Results

Experiment 1

Table 1 presents the average number of correctly completed sequences and the average number of errors summed across the *test* blocks at the beginning of training, by the end of training and at 24 h post-training, in each of the two conditions for each group. All analyses were designed as within-subject comparisons because of the small groups and the individual differences in the speed and accuracy of performance. Only the effect of the order of conditions was tested in a between-subject comparison, as each participant was tested in one of two possible orders of conditions. Two separate repeated measures analyses were run for each group, with either the number of sequences performed correctly during the block (speed) or the number of errors per block (accuracy) i.e., number of sequences performed incorrectly, as the dependent variables. Here, and elsewhere, results were corrected for non-sphericity violation using Greenhouse-Geisser adjustment.

To test for order effects (i.e., whether initial performance and the gains accrued in training within the session differed when baseline condition or the interference condition were tested first) across both groups, a repeated measures general linear model was applied in which condition (with two levels baseline or

Table 1 Performance of the FOS task before training (*test1*), after the training session (*test2*) and on the following day (*test3*) in the two groups (mean and standard deviations). P values refer to comparisons (dependent t-tests) between the relative gains in the baseline and corresponding interference conditions, i.e., for Δ1–2 and Δ2–3

	Test1	Test2	Δ1–2	*P* value	Test3	Δ2–3	*P* value
Experiment 1							
Speed (no. of sequences)							
Hebrew group							
Baseline condition	54.1 ± 14.5	65.1 ± 14.5	11.0 ± 6.2	0.320	72.8 ± 14.7	7.7 ± 4.6	0.045*
Interference condition	55.1 ± 14.4	67.9 ± 14.7	12.9 ± 7.4		72.3 ± 15.1	4.4 ± 5.6	
Heblatin group							
Baseline condition	53.7 ± 12.1	63.6 ± 10.3	9.9 ± 6.0	0.157	71.5 ± 11.8	8.0 ± 5.1	0.976
Interference condition	50.0 ± 13.1	63.0 ± 13.4	13.0 ± 6.5		71.0 ± 12.8	8.0 ± 6.0	
Accuracy (no. of errors)							
Hebrew group							
Baseline condition	3.3 ± 2.2	1.9 ± 1.5	1.4 ± 2.5	0.378	1.2 ± 1.4	0.70 ± 1.6	0.174
Interference condition	2.3 ± 1.9	1.3 ± 1.2	.95 ± 2.1		1.2 ± 1.4	0.01 ± 1.8	
Heblatin group							
Baseline condition	3.8 ± 4.0	.62 ± .56	1.3 ± 3.0	0.341	1.4 ± 1.4	1.1 ± 2.1	0.407
Interference condition	3.2 ± 2.6	2.8 ± 2.5	0.45 ± 3.1		1.1 ± 0.89	1.7 ± 2.1	
Experiment 2							
Speed (no. of sequences)							
Baseline condition	57.9 ± 26.9	69.3 ± 26.3	11.4 ± 7.9	0.918	80.2 ± 25.0	10.8 ± 6.5	0.012*
Interference condition	62.2 ± 23.2	73.2 ± 24.4	11.0 ± 7.2		75.8 ± 21.9	2.6 ± 7.1	
Accuracy (no. of errors)							
Baseline condition	3.3 ± 2.4	2.8 ± 2.5	0.50 ± 2.7	0.949	0.41 ± .66	2.3 ± 2.7	0.203
Interference condition	2.6 ± 1.9	2.0 ± 2.0	0.58 ± 2.2		1.3 ± 1.1	0.75 ± 2.2	

interference), *test* (with two levels *test* 1, *test* 2, corresponding to initial performance and the performance at the termination of the training session, respectively) and *block* (with four levels 1st, 2nd, 3rd, and 4th block) were within-subjects variables and *order* (with two levels baseline first or interference first) was a between-subjects variable. No significant order effects were found for either speed [$F(1,41) = 2.7$, $P = 0.106$] or accuracy [$F(1,41) = 0.12$, $P = 0.730$].

Training on a given sequence of movements resulted in robust within-session (early) gains in both speed and accuracy, in the two groups (Table 1). This held true, irrespective of whether interference experience was given after the termination of the training session. A repeated measures general linear model was applied for each group separately, in which *condition* (with two levels baseline or interference), *test* (with two levels *test* 1, *test* 2, corresponding to initial performance and the performance at the termination of the training session, respectively) and *block* (with four levels 1st, 2nd, 3rd, and 4th block) were within-subjects variables. There was no significant difference between the two conditions in each of the two groups in terms of within session gains. For speed, the main effect for *test* were significant [Hebrew group, $F(1,20) = 103.6$, $P < 0.001$; Heblatin group, $F(1,21) = 194.3$, $P < 0.001$], with superior performance in *test2* compared to *test1*. For accuracy, the main effect of *test* was significant in the Hebrew group [$F(1,20) = 7.8$, $P = 0.011$], but showed only a trend for improvement in the Heblatin group [$F(1,21) = 3.0$, $P = 0.096$], although overall participants made only a small number of errors in either test periods (Table 1). Finally, the interaction of *condition* and *test* was not significant, in both groups, for speed [Hebrew group, $F(1,20) = 1.0$, $P = 0.320$; Heblatin group, $F(1,21) = 2.2$, $P = 0.157$] and accuracy [Hebrew group, $F(1,20) = 0.81$, $P = 0.378$; Heblatin group, $F(1,21) = 0.95$, $P = 0.341$].

Training also resulted in significant gains in both speed and accuracy, when performance at 24 h post-training was compared to performance at the end of the training session; i.e., significant gains have evolved after the termination of training, during this interval, in both groups (delayed, between-sessions, gains). However, the delayed gains were significantly reduced when an interference experience of, specifically, writing in Hebrew was given. A repeated measures general linear model was applied for each group separately, in which *condition* (with two levels baseline or interference), *test* (with two levels *test* 2 and *test* 3, corresponding to the performance at the termination of the training session and on the following day, respectively), and *block* (with four levels 1st, 2nd, 3rd, and 4th block) were within-subjects variables. Two separate analyses were run, with either speed or accuracy as the dependent variables. For performance speed, there was a significant main effect for *test* in both groups [Hebrew group, $F(1,20) = 54.5$,

$P < 0.001$; Heblatin group, $F(1,21) = 75.7$, $P < 0.001$], with superior performance in *test3* compared to *test2*. However, the interaction of *condition* and *test* was significant in the Hebrew group [$F(1,20) = 4.5$, $P = 0.045$], with smaller delayed performance gains when interference was given. This interaction was not significant in the Heblatin group [$F(1,21) = 0.00$, $P = 0.976$]. Furthermore, the main effect for accuracy, i.e., a decrease in the number of errors at *test3*, was significant in the Heblatin group [$F(1,21) = 24.8$, $P < 0.001$] but not in the Hebrew group [$F(1,20) = 1.9$, $P = 0.187$]. The interaction of *condition* and *test* was not significant for accuracy presumably because accuracy was almost at ceiling, in both groups [Hebrew group, $F(1, 20) = 1.9$, $P = 0.174$; Heblatin group, $F(1,21) = 0.71$, $P = 0.407$]. No significant between-subjects effect of order was found for either speed [$F(1,41) = 2.0$, $P = 0.163$] or accuracy [$F(1,41) = 0.09$, $P = 0.762$].

Since testing constituted by necessity additional training in the task, the block-by-block improvement in speed was examined in the three tests. As previously described (Korman et al. 2003), there was a significant improvement in speed only in *test1* (Hebrew group $F(1,20) = 4.4$, $P = 0.048$, $F(1,20) = 15.7$, $P < 0.001$, baseline and interference condition, respectively; Heblatin group $F(1,21) = 7.7$, $P = 0.011$, $F(1,21) = 30.7$, $P < 0.001$), baseline and interference condition, respectively). There was no significant trend for improvement between blocks in *test2* and *test3*, in both groups, in both conditions. The significant delayed gains in performance cannot, therefore, be ascribed to practice effect that stem from the testing.

To further test the difference between the delayed gains accrued in the interference condition compared to the gains accrued in the baseline condition, the absolute gains in performance (i.e., the difference between tests 2 and 3 (Δ2–3) was computed in each condition (baseline or interference). For accuracy, the number of errors made in a given *test* was subtracted from the number of errors made in the preceding *test* (i.e., a reduction in errors = a positive Δ). Paired-samples *t* tests were used to compare the Δs achieved in the baseline and the corresponding interference conditions separately for the two groups (Hebrew or Heblatin) (Table 1). As can be seen in Table 1, the relative delayed gains (Δ2–3) were reduced in the Hebrew interference condition (on average only 4.4 sequences compared to 7.7, 8 and 8 sequences in the baseline and the Heblatin interference condition and corresponding baseline, respectively). The differential effect of writing Hebrew or Heblatin on the learning of the movement sequence can be seen in Fig. 2, which presents the average delayed gains for speed and accuracy, in both groups (Hebrew or Heblatin). While writing in Heblatin after the termination of the training session resulted in as robust gains as in the corresponding baseline condition, writing in Hebrew resulted in clearly reduced gains in speed, compared to the corresponding baseline condition gains. The absolute gains accrued during the training session (within-session, between tests 1 and 2, Δ1–2) showed that the gains for both speed and accuracy were not significantly different in the interference conditions, as compared to their corresponding baseline conditions in both groups (Table 1).

In the interference condition, six participants of the Hebrew group failed to show any improvement in speed (and even demonstrated some loss of performance relative to the end of the practice session; i.e., negative delayed gains) at *test3* as compared to *test2*, while only one to two participants failed to improve in the Heblatin interference condition and in the two baseline conditions (Fig. 3a). There was no significant difference between each interference condition and its corresponding baseline in terms of accuracy (Table 1 and Fig. 3b).

The absolute gains within the training session and between-sessions (Δ1–2 and Δ2–3, respectively) were not correlated with either the *order* of conditions (baseline condition completed before interference condition or vise versa) or the specific *sequence* of opposition movements used in training (43124, 42314, or 41324) (for performance speed $r = 0.03$, $P = 0.789$, and $r = 0.11$, $P = 0.309$, between *order* and Δ1–2 or Δ2–3, respectively; $r = -0.19$, $P = 0.071$, and $r = 0.02$, $P = 0.894$, *sequence* and Δ1–2 or Δ2–3, respectively). In addition, no significant correlations were found between *order* and Δ1–2 or Δ2–3 ($r = 0.17$, $P = 0.108$, and $r = -0.08$, $P = 0.445$, respectively) and between *sequence* and Δ1–2 or Δ2–3 ($r = 0.01$, $P = 0.929$, and $r = 0.00$, $P = 0.977$, respectively) for accuracy.

There were no significant correlations between the performance gain of individual participants in *test2* and their performance gains in *test3* in any of the three conditions; baseline ($r = 0.06$, $P = 0.709$), Hebrew interference ($r = -0.32$, $P = 0.147$), or Heblatin interference ($r = -0.18$, $P = 0.434$). Thus, the within-session gains were not correlated with the delayed, between-session gains in performance.

Experiment 2

In Experiment 2, we replicated the Hebrew condition of Experiment 1. Experiment 2 was run to substantiate the finding that handwriting in the participants' native script could significantly reduce the expected delayed gains in the FOS task and moreover, result in an actual

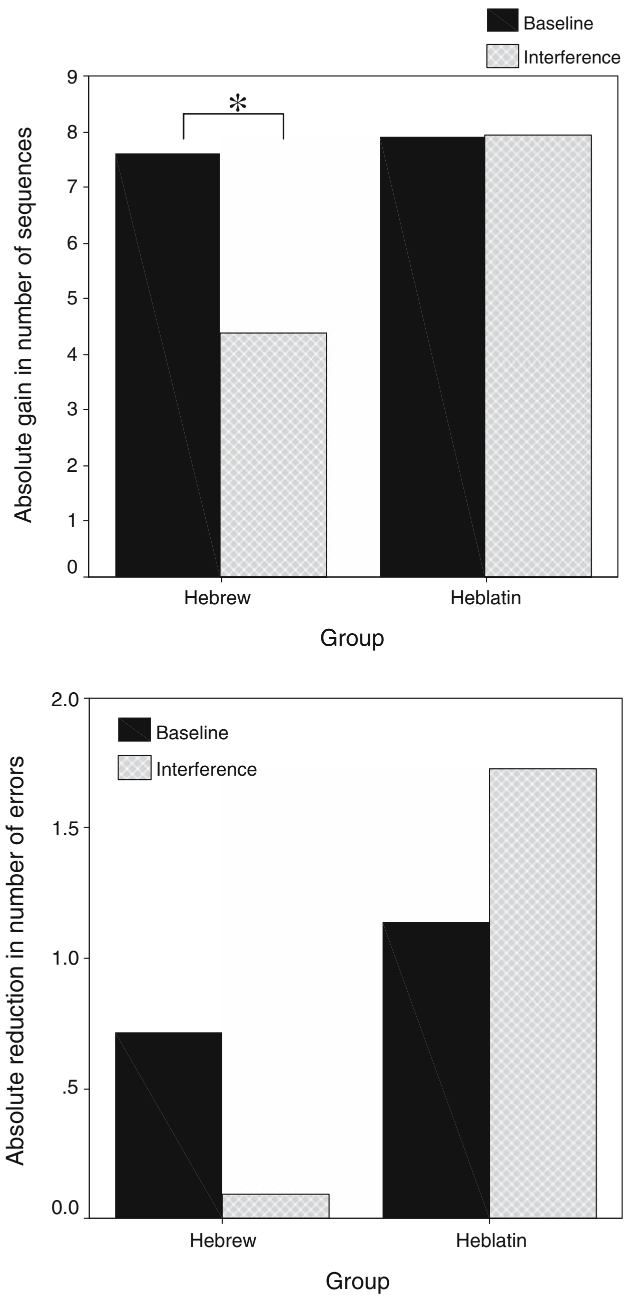

Fig. 2 Delayed gains (Δ2–3) in speed (number of sequences, *upper panel*) and accuracy (reduction in errors, *lower panel*) in the *baseline* and corresponding *interference* conditions, in the Hebrew and Heblatin groups, in experiment 1

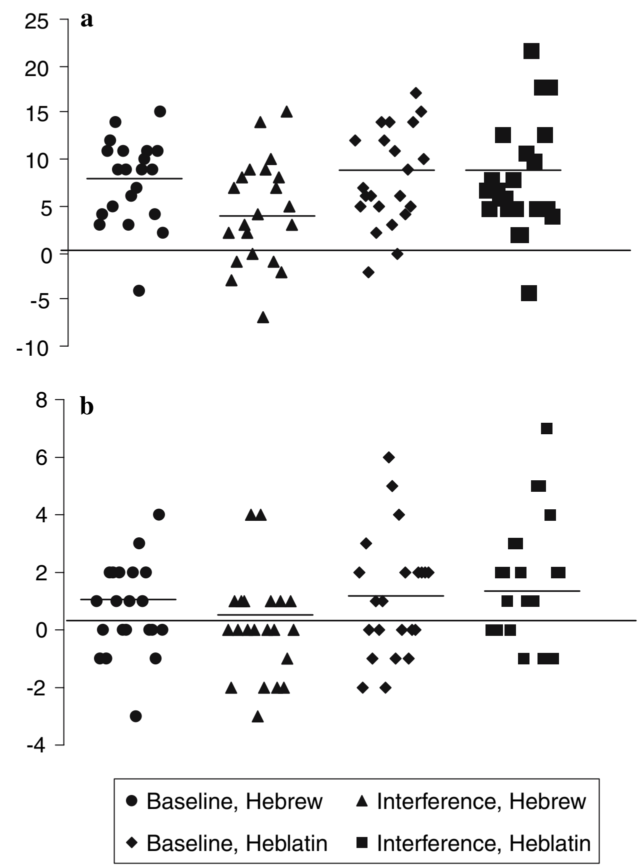

Fig. 3 Individual data: the difference (Δ2–3) in number of completed sequences in *test3* relative to *test2* (**a**) and the difference in the total number of errors in *test2* relative to *test3* [note that the number of errors made in the preceding test was subtracted from the number of errors made in the following test (i.e., a reduction in errors = a positive Δ)] (**b**) performed by each participant in the Hebrew, Heblatin and the corresponding baseline conditions, in experiment 1. The *horizontal lines* indicate the group average differences in each condition. Note that negative scores (locate under the *zero line*) indicate negative delayed gains, e.g., an inferior performance in *test* 3 relative to *test* 2

loss of performance, relative to the performance at the end of the practice session (negative delayed gains), by 24 h post-training. There was no significant difference between the baseline and the Hebrew interference conditions in the early, within-session gains (Fig. 4). A repeated measures general linear model was run separately for speed and for accuracy, with *condition* (with two levels baseline or interference), *test* (with two levels *test* 1, *test* 2) and *block* (with four levels 1st, 2nd, 3rd, and 4th block) as within-subjects variables and *order* (with two levels baseline first or interference first) as a between-subjects variable. No significant order effect for either speed [$F(1,10) = 0.02$, $P = 0.886$] or accuracy [$F(1,10) = 0.87$, $P = 0.371$] was found. Significant main effects of *test* and *block* were found for speed [$F(1,10) = 138.9$, $P < 0.001$; $F(1,10) = 7.2$, $P = 0.023$] showing that on both conditions, participants performed better in *test2* compared to *test1*. No significant effects were found for accuracy, however the error rate was small in all phases of training (0.812 ± 0.18, 0.687 ± 0.18, mean and SD of number of errors in *test1* and *test2*, respectively, in the baseline condition; 0.646 ± 0.15, 0.500 ± 0.14, mean and SD of number of errors in *test1* and *test2*, respectively, in the Hebrew interference condition). There was a significant *test* and *block* interaction in speed, reflecting the

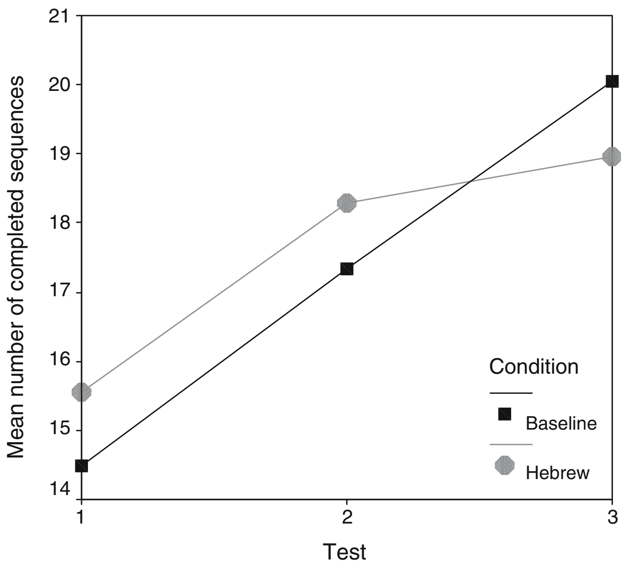

Fig. 4 Group performance (average number of completed sequences in a block) at tests 1, 2 and 3 in the *baseline* and *Hebrew* conditions, in Experiment 2

finding that there was block-by-block improvement in *test1* but not in *test2* ($F(1,10) = 6.164$, $P = 0.032$). All the other main effects and their interactions were not significant for either speed or accuracy.

To examine the differences between the baseline and the Hebrew interference conditions in terms of the delayed, between-sessions gains (speed and accuracy), a similar analysis was used with *condition* (with two levels baseline or interference), *test* (with two levels *test2*, *test3*) and *block* (with four levels 1st, 2nd, 3rd, and 4th block) as within-subjects variables and *order* (with two levels baseline first or interference first) as a between-subjects variable. No significant order effects were found for speed [$F(1,10) = 0.00$, $P = 0.954$], however, order did have a significant effect for accuracy [$F(1, 10) = 7.3$, $P = 0.022$] though here also, the error rates were very small (0.313 ± 0.46, 0.490 ± 0.46, mean and SD of number of errors; baseline before interference, and reversed order, respectively). For performance speed, there was a significant main effect of *test* [$F(1,10) = 20.4$, $P < 0.001$] with participants performing better in *test3* then in *test2*, irrespective of condition. The main effect of *test* for accuracy was also significant [$F(1,10) = 13.7$, $P = 0.004$]. However, a significant interaction between *condition* and *test* was found [$F(1,10) = 8.4$, $P = 0.016$] indicating the inferior performance in the Hebrew interference condition compared to the baseline condition at *test3* (Table 1 and Fig. 4). No additional significant main effects or interactions were found either for speed or for accuracy.

As in experiment 1, the absolute gains in performance [i.e., the difference between tests 1 and 2 (Δ1–2) and between tests 2 and 3 (Δ2–3)] were computed in each condition (baseline or interference) for speed and accuracy. For Δ1–2, a measure of the within-session gains, there was no significant difference between the two conditions in either speed or accuracy [paired *t* test, $t(11) = 0.10$, $P = 0.918$; $t(11) = 0.07$, $P = 0.949$, respectively]. For Δ2–3, i.e., the delayed gains, however, there was a significant difference in speed between the two conditions [$t(11) = 3.0$, $P = 0.012$). The difference in the delayed gains, for accuracy, was not significant [$t(11) = 1.3$, $P = 0.203$)].

Figure 5 depicts the absolute gains in performance speed at *test2* relative to *test1* (Δ1–2) and at *test3* relative to *test2* (Δ2–3) in the Hebrew condition, on an individual basis. In the baseline condition, all of the participants showed some improvement during the 24 h post-training interval. However, in the Hebrew interference condition, 6 participants out of the 12 (50%) showed an actual loss of performance, in terms of speed, by 24 h post training, relative to performance speed at the end of the practice session (Fig. 5).

Discussion

Altogether, the results of the current experiments show that the evolution of delayed gains in performance, accrued in practice on the FOS, could be significantly interfered with if, shortly after the termination of the training session, the participants wrote a small number of common words in their native handwriting. In a number of participants (28–50%), an actual loss of the within-session performance gains

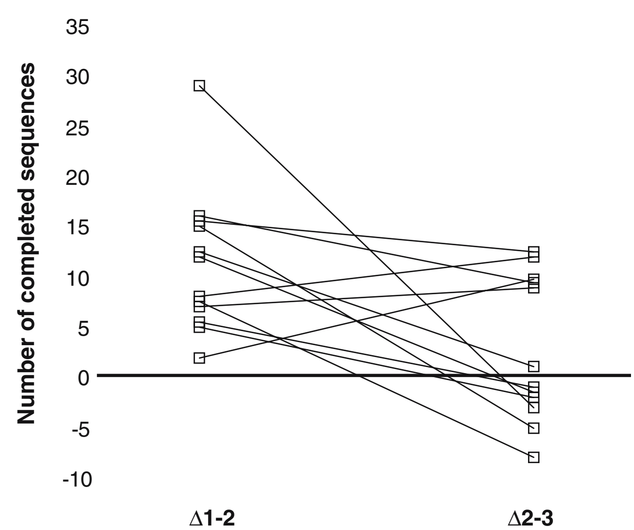

Fig. 5 Individual data: the absolute gains, for speed, at test2 relative to test1 (Δ1–2) and at test3 relative to test2 (Δ2–3) in the Hebrew condition, in Experiment 2

occurred in the 24 h post-training interval in the Hebrew interference condition (negative delayed gains). However, the same number of words in a less practiced mode of handwriting—Heblatin—resulted in no interference, with as robust within and between session gains as those accrued when no interference was introduced.

The strength of the current results derives from the within-subjects comparisons afforded by the study design with each participant providing his or her own control data. Thus, although the interference effects in both experiments were small in absolute terms (each additional sequence in a test block stands, nevertheless, for five additional correct opposition movements), the interference by handwriting in the participants native script resulted on average in a 50% reduction in the expected delayed gains, and often in no gains whatsoever.

Recent studies reported significant interference when shortly after the training on a given FOS, training on a different (reversed movement) sequence (Walker et al. 2003) or the performance of the Tower of Hanoi task (E. Vakil et al., Psychonomics Society abstracts 2002) was introduced. The within-session gains however, were maintained in both studies. Interference related loss of both the within-session and the delayed gains was reported in tasks other than the FOS (Shadmehr and Brashers-Krug 1997; Hauptmann and Karni 2002; Tong et al. 2002).

It is not clear which factors determine the establishment and the magnitude of interference effects (Adams 1987; Flanagan et al. 1999; Krakauer et al. 1999; Goerdert and Willingham 2002; Hauptmann and Karni 2002; Krakauer et al. 2005). A leading notion is that, an effective interference experience is one that shares some critical motor representation, or internal model, with the initial, interfered, task (e.g., Shadmehr and Brashers-Krug 1997; Tong et al. 2002). The conjecture is that, both the initial training and the subsequent interference experiences activate overlapping neural representations in specific brain areas, but the two experiences differ in the sense that each requires quite different adaptation parameters (Robertson et al. 2004). The need to adapt to the demands of the second task may therefore, eliminate or supersede the settings of the initial one with an advantage for the gains attained in the latest experience (Brashers-Krug et al. 1996; Krakauer et al. 1999; Hauptmann and Karni 2002).

The notion of consolidation was recently challenged by studies showing no diminution of the interference effect with time. Interference was found when the interfering task was carried out 24 h or even a week after the termination of training on the initial task (Goedert and Willingham 2002; Caithness et al. 2004). It may be the case that in both studies, skill learning effects (by necessity requiring memory consolidation) and adaptation effects (which may be long-lasting but do not necessitate consolidation effects, see Hauptmann and Karni 2002) were interchangeably measured. When insufficient training was afforded and presumably when two tasks are interleaved within a session, consolidation processes may not be triggered or alternatively slowed down (Adams 1987; Hauptmann and Karni 2002). Because interference can occur at the adaptation phase, irrespective of consolidation, Hauptmann and Karni (2002) have argued that the evolution of delayed gains is the more sensitive measure for the triggering of consolidation processes.

Motor sequence learning may involve changes in primary motor cortex (M1) activation (Ungerleider et al.2002). Although other areas have also been implicated, learning related effects in M1 were shown to occur both within a short practice session, corresponding to the within-session performance gains and corresponding to multi-session gains and the long-term retention of some skills (e.g., Friston et al. 1992; Grafton et al. 1992; Kawashima et al. 1994; Karni et al. 1995; Nudo et al. 1996; Doyon et al. 2002; Muellbacher et al. 2001; Robertson et al. 2005; Koeneke et al. 2006). In humans (e.g., Karni et al. 1995, 1998a, b) and monkeys (Nudo et al. 1996) extended motor practice was shown to result in the recruitment of additional M1 units into a local network specifically representing the trained motor sequence. Based on these results, it was proposed that M1 might code not just for simple, single, movements, but also for complex movement sequences (Tanji and Shima 1994; Karni et al. 1998a, b; Georgopoulos 2000). Furthermore, it was suggested that given extensive training, even complex movement sequences may come to be represented in part by low-level, presumably M1, movement modules (e.g., Karni et al. 1998a, b; Sosnik et al. 2004). Based on this notion, Ungerleider et al. (2002) suggested that a given subpopulation of neurons within a representational domain, such as the hand's, participate in the representation of different movement sequences but that different movement sequences are realized by differential recruitment of these units. The advantage of such a parsimonious system may lay in the potential to support the learning of many parallel skills within a given restricted representation. However, such a system may be more susceptible to interference in a way that even movement sequences of very different attributes can interfere with each other.

The current results suggest that the ordering and scheduling of tasks during training and also in the hours following an effective training session may be critical for long-term motor memory, raising concerns about arbitrary scheduling in laboratory, academic and neurological rehabilitation practice. Thus, writing immediately after practice on a musical instrument may decrease the long-term effectiveness of the music lesson.

Our results also show, that behavioral interference might occur also when the two tasks are apparently very dissimilar and seem to share little or no kinematic or dynamic features. Both writing modes that were used as interference were complex and presumably involved a rather similar set of strokes (Namboodiri and Jain 2004). Given the logic of the representational overlap conjecture, our results suggest that the two handwriting modes do not activate the same motor representations, or rather, that these representations diverge in the extent of their overlap with the FOS representation. One critical difference between the two modes of writing may lie in the participants' expertise level—they were less skilled in Heblatin writing compared to Hebrew writing. The proposal therefore is that the differential effect of the two handwriting scripts tested in the current study, on the very same motor representation of the FOS, reflects a difference in the respective brain representations of well trained, versus relatively novel sequences of handwriting.

There is some support for the notion that while the representation of well-practiced handwriting sequences is effector dependent and necessitates the activation of low-level motor areas (e.g., M1) rather than more high-level ones for fluent performance, unpracticed writing sequences may require more activation of high-level areas (e.g., the SMA) and depend less on M1 based fluency (Karni et al. 1998a, b; Sosnik et al. 2004, Society for Neuroscience abstract 533.17, 2004). As opposed to well-practiced handwriting, controlled, less practiced handwriting is associated with kinematic non-fluency and shows increased neuronal activity in the contralateral primary sensorimotor cortex, frontal premotor area (lateral pre-motor cortex and SMA), parietal cortex, and the putamen. It was suggested, that during controlled processing, these brain regions might be involved in the generation of the motor output, in sensorimotor integration and in attentional processes (Siebner et al. 2001). Support for the notion of different brain activation patterns underlie the performance of well-practiced versus less practiced handwriting comes from studies that compared well-practiced handwriting in the dominant hand to handwriting in the non-dominant hand (e.g., Hoshiyama and Kakigi 1999; Karni et al. 1998a, b; Robertson et al. 2005). A similar notion has been advanced in motor learning in the monkey (Pavlides et al. 1993; Tanji and Shima 1994).

The extent, to which one task may interfere with another, may be related to the learner's level of expertise in both tasks (Schmidt 1975; Del-Rey et al. 1982; Shea et al. 1990). Others, (e.g., Guadagnoli and Lee 2004) have interpreted the finding that novices, as opposed to experts, show reduced delayed gains following training on multiple variations of the same task (contextual interference) in terms of a competition on "limited processing capacity" such as attention resources. Our results do not support either explanation, which would predict that the Heblatin condition, both relatively novel and likely to require more attention in its execution compared to the well-practiced Hebrew, was more likely to interfere with the FOS. Thus, one or more of the successive task variations that followed each other within a short time interval, could have constituted an effective interference to the initial task conditions. In experts, the representation of each task variation may be subserved by a specific, well-established routine (e.g., Karni et al. 1998a, b; Korman et al. 2003; Sosnik et al. 2004). Moreover, these routines may be subserved by specific motor representations perhaps embodied in a module consisting of a sub-population of neurons in a given shared representation (e.g., Ungerleider et al. 2002).

Taken together, our results suggest the notion that well-trained handwriting sequences are represented at some critical neuronal level in a manner more overlapping the execution of a recently acquired sequence of finger movements compared to the representation of much less practiced handwriting sequences. These results support the proposal (Korman et al. 2003; Sosnik et al. 2004) that, with extended practice, well-practiced movement sequences undergo not only qualitative changes, movement chunking and co-articulation, but also shift in the hierarchical sense, and come to be represented, at least in part, as novel motor primitives in motor cortex.

Acknowledgments This study was partially supported by a grant from the Scientific Director, Israeli Ministry of Health (to N. G and A. K.).

References

Adams JA (1987) Historical review and appraisal of research on the learning, retention, and transfer of human motor skills. Psychol Bull 101(1):41–74

Brashers-Krug T, Shadmehr R, Bizzi E (1996) Consolidation in human motor memory. Nature 382:252–255

Caithness G, Osu R, Bays P, Chase H, Klassen J, Kawato M, Wolpert DM, Flanagan JR (2004) Failure to consolidate the consolidation theory of learning for sensorimotor adaptation tasks. J Neurosci 24(40):8662–8671

Del Rey P (1982) Effects of contextual interference on the memory of older females differing in levels of physical activity. Percept Mot Skills 55(1):171–180
Doyon J, Song AW, Karni A, Lalonde F, Adams MM, Ungerleider LG (2002) Experience-dependent changes in cerebellar contributions to motor sequence learning. Proc Natl Acad Sci USA 99(2):1017–1022
Fischer S, Hallschmid M, Elsner AL, Born J (2002) Sleep forms memory for finger skills. Proc Natl Acad Sci USA 99(18):11987–11991
Flanagan JR, Nakano E, Imamizu H, Osu R, Yoshioka T, Kawato M (1999) Composition and decomposition of internal models in motor learning under altered kinematic and dynamic environments. J Neurosci 19(20):RC34:1–5
Fonseca R, Nagerl UV, Morris RG, Bonhoeffer T (2004) Competing for memory: hippocampal LTP under regimes of reduced protein synthesis. Neuron 44:1011–1020
Friston KJ, Frith CD, Passingham RE, Liddle PF, Frackowiak RS (1992) Motor practice and neurophysiological adaptation in the cerebellum: a positron tomography study. Proc Biol Sci 248(1323):223–228
Georgopoulos AP (2000) Neural aspects of cognitive motor control. Curr Opin Neurobiol 10:238–241
Goedert KM, Willingham DB (2002) Patterns of interference in sequence learning and prism adaptation inconsistent with the consolidation hypothesis. Learn Mem 9:279–292
Grafton ST, Mazziotta JC, Presty S, Friston KJ, Frackowiak RSJ, Phelps ME (1992) Functional anatomy of human procedural learning determined with regional cerebral blood flow and PET. J Neurosci 12(7):2542–2548
Guadagnoli MA, Lee TD (2004) Challenge point: a framework for conceptualizing the effects of various practice conditions in motor learning. J Mot Behav 36(2):212–224
Hauptmann B, Karni A (2002) From primed to learn: the saturation of repetition priming and the induction of long-term memory. Brain Res Cogn Brain Res 13(3):313–322
Hoshiyama M, Kakigi R (1999) Changes of somatosensory evoked potentials during writing with the dominant and non-dominant hands. Brain Res 833:10–19
Jueptner M, Stephan KM, Frith CD, Brooks DJ, Frackowiak RSJ, Passingham RE (1997) Anatomy of motor learning. I. Frontal cortex and attention to action. J Neurophysiol 77:1313–1324
Karni A, Meyer G, Jezzard P, Adams M, Turner R, Ungerleider LG (1995) Functional MRI evidence for adult motor cortex plasticity during motor skill learning. Nature 377:155–158
Karni A, Kushnir T, Bitan T, Manor D, Yitzhak Y (1998a) An fMRI investigation of the representation of movement sequences in the adult motor cortex: effector independence. Neuroimage 7(2):S969
Karni A, Meyer G, Rey-Hipolito C, Jezzard P, Adams M, Turner R, Ungerleider LG (1998b) The acquisition of skilled motor performance: fast and slow experience-driven changes in primary motor cortex. Proc Natl Acad Sci USA 95:861–868
Kawashima R, Roland PE, O'Sullivan BT (1994) Fields in human motor areas involved in preparation for reaching, actual reaching, and visuomotor learning: a positron emission tomography study. J Neurosci 14(6):3462–3474
Koeneke S, Lutz K, Herwig U, Ziemann U, Jancke L (2006) Extensive training of elementary finger tapping movements changes the pattern of motor cortex excitability. Exp Brain Res (in press)
Korman M, Raz N, Flash T, Karni A (2003) Multiple shifts in the representation of a motor sequence during the acquisition of skilled performance. Proc Natl Acad Sci USA 100(21): 12492–12497
Krakauer JW, Ghilardi MF, Ghez C (1999) Independent learning of internal models for kinematic and dynamic control of reaching. Nat Neurosci 2(11):1026–1031
Krakauer JW, Ghez C, Ghilardi MF (2005) Adaptation to visuomotor transformations: consolidation, interference, and forgetting. J Neurosci 25(2):473–478
Maquet P, Laureys S, Perrin F, Ruby P, Melchior G, Boly M, Vu TD, Desseilles M, Peigneux P (2003). Sleep-related consolidation of a visuomotor skill: brain mechanisms as assessed by functional magnetic resonance imaging. J Neurosci 23(4): 1432–14440
McGaugh JL (2000) Memory—a century of consolidation. Science 287:248–251
Miall RC, Jenkinson N, Kulkarni K (2004) Adaptation to rotated visual feedback: a re-examination of motor interference. Exp Brain Res 154:201–210
Muellbacher W, Ziemann U, Boroojerdi B, Cohen L, Hallett M (2001) Role of the human motor cortex in rapid motor learning. Exp Brain Res 136:431–438
Namboodiri AM, Jain AK (2004) Online handwritten script recognition. IEEE Trans Pattern Anal Mach Intell 26(1):124–130
Nudo RJ, Miliken GW, Jenkins WM, Merzenich MM (1996) Use-dependent alterations of movement representations in primary motor cortex of adult squirrel monkeys. J Neurosci 16(2):785–807
Pavlides C, Miyashita E, Asanuma H (1993) Projection from the sensory to the motor cortex is important in learning motor skills in the monkey. J Neurophysiol 70(2):733–741
Robertson EM, Pascual-Leone A, Miall RC (2004) Current concepts in procedural consolidation. Neuroscience 5:1–7
Robertson EM, Press DZ, Pascual-Leone A (2005) Off-line learning and the primary motor cortex. J Neurosci 25(27):6372–6378
Schmidt RA (1975) A schema theory of discrete motor skill learning. Psychol Rev 82:225–260
Shadmehr R, Brashers-Krug T (1997) Functional stages in the formation of human long-term motor memory. J Neurosci 17(1):409–419
Shadmehr R, Holocomb HH (1997) Neural correlates of motor memory consolidation. Science 277:821–825
Shea JB, Morgan RL (1979) Contextual interference effects on the acquisition, retention, and transfer of a motor skill. J Exp Psychol Hum Learn 5(2):179–187
Shea CH, Kohl RM, Indermill C (1990) Contextual interference: contributions of practice. Acta Psychol 73:145–157
Siebner HR, Limmer C, Peinemann A, Bartenstein P, Drzezga A, Conard B (2001) Brain correlates of fast and slow handwriting in humans: a PET-performance correlation analysis. Eur J Neurosci 14:726–736
Sosnik R, Hauptmann B, Karni A, Flash T (2004) When practice leads to co-articulation: the evolution of geometrically defined movement primitives. Exp Brain Res 156:422–438
Tanji J, Shima K (1994) Role for supplementary motor area cells in planning several movements ahead. Nature 371(6496): 413–416
Tong C, Wolpert DM, Flanagan R (2002) Kinematics and dynamics are not represented independently in motor working memory: evidence from an interference study. J Neurosci 22(3):1108–1113
Ungerleider LG, Doyon J, Karni A (2002) Imaging brain plasticity during motor skill learning. Neurobiol Learn Mem 78: 553–564
Walker MP, Brakefield T, Morgan A, Hobson JA, Stickgold R (2002) Practice with sleep makes perfect: sleep-dependent motor skill learning. Neuron 35:205–211
Walker MP, Brakefield TA, Hobson JA, Stickgold R (2003) Dissociable stages of human memory consolidation and reconsolidation. Nature 425:616–620