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RESEARCH ARTICLE | *Control of Movement*

Fast and specific: insights into the acquisition and generalization of motor acuity

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Gonda S, Shkedy Rabani A, Horesh N, Shmuelof L. Fast and specific: insights into the acquisition and generalization of motor acuity. *J Neurophysiol* 122: 2354–2363, 2019. First published October 16, 2019; doi:10.1152/jn.00558.2018.—Motor acuity is considered to be the outcome of prolonged practice and to involve morphological changes in the motor cortex. We have previously designed a curved pointing task, the arc pointing task (APT), to study motor acuity acquisition, defined as a change in the speed-accuracy tradeoff function (SAF) of the task. Here, we studied the generalization of motor acuity between hands and between tasks (drawing the arc in the opposite direction and with the untrained hand) and the effect of training duration on motor acuity. We report that training-induced motor acuity improvement did not generalize across hands and across tasks performed with the same hand, suggesting a task-specific representation of motor acuity. To our surprise, the largest gains in motor acuity, measured both by changes in SAF and by improvement in multiple kinematic variables, were seen following a short exposure to the task. Our results suggest that motor acuity training-induced improvement is task specific and that motor acuity starts to improve following a very short practice.

NEW & NOTEWORTHY We report that training induced motor acuity improvement does not generalize from one hand to another or between movements that are performed with the same effector. Furthermore, significant improvements in acuity were found following a very short exposure to the task (~20 trials). Therefore, our results suggest that the nervous system has the capacity to rapidly improve motor acuity.

motor control; motor learning; motor skill; reaching

INTRODUCTION

Mastering a motor skill, such as playing a musical instrument, takes years of deliberate practice (Ericsson et al. 1993). Motor skill acquisition is a complex process in which the actor acquires multiple abilities, such as knowledge about the task (Stanley and Krakauer 2013), the ability to select the proper actions (Nissen and Bullemer 1987), and the ability to execute them reliably (Müller and Sternad 2004). Indeed, a central aspect of skill is motor acuity, the ability of the subject to reliably perform dexterous movements. We have previously shown that motor acuity, defined as a change in speed-accuracy tradeoff function (SAF) in a precision task performed with a single joint, can be acquired following 3 days of practice and suggested that motor acuity could be the bottleneck in acquisition of complex motor skills (Shmuelof et al. 2012). Nevertheless, the effect of training duration, and specifically, the effect of a short exposure to the task on motor acuity, is not well documented. This component is often overlooked in studies that compare the performance of subjects before and after training, with no proper examination of the effect of the task's exposure on the performance in the task.

Another open question in motor acuity learning relates to the neural and cognitive representations that are modulated with training. Direct and indirect neural recording methods have shown involvement of the primary motor cortex, the premotor cortex, and the cerebellum in motor acuity acquisition (Hardwick et al. 2013; Karni et al. 1995; Nudo et al. 1996; Shmuelof et al. 2014). A primary approach to studying the nature of the representations that change with training is to examine the generalization of the improvement to other tasks and effectors (Shadmehr 2004). Motor acuity gains could potentially result from a general improvement in the control over the specific muscle groups that are involved in performing the trajectory or from improvement in the control over the performed trajectory. These alternatives could be examined by investigating the performance gains when training on one variant of the task and testing on another (transfer). We have previously shown that motor acuity generalizes across speeds and involves improvement in feedforward and feedback control components (Shmuelof et al. 2012), but it is still unknown to what degree motor acuity improvement is specific to the performed trajectory and to the performing effector. Furthermore, recent results indicate that task's generalization is dynamic, and changes with training (Karni et al. 1995; Perez et al. 2007a). Thus, changes in generalization functions may also be indicative of stages of learning (Fitts and Posner 1967).

The goal of this study is to characterize the acquisition and generalization of motor acuity by comparing the effect of training duration on the improvement and generalization of improvement in the arc pointing task (APT), a pointing task that emphasizes motor acuity (Shmuelof et al. 2012). To gain a better understanding of the underlying components of motor acuity improvement under the different conditions, multiple

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kinematic variables were examined. Trial-by-trial variability and sum of deviations from the channel were measured to quantify the ability of the subjects to control the cursor. Integrated squared jerk was computed as a measure of movement efficiency, and entry angle to the target was measured to approximate sensorimotor calibration in the task.

METHODS

Subjects. Sixty-six right-handed subjects (20–32 yr of age, 20 males), naïve to the task, participated in the study. All subjects gave written, informed consent and received a small compensation for their participation in the study, which was approved by the Ben-Gurion University Human Subjects Research Committee.

The arc pointing task. The APT (Shmuelof et al. 2012) requires subjects to guide a cursor from one circle to another through a semicircular channel, presented on a monitor, by moving their wrist without crossing the borders of the channel (Fig. 1). Movements were constrained to the wrist joint by splinting the arm of the subjects to a table (Shmuelof et al. 2012). Only one channel was presented in each trial. Channels alternated between successive trials. At the beginning of each trial, a channel appeared, and the subject had to bring the cursor into the starting point circle, colored in white. Following a 1-s delay, the target circle turned green, accompanied by a sound, signaling to the subject that she could begin the movement. The cursor was visible throughout the movement. After the trial, the entire trajectory of the cursor appeared on the screen. In all conditions, subjects were required to make the movements in predefined movement time (MT) ranges. The required MT was indicated to the subject using a computer-generated demonstration of the cursor moving through the channel at the required MT. This demonstration was presented at the beginning of each session block. Valid movements (inside the channel and within MT range for the constrained blocks) were followed by a pleasant sound and rewarded with symbolic coins. To increase the motivation of the subjects, the number of coins that the subjects received for a successful performance depended on MT (e.g., movements that were faster than 350 ms were rewarded with 6 coins; 350–618 ms, 5 coins; 618–827 ms, 4 coins; 827–1,060 ms, 3 coins; 1,060–1,440 ms, 2 coins; 1,440–10,000 ms, 1 coin). For trials that were within MT, the entire trajectory of the cursor appeared as a series of circles on the screen ["knowledge of performance" (KP)]. The cursor path was colored according to the position of the cursor with respect to the channel; the parts of the path inside the channel were colored in white, and the parts outside the channel were colored in yellow. For trials outside the required MT boundaries, a remark appeared on the screen ("move faster"/"move slower"). In these trials, KP was not given to motivate subjects to follow the movement time constraints.

Study design. Subjects participated in multiple sessions in the laboratory. The sessions in the laboratory were composed of test sessions (first and last days, length depending on group), in which the performance of subjects in the APT was assessed at 4 MTs to derive an SAF, and training sessions (1 each day), in which subjects were required to perform the APT at a single MT (800 ± 20% ms). In *experiment 1*, subjects were randomly assigned to two control and two trained groups. The control groups did only the test sessions, and the trained groups did both the test and the training sessions. In *experiment 2*, subjects were randomly assigned to two groups that conducted only a short test session, with different time intervals between the first and second test sessions.

Test sessions. On the first and last sessions, subjects' SAF was sampled by testing their performance at four different MTs (500 ± 30, 733 ± 20, 966 ± 20, and 1,200 ± 20% ms) presented in different blocks. For all speeds but the fastest, MT ranges were chosen to be 20% below and above the required MT. For the fastest speed, which was the hardest to follow, the range was chosen to be slightly wider (30%). Twelve movements within each time range were collected in each test session. Movements outside the required MT ranges were not included in SAF calculations. For the calculation of trial-by-trial variability, movements outside the MT range were included to improve the estimation of the variability measure. At the beginning of each block, four demonstration trials (demo), in which the cursor moved within the channel at the required speed were shown. In *experiment 1*, subjects (see test protocols; Table 1) were tested on four variants of the APT: movements with the left (L; nondominant) and right (R; dominant) hands in a counterclockwise (LCCW and RCCW, respectively) or clockwise (LCW and RCW, respectively) direction. Participants in *experiment 2* were tested only on the LCCW variant.

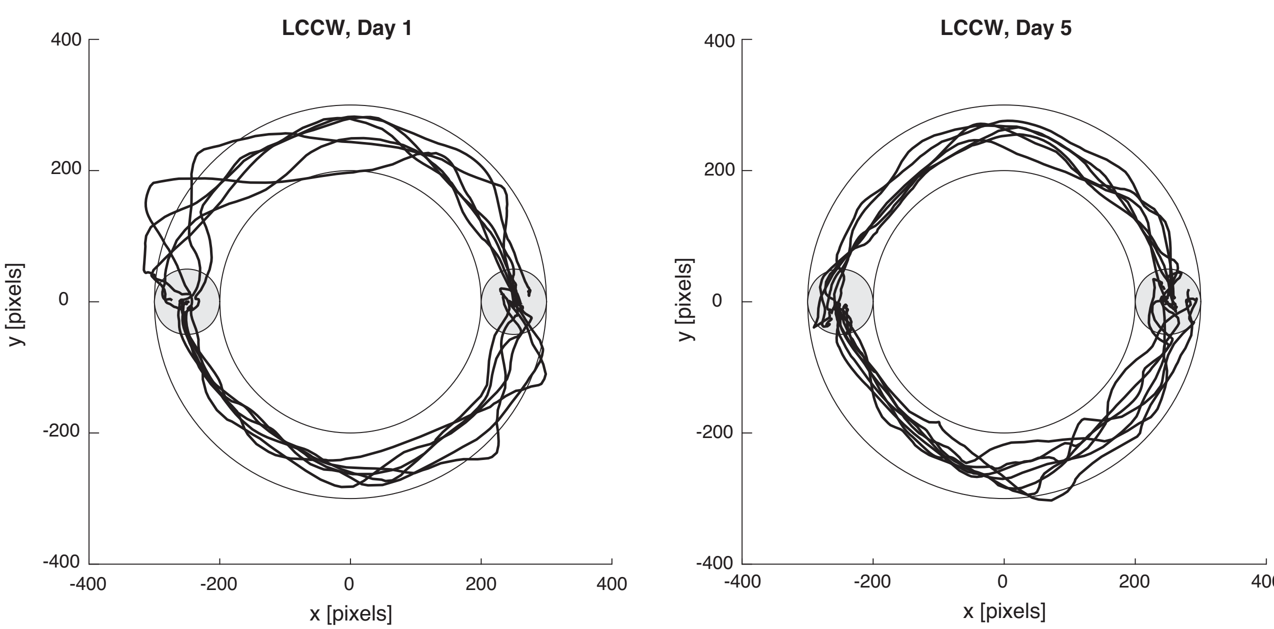

Fig. 1. Performance in the arc pointing task (APT) in *experiment 1*. Trajectories of a representative subject from the 3-day trained group. *Left*: trajectories from the 1st test session. *Right*: trajectories from the retest session of the trained task [left hand in a counterclockwise (LCCW) direction] from a movement time (MT) that is the closest to the training speed (966 ms). Only trials within the required MT range are depicted.

Table 1. *Experimental protocol*

Group	*Day 0*	*Day 1*	*Day 2*	*Day 3*	*Day 4*
			Experiment 1		
2 Day control ($n = 8$)	Test (4 tasks, 4 MT ranges)			Retest (4 tasks, 4 MT ranges)	
2 Day trained ($n = 8$)	Test (4 tasks, 4 MT ranges)	Training (LCCW, 800 ms, 270 trials)	Training (LCCW, 800 ms, 270 trials)	Retest (4 tasks, 4 MT ranges)	
3 Day control ($n = 10$)	Test (4 tasks, 4 MT ranges)				Retest (4 tasks, 4 MT ranges)
3 Day trained ($n = 17$)	Test (4 tasks, 4 MT ranges)	Training (LCCW, 800 ms, 270 trials)	Training (LCCW, 800 ms, 270 trials)	Training (LCCW, 800 ms, 270 trials)	Retest (4 tasks, 4 MT ranges)
			Experiment 2		
2 Day control ($n = 11$)	Test (LCCW, 4 MT ranges)			Retest (LCCW, 4 MT ranges)	
0 Day control ($n = 12$)	Test (LCCW, 4 MT ranges) and retest (LCCW, 4 MT ranges)				

LCCW, left hand, counterclockwise; MT, movement time. All groups participated in 2 test sessions. Two groups also performed training sessions between the test sessions.

Estimation of the SAF for each variant of the task was conducted in a block that lasted ~20 min. Thus, the test session in *experiment 1* lasted 80 and 20 min in *experiment 2*. At the beginning of each test variant, subjects performed a warm-up epoch, where they observed demos of the cursor moving within the arc, and performed 12–13 APT trials.

Training. Training sessions were conducted only in *experiment 1*. Training was carried out for 2 and 3 days in two groups (see protocols in Table 1). Each day's training was composed of 3 blocks of 90 movements each in a constrained MT range (training sessions, 800 ± 20% ms). A demo, presenting the cursor moving at the required MT (800 ms), was presented every 30 trials. Between blocks, the subjects were allowed to rest for 5 min. Coins for each block were accumulated separately to allow the subjects to discern their improvement within a session. The total duration of a training session was ~45 min.

Experiment 1. Subjects were randomly assigned to one of four groups. All groups did two test sessions (test and retest) that were composed of all four variants of the APT: clockwise (CW) and counter clockwise (CCW) APT movements with the right and left hands. The 2-day control group did only test sessions separated by 2 days. The 2-day trained group did 2 days of training with tests before and after. The 3-day control group did two test sessions separated by 3 days. The 3-day trained group did 3 days of training with tests before and after. The training was performed only on one variant of the task (LCCW).

Experiment 2. To further investigate the effect of the test session on performance, two additional control groups were examined. These groups did not go through any training, and were tested on only one variant of the task (LCCW). The 2-day control group did test sessions separated by 2 days. The 0-day control group was tested twice on the same day, with a 2.5-h time interval between tests.

Data analysis. Data were collected using three motion capture cameras (Oqus5+ by Qualisys) positioned on a wall in front of the subjects and recorded at a frequency of 60 Hz. First, trials in which the subjects were not following the task (either moving in a straight line between targets or moving in the wrong direction) were manually excluded. Approximately 2.5% of trials were excluded.

Accuracy measures were calculated as the proportion (p) of valid trials (within MT and inside the channel) out of all trials within the MT in each MT condition. Because this number is bounded between 0 and 1 and suffers from floor and ceiling effects when approaching the lower and upper limit of performance, these results were further transformed to z values using the logit transformation: $z = \ln[p/(1 - p)]$. The resulting variable z can be considered a more accurate reflection of skill, because it is not bounded at either end of the SAF. Because the logit transformation is not defined for $P = 0$ and $P = 1$, these specific values were replaced before applying the logit transformation by $P = 1/2n$ and $P = 1–1/2n$, respectively, where n denotes the number of trials in a condition (Shmuelof et al. 2012). To check that the transformed variables follow a normal distribution, we estimated the symmetricity of the distribution of residuals of each one of the variables (4 variants × 4 speeds × 2 time points) using inspection of the qq plots and computed the normalized skewness and kurtosis. In six of the 32 distributions, normalized skewness or kurtosis exceeded ±2, indicating that these distributions are not symmetrical. Importantly, three of these cases were from the slowest speed, suggesting that the asymmetry stems from a ceiling effect, and two of the six came from the fastest speed due to a floor effect. Thus, five of six deviations came from the extreme test speeds. Notably, because our statistical effects were based on conditions that were computed on multiple repeated-measures variables (such as the 4 speeds), the estimation of performance in each condition in each subject was based on ~48 trials. Therefore, according to the central limit theorem, the estimation of the probabilities across speeds tends toward a normal distribution, even when the distribution of the probabilities themselves may not be normal. In other words, although in some cases the residuals did not have a Gaussian distribution, the contrasts did, and inference is therefore valid. Additionally, to verify that the results do not depend on the variables that show deviation from symmetricity, we ran the same repeated-measures ANOVA analysis on the accuracy measures using only the two central MT conditions. Results were qualitatively identical; training-related improvement was observed only on the trained variant of the task [retest × condition for the LCCW, $F_{(1, 39)} = 5.97$, $P = 0.019$, and $P > 0.6$ for the other three variants].

Trial-by-trial variability. Trial-by-trial variability was calculated from the time-normalized radial positions.

After all the examined trajectories were transformed to clockwise movement on the upper arc using sign changes of x- and y-coordinates, trajectories were normalized by interpolating the sampled radial position between 10 and 170° to 50 points evenly spaced in time. Variance and average radial position were computed for each time-normalized point for every subject, day, and test speed. To avoid multiple comparisons, we focused our analysis on the last section of the movement. This selection was motivated by our previous work on the APT (Shmuelof et al. 2012), in which the effect of practice was examined along the entire trajectory and was highly significant at the end of the movement. Therefore, the trial-by-trial variability measure was defined as the mean variance between 70 and 90% of the time-normalized trajectory.

Target entrance angle. Target entrance angle was defined as the angular position of the entry point of the trajectory to the target with respect to the center of the target (Fig. 6*A*). In cases where there was no data point on the border of the target, a linear fit was computed for the closest points to the target before and after the cursor crossed the boundary of the target, and its intersection with the target boundary was denoted as the crossing point. To allow comparison between movement in the upper and lower channel and across directions, all trajectories were transformed to the counterclockwise direction in the upper channel (e.g, for the lower channel, the clockwise trajectory was transformed as follows: $x = x$, $y = -y$).

Sum of deviations from the channel. Sum of deviations from the channel was computed using a root mean square (RMS) measure. After transforming all the examined trajectories to counter-clockwise movement on the upper arc using sign changes of x and y coordinates, the radial potion of the cursor was calculated at the range of 10°-170° of the movement within the channel. All radial positions that exceeded the channel boundaries, R_{out}, were squared, summed, and the total square root was reported (*Eq. 1*).

$$\mathrm{RMS} = \sqrt{\sum_{k=1}^{n} {R_{out}}^2}. \qquad (1)$$

Integrated squared jerk. Jerk, the third derivative of the position, was calculated for each trial in the range of 10–170° (after all the examined trajectories were transformed to counterclockwise movement on the upper arc using sign changes of *x*- and *y*-coordinates). The *x*- and *y*-positions were derived three times using numeric differentiation. After each differentiation, data were filtered using a third-order Butterworth LPF with a 14-Hz cutoff frequency. After the third derivation, radial jerk was calculated. Eventually, for each trial, the integrated squared jerk (ISJ) was calculated (*Eq. 2*)

$$ISJ = \int_{t1}^{t2} \ddot{x}(t)^2 dt. \qquad (2)$$

Statistics. Statistical analysis was performed in JASP 0.9 (JASP Team, 2018) and SPSS 23 (IBM Corp., Armonk, NY). Data were analyzed using repeated-measures ANOVA.

RESULTS

Experiment 1. The aim of this experiment was to study the effect of the duration of training on the LCCW version of the task on the improvement in APT and on the generalization to other variants of the task that were performed with the same hand (LCW) or with the other hand (RCW, RCCW).

Retest effect. Four groups were tested and retested on the task. All groups showed an improvement between the test and retest sessions [retest effect $F_{(1,\ 39)} = 31.86$, $P < 0.001$; Figs. 1 and 2]. This is the first indication of a rapid improvement in APT following a short exposure. This effect will be further investigated in *experiment 2*.

Effect of training. The training effect was examined by comparing the improvement in the LCCW task between the trained and the control groups (Figs. 2 and 3*A*). We found a significant retest × condition interaction [$F_{(1,39)} = 4.847$, $P = 0.033$], indicating that training had an additional effect on the performance of the task.

Effect of training duration. The length of training did not show a significant effect when the effect of training for 2 days

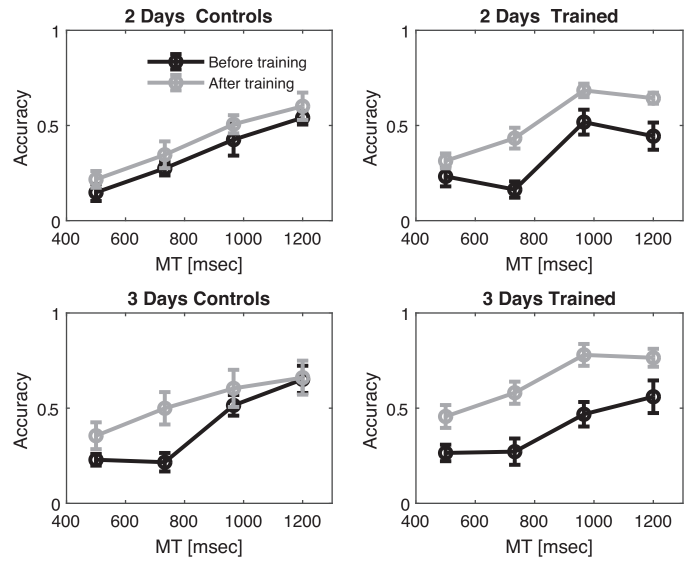

Fig. 2. Performance curves before and after training in *experiment 1* (for test and retest, respectively) in trained and control groups performing the left hand in a counterclockwise (LCCW) direction (trained) task. MT, movement time. Error bars denote SE.

was compared with the effect of training for 3 days [retest × duration × condition, $F_{(1,\ 39)} = 0.161$, $P = 0.69$; Fig. 3*A*].

Transfer within effector. The performance in the transfer task with the same hand (LCW) improved between test and retest [$F_{(1,\ 32)} = 22$, $P < 0.001$], but this improvement was not enhanced in the groups that trained compared with the groups that did not [retest × condition, $F_{(1,\ 39)} = 0.0029$, $P = 0.957$; Fig. 3*B*]. This result suggests that the improvement in the LCW condition was driven primarily by the retest effect and not by transfer of training-induced performance gains.

Transfer between effectors. Analysis of performance in the right hand tasks showed a retest effect, marking an improvement from one test session to the other [$F_{(1,\ 39)} = 22.88$, $P < 0.001$, Fig. 3*C*], but here again, the magnitude of the effects was comparable between the groups that trained and the control groups [retest × condition interaction, $F_{(1,\ 39)} = 0.058$, $P = 0.81$). Additionally, no difference was found between the improvement levels in the two tasks that were performed with the right hand [retest × task, $F_{(1,\ 39)} = 1.27$, $P = 0.267$, Fig. 3*C*]. These results clearly demonstrate a lack of transfer of skill between the right and the left wrists.

Variability. To test whether the accuracy changes were driven by improvement in task's execution, trial-by-trial variability was measured along the trajectory. This analysis focused on the variability in the last quarter of the movement (see METHODS).

Test-retest variability effect. A robust reduction in variance between the two test sessions (retest effect) was found in all variants of the task: LCCW [$F_{(1,\ 39)} = 11.38$, $P = 0.0017$], LCW [$F_{(1,\ 39)} = 10.17$, $P = 0.0028$], RCW [$F_{(1,\ 39)} = 7.08$ $P = 0.0113$], and RCCW [$F_{(1,\ 39)} = 4.793$ $P = 0.0346$] (Fig. 4). Nevertheless, this reduction was not affected by training (retest × condition interaction, $P < 0.19$). These results suggest that the reduction in variability occurred relatively quickly and contributed to the initial improvement in performance. Apparently, the effect of training on performance was

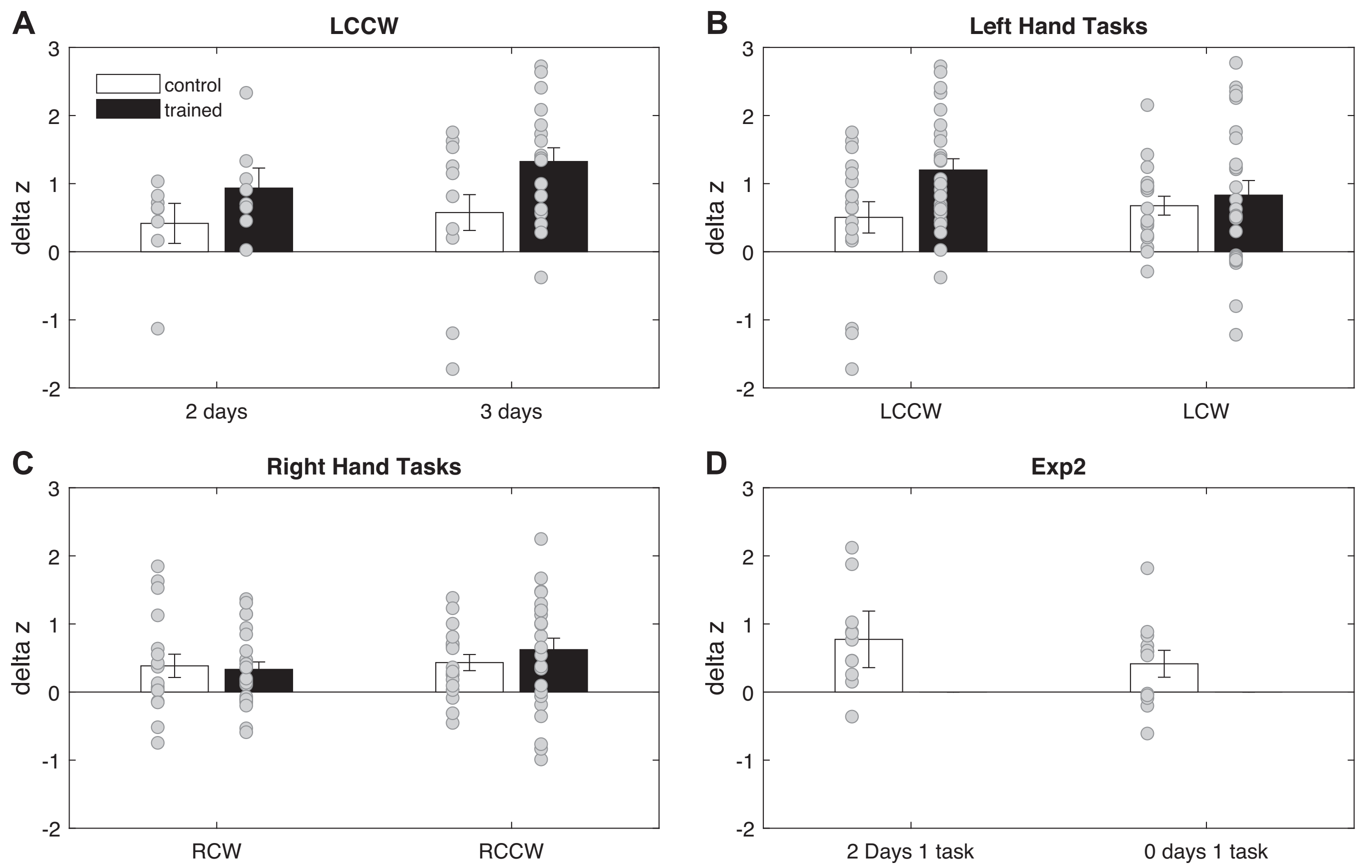

Fig. 3. Improvement in performance in all arc pointing task (APT) variants. *A*: *experiment 1*; improvement in the trained task [left hand in a counterclockwise (LCCW) direction] across test and retest for the 2 training durations (2 days vs. 3 days) for the trained and control groups. Although all improvements are greater than zero, the trained groups improved more than the untrained ones. *B*: *experiment 1*; improvement in the 2 left-hand tasks over both training durations. Training effect is seen in the trained but not in the untrained task. *C*: *experiment 1*; improvement in the 2 right-hand tasks over both length conditions. *D*: improvement in performance in *experiment 2*, where subjects were tested on only 1 task variant. Bars represent average performance. Gray circles represent performance of individual subjects.

not mediated by a further reduction in variability at the end of the movement.

Despite the notable difference between the averaged variability measures of the experimental groups between *days 2* and *3* (Fig. 5*A*), training duration did not have a significant effect on the variability reduction in the trained variant of the task [LCCW, retest × condition × duration, $F_{(1,\ 39)} = 2.54$, $P = 0.11$]. As can be appreciated from the single-subject results (Fig. 5*A*), the sensitivity of the variability analysis is limited due to the large intersubject variance.

Target entrance angle. In search of a kinematic measure that would capture the rapid calibration between the movement of the wrist and the feedback of the cursor on the screen, we quantified the angle of entry of the cursor to the target (Fig. 6*A*). We reasoned that the entry angle during the first test condition, which was the second-fastest speed, would be affected by sensorimotor calibration and would improve rapidly with exposure to the task, such that it would not show sensitivity to training. Indeed, the entry angles under the first test condition (733 ms) improved between test and retest [$F_{(1,\ 41)} = 5.43$, $P < 0.025$], such that in the first exposure movements tended to overshoot the target, and in the second exposure (retest) movements entered the target closer to its center (closer to 90°). This difference was consistent across the experimental and control groups [$F_{(1,\ 41)} = 0.051$, $P = 0.823$] and was not effected by training. Assuming that the examined fast movements (733-ms duration) are driven by feedforward control, our results suggest that calibration took place rapidly and was not affected by additional training on the task.

Sum of deviations from the channel. To better approximate the ability of subjects to stay in the channel, we quantified the sum of deviations from the channel using a root mean square (RMS) measure (see METHODS). Deviations decreased as a function of movement time [$F_{(3,\ 123)} = 8.82$, $P < 0.001$; Fig. 7], and from test to retest [$F_{(1,\ 41)} = 28.47$, $P < 0.001$]. Importantly, this measure also showed sensitivity to training [retest × condition, $F_{(1,\ 41)} = 4.56$, $P = 0.039$], reflecting the training gains on the performance of the subjects. Improvement in sum of deviations from the channel did not transfer to the other variants of the task ($P > 0.29$). Therefore, RMS partially reflects the effect of training induced improvement in the APT. The increased RMS value for the second MT of the test session of the trained group could be partially attributed to the fact that this was the first test condition that the subjects performed in the session, and that therefore, their warm-up was not complete.

Trajectory smoothness. Skilled movements are characterized by their smoothness, which has been also suggested as an optimization criterion for motor planning (Flash and Hogan 1985). To test of the evolvement of smoothness in the APT, we

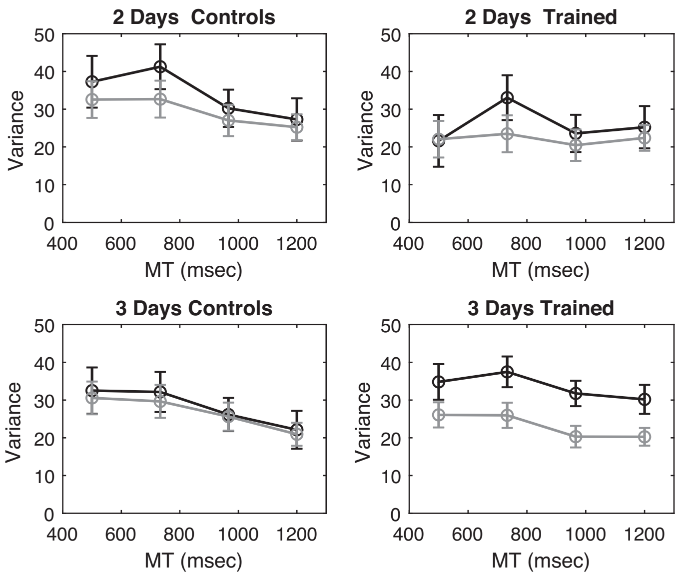

Fig. 4. Trial-by-trial variability reduction in the trained variant of the arc pointing task (APT) in *experiment 1*. Variability measures from the 4 examined movement durations before (black) and after (gray) training. Error bars denote SE.

followed the reduction of integrated squared jerk measure in the task (see METHODS). As can be appreciated from Fig. 8, integrated squared jerk was reduced with movement time [$F_{(3,\ 123)} = 18.45, P < 0.001$] and from test to retest [$F_{(1,\ 41)} = 8.9, P = 0.005$]. Training did not have a significant effect on the reduction in integrated squared jerk [retest × condition, $F_{(1,\ 41)} = 2.77, P = 0.1$]. Therefore, training-induced improvement in the APT is not reflected in the smoothness measure. There was a marked difference between the groups due to two subjects in the trained group that presented movements with high jerk values. Because this was a within-subject comparison, we chose not to exclude them from the analysis.

Experiment 2. Following the considerable size of the retest effect in *experiment 1*, we checked whether this effect was related to the long test session, which was composed of four variants of the task, and the degree to which the retest effect was driven by offline consolidation. Therefore, we ran two additional groups that did not go through any training and were tested only on one variant of the APT, with two different time durations between tests (2 days, 2.5 h; Table 1).

Retest effect. Retest effect was found to be significant [$F_{(1,\ 21)} = 17.28, P < 0.001$; Fig. 3*D*]. This result shows that ~15 min of exposure to the task is sufficient to drive an improvement in performance. The magnitude of improvement was comparable with the magnitude that was seen for the 2-day control group in *experiment 1* (Fig. 3*A*) and was not statistically distinguishable from it [$F_{(1,\ 51)} = 1.16, P = 0.29$].

Effect of the duration of the interval between rest and retest sessions. A 2.5-h interval between the test and retest sessions was enough for achieving an improvement (Fig. 3*D*). A longer interval between the tests did not affect the improvement [$F_{(1,\ 21)} = 1.57, P = 0.22$]. This result does not support the existence of a sleep-dependent consolidation process in motor acuity.

Variability change. The trial-to-trial variability of subjects in the short test groups was reduced from test to rest [$F_{(1,\ 21)} = 9.39, P = 0.006$; Fig. 5*C*] and was also not affected by the time interval between the test and retest sessions [$F_{(1,\ 21)} = 0.191, P = 0.667$].

DISCUSSION

Motor acuity acquisition was examined through multisession experiments with control groups for the effect of exposure to the task during the initial test session. When carefully controlling for the effect of exposure to the task, we found that motor acuity improvement is specific to the trained trajectory and to the trained hand. Unexpectedly, large and significant

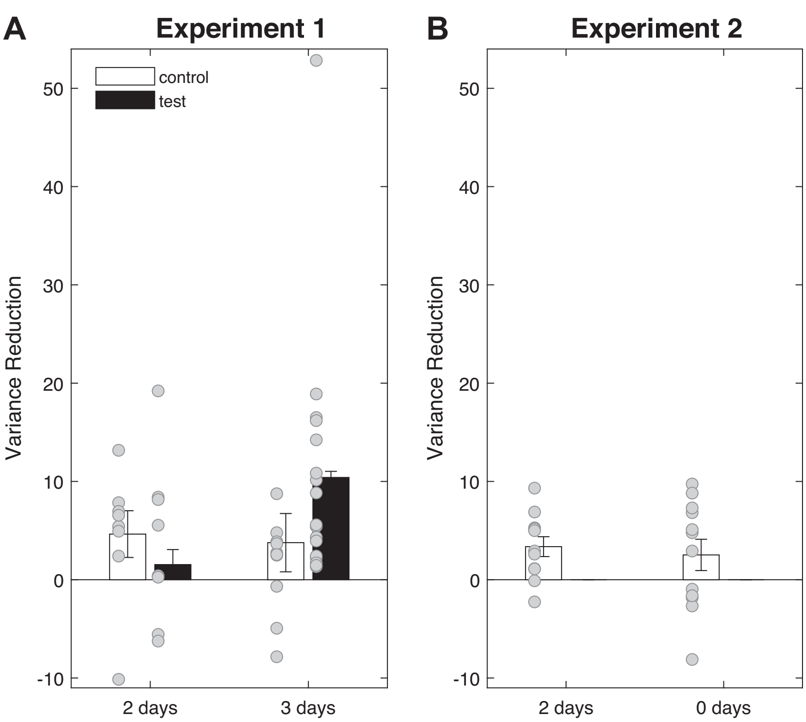

Fig. 5. Average variability changes in *experiments 1* (*A*) and *2* (*B*). Bars denote averaged variabilities. Gray circles represent performance of individual subjects.

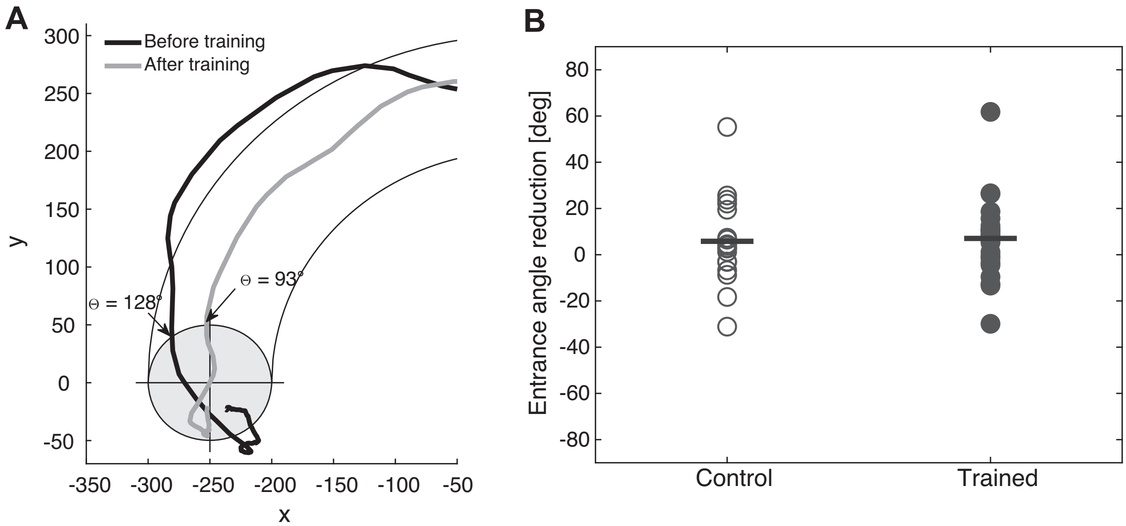

Fig. 6. *A*: entrance angle was defined as the angular position of the trajectory entrance to the target, computed with respect to the center of the target. Black trajectory is taken from a test session and the gray trajectory from a retest session of a representative subject. *B*: reduction in entrance angles between test and retest sessions for the control groups (*left*) and trained groups (*right*) in *experiment 1* from the first test condition (733-ms duration). Horizontal lines represent averages. Gray filled and open circles represent individual subjects.

improvements were found in all variants of the task in the retest sessions. These effects were observed both in the groups that trained between the test sessions and in the groups that did not, indicating that this improvement is not a generalization of the training-induced gains. Therefore, our results point to an initial and rapid improvement in motor acuity, which is followed by a slower improvement. We suggest that this rapid improvement reflects improvement in motor acuity and not task's familiarization or warm-up, since every test variant was preceded by a warm-up epoch, and since this improvement was associated with an improvement in kinematic measures such as integrated squared jerk, sum of deviations from the channel, and with a marked reduction in trial-by-trial variability. In fact, all the kinematic measures that were examined in this study showed a significant retest effect.

Our results are consistent with the view that motor acuity is acquired through a rapid initial process, which is followed by a slower process ("power law of practice;" see Newell and Rosenbloom 1981). This observation is similar to what we are accustomed to see in tasks in which there is a marked transition between failure and success, such as riding a bicycle, juggling, or mastering a sequence of actions, and is consistent with the implementation of the self-organized criticality theory in the field of motor learning (Korman et al. 2003; Newell et al. 2001). The existence of such an apparent criticality in a pointing task that has no apparent initial boundary suggests that the acquisition of any skill may be composed of multiple separate abilities that are acquired at different speeds. The suspected processes underlying improvement in the APT are improved state estimation, improvement in the representation

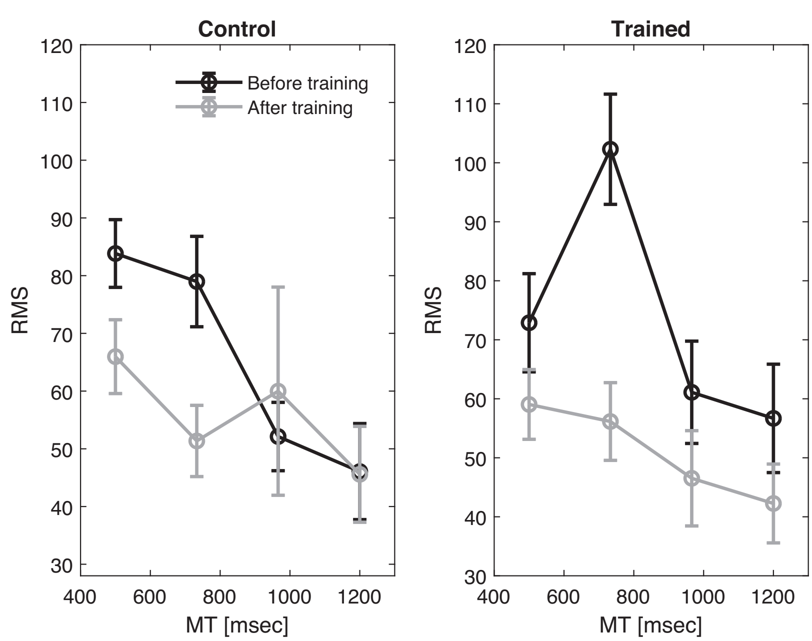

Fig. 7. Sum of deviations from the channel was quantified using a root mean square (RMS) measure. RMS is presented as a function of movement time (MT) before and after training for the control groups (*left*) and experimental groups (*right*) for the trained variant [left hand in a counterclockwise (LCCW) direction] in *experiment 1*. Following the test session, RMS decreased in both groups, but to a greater extent in the trained group. Error bars denote SE.

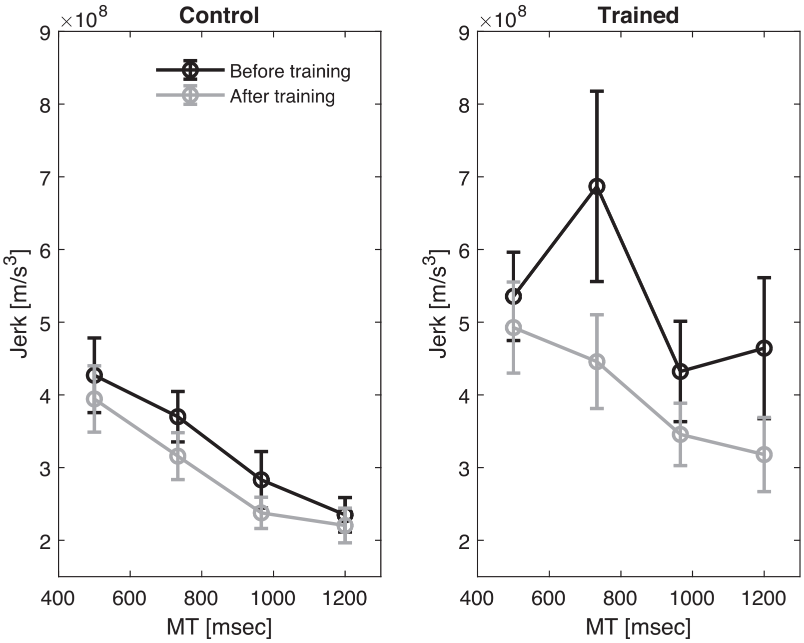

Fig. 8. Integrated squared jerk is presented as a function of movement time (MT) before and after training for the control groups (*left*) and trained groups (*right*) for the trained variant [left hand in a counterclockwise (LCCW) direction] in *experiment 1*. Following the first test, integrated squared jerk decreased in both groups, but to a greater extent in the trained group. Error bars denote SE.

of the motor plan, and improved feedback control (Shmuelof et al. 2012). In our study, a short exposure to the APT was associated not only with improved sensorimotor calibration, as can be seen in the entry angle analysis, but also with an increase in trajectory smoothness and trial-by-trial variability. These findings suggest that the initial improvement of the subjects involves a control component of the task. Notably, training was associated with a reduction in the sum of deviations from the channel, pointing to the fact that 2–3 h of additional training contributes further to the ability of subjects to control the cursor. One interpretation of our results is that the improvement that the trained and the control groups is driven by changes in the same underlying processes and that the extent of the training-related gains could be demonstrated only following longer training periods or when comparing bigger groups. Alternatively, it could be that the contribution of the suggested processes to performance changes with time and that the gains of the training are driven by different processes than the ones underlying the initial improvement. Further investigation using perturbations that target specific control components, such as online perturbations of the position of the cursor to probe feedback corrections, should be attempted to address this suggested modularity in skill learning.

One of the characteristics of procedural learning has been offline learning, which is thought to be an outcome of the consolidation of the new memory. In sequence learning tasks, consolidation was shown to be sleep-dependent, such that subjects show a greater improvement in sequence performance following sleep, even when the duration between the examinations is controlled for (Fischer et al. 2002; Korman et al. 2003; Walker et al. 2002, 2003). In fact, passage of time without sleep did not result in offline consolidation at all (Walker et al. 2002). Although our results cannot address offline learning directly, since subjects' performance was examined in a series of MTs, and the last MT in the first test session was not identical to the first MT on the subsequent day, the results of *experiment 2* do address sleeping-dependent offline learning as they indicate a comparable retest effect when a group that was retested 2.5 h after the initial test was compared with a group that was retested 72 h after training. We suggest that this apparent inconsistency between the sequence learning experiments and the APT is due to task differences; whereas the sequence learning task emphasizes the improved ability to select the specified sequence of finger movements and may include a declarative component, the APT emphasizes the improvement in the execution of a single movement. Thus, based on these findings, we suggest that offline sleep-dependent learning underlies improvement in action selection and not action execution. The existence of offline sleep-dependent processes in perceptual learning tasks (Stickgold et al. 2000), which are likely to share similar mechanisms to motor acuity tasks (Censor et al. 2012), may challenge this conjecture.

Generalization of learning provides insight into the functional and neural bases of the learned ability (Shadmehr 2004; Tanaka et al. 2009). In sequence learning tasks, generalization is typically examined along the movement (effector) and goal dimensions (Cohen et al. 1990; Grafton et al. 1998; Verwey and Wright 2004) (Waters-Metenier et al. 2014), delineating contributions of abstract and effector-dependent representations to motor learning, respectively. Accordingly, the generalization of acuity can provide insight into the unknown representation of motor acuity. Our results point to a selective improvement in motor acuity that does not generalize to an opposite movement of the wrist or to the same movement performed with the contralateral wrist and, therefore, suggest that motor acuity is effector and trajectory specific. This limited generalization may cast doubt on the utility of motor acuity training protocols that emphasize repetitions in rehabilitation.

A more recent view of generalization suggests that the extent of generalization is affected by the conditions that subjects are exposed to during training and pretraining and that generalization changes with training (Shea and Morgan 1979). For example, sequence learning studies have shown that after a short practice session, improvement in performance of one hand transfers to the untrained hand (Japikse et al. 2003; Perez et al. 2007a, 2007b), whereas after prolonged training of weeks it does not (Karni et al. 1995; Verwey and Wright 2004). These results were taken as support for the fact that extended practice enhances a particular mode of execution, reducing a more abstract representation of the task (Clark and Ivry 2010; Hikosaka et al. 2002). Importantly, reduced generalization with training has also been reported in perceptual learning, where a short training session results in greater generalization to an untrained visual field (Censor and Sagi 2009). Both lines of results have been recently interpreted as an outcome of an "overfitting" of the system to the presented stimuli, which leads to increased specificity of the representation and hence, to a restricted generalization to variants of the presented stimuli (Sagi 2011). The fact that we saw that training for 2 and 3 days resulted in a similarly narrow generalization suggests that either this phenomenon does not exist in motor acuity, or that overfitting occurs rapidly in this task. Furthermore, we report that the improvement that was gained following a test session with a single variant (*experiment 2*) was comparable with the improvement that was gained in a test session with four task variants. This result suggests that even at the beginning of training, practicing three additional variants of the task does not lead to a significant modulation of the performance in a fourth task. One interpretation of this result is that it reflects a ceiling of a task-invariant effect of exposure to a task in a manner similar to motivation effects in sequence learning (Wong et al. 2015). An alternative explanation is that, just like the training effect, the retest (exposure) effect is task specific, and improvement in the performance in each one of the variants is invariant to the amount of training that was performed with other variants.

To conclude, although intuitively motor acuity is considered to be the bottleneck in acquiring complex motor skills, and improvement in acuity is thought to be the outcome of a prolonged practice, we report here that performance in the control of a trajectory is significantly facilitated following a short exposure to the task and that the gains that are acquired through extended practice are specific to the performed effector and trajectory.

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

AUTHOR CONTRIBUTIONS

S.G., N.H., and L.S. conceived and designed research; S.G. and N.H. performed experiments; S.G., A.S.R., N.H., and L.S. analyzed data; S.G., A.S.R., N.H., and L.S. interpreted results of experiments; S.G., A.S.R., and L.S. prepared figures; S.G. and L.S. drafted manuscript; A.S.R. and L.S. edited and revised manuscript; S.G., A.S.R., N.H., and L.S. approved final version of manuscript.

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