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RESEARCH ARTICLES

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When practice leads to co-articulation: the evolution of geometrically defined movement primitives

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Abstract The skilled generation of motor sequences involves the appropriate choice, ordering and timing of a sequence of simple, stereotyped movement elements. Nevertheless, a given movement element within a well-rehearsed sequence can be modified through interaction with its neighboring elements (co-articulation). We show that extensive training on a sequence of planar hand trajectories passing through several targets resulted in the co-articulation of movement components, and in the formation of new movement elements (primitives). Reduction in movement duration was accompanied by the gradual replacement of straight trajectories by longer curved ones, the latter affording the maximization of movement smoothness. Surprisingly, the curved trajectories were generated even when new target configurations were introduced, i.e., when target distances were scaled, movement direction reversed or when different start and end positions were used, indicating the acquisition of geometrically defined movement elements. However, the new trajectories were not shared by the untrained hand. Altogether, our results suggest that novel movement elements can be acquired through extensive training in adults.

Keywords Motor control · Sequence learning · Co-articulation · Movement primitives

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Introduction

When moving a hand between pairs of targets, subjects tend to generate straight hand paths with single-peaked, bell-shaped velocity profiles. These stereotyped movements are invariant with respect to rotation, translation, temporal and size scaling (Morasso 1981; Abend et al. 1982; Hollerbach and Flash 1982; Flash and Hogan 1985; Gordon et al. 1994; Ghilardi et al. 1995; Wolpert et al. 1995). Studies of visually guided movements under altered visuospatial (Flanagan and Rao 1995; Wolpert et al. 1995; Gharamani and Wolpert 1997) or sensorimotor mapping conditions, as well as in the presence of unpredicted loads (Flash and Gurevich 1992; Shadmehr and Mussa-Ivaldi 1994) have shown that, following practice, subjects tend to re-converge on the straight trajectories generated in the unperturbed conditions. Thus, straight hand-paths with bell-shaped velocity profiles can be regarded as simple basic motor elements (“primitives”). It was found that arm trajectory modification in a double-target displacement paradigm might involve the vectorial summation of two such basic movement elements, each planned with the objective of maximizing movement smoothness (Flash and Henis 1991). Similarly, the movements of children in their first year of life can be decomposed into a sequence of stereotyped movements each resembling simple basic movements of adults (Hofsten 1991; Konczak et al. 1995; Berthier 1996). Other supportive evidence for the existence of basic movement elements has come from the study of hemiplegic stroke patients, whose initial movements were found to be clearly segmented and exhibited remarkably invariant velocity profiles (Krebs et al. 1999) similar to those seen in infants. It was recently suggested that such modular architecture might exist within the spinal cord as well as within higher brain structures. Moreover, the concept of a repertoire of movement primitives was suggested to include not only kinematic elements of movements but also dynamic ones (Mussa-Ivaldi and Bizzi 2000). Experimental evidence from the frog and the rat indicated that complex limb movements may be generated by a vectorial summation of modular force fields in the spinal cord (Bizzi et al. 2000; Mussa-Ivaldi and Bizzi 2000), suggesting the use of modular primitives both in the planning and execution of multi-joint limb movements.

In addition to the stereotypical straight trajectories seen in point-to-point movements, multiple studies were conducted in order to describe the kinematic features of curved and complex drawing movements with the aim of characterizing such movements and gaining insight into the nature of the basic elements comprising them (Edelman and Flash 1987; Wada and Kawato 1995; Wada et al. 1995; Adi-Japha et al. 1998). It is not clear, however, what type of movement elements, in addition to the straight ones described above, constitute basic building blocks for drawing and complicated scribbles or curved movements.

There is clear evidence in support of the notion that skilled movements might also reflect a process for the concatenation of consecutive movement elements into complex movements. A relatively well-studied mechanism for movement concatenation is represented by the notion of co-articulation. The term refers to the phenomenon that in a well-trained motor sequence the basic units are influenced by the anticipated adjacent units, resulting in spatial and temporal overlap of the units, and thus creating a new entity that is different from the sum of the elements that comprise it (Engel et al. 1997). This mechanism was first described for speech, wherein the articulator movements for a given speech sound were shown to vary systematically with the surrounding sounds and their associated articulatory movements, thus increasing speech fluency (Kent and Minifie 1977; MacNeilage 1980; Hardcastle and Marchal 1990; Blackburn and Young 2000). Moreover, it was shown that rather than simply an interaction whereby a preceding movement affects the one following, the anticipated movement in a sequence could systematically affect the one preceding it (Jerde et al. 2003). The concept was expanded to include also hand and digit movements, e.g., it was shown that pianists could anticipate notes in a well-rehearsed sequence, which resulted in hand and finger kinematic divergence (by assuming an “anticipatory” position) prior to the depression of a common note (Engel et al. 1997).

Assuming that we generate complex movements by combining existing, basic movement elements—”movement primitives”, strokes—to achieve fluency, the purpose of the present study was to test the possibility that extensive training may lead to the formation and addition of new movement elements (strokes) to the basic movement vocabulary in adults, i.e., that a qualitative change in motor performance can occur with practice. It may be the case that, due to our ability to tailor the existing strokes or to apply simple operations such as the superposition of temporally overlapping and time-shifted point-to-point movement units (Morasso and Mussa-Ivaldi 1982; Flash and Henis 1991; Roher et al. 2002), the modification of existing strokes or the evolvement of new movement elements may not be essential. However, the notion of co-articulation suggests the possibility that with extensive experience a new movement primitive can be generated, which would be different from the sum of the elements that comprised the sequence of movements initially, yet will be an effective (or perhaps more effective) means to perform the task. If true, this would imply a profound hierarchical change in motor planning: from syntax-dependent performance, to unitary (specific) element-dependent movement. Depending on the operational definition of co-articulation, one may either consider this latter outcome (the possible replacement of two movements by a single one) as a step superceding co-articulation or as the final stage of co-articulation (Engel et al. 1997).

A variety of motor tasks can be conceptualized as consisting of a serial sequence of simple movement components; the skilled generation of such a sequence can be reduced to the problem of choosing the correct components in the proper order, determining the time at which each component movement is initiated, and ensuring smooth continuity from one component movement to the next. However, there are some indications that this scheme may not hold true in all cases of sequence performance (Engel et al. 1997; Karni et al. 1998; Blackburn and Young 2000). A recent study has shown that practice on a given sequence of finger-opposition movements resulted in robust gains in performance, with both speed and accuracy more than doubled, over the course of several sessions (Karni et al. 1995; 1998). Both the behavioral and the functional brain imaging data indicated that practice resulted in a specific representation of the trained sequence of movements, rather than changes pertaining to the performance or cortical representation of the component movements per-se. Moreover, the results supported the conjecture that a specific representation of the sequence, as a functional unit, may be implemented at the level of primary motor cortex, in parallel to and differentially from the representation of the component movements (Karni et al. 1998). This interpretation is in agreement with the finding in monkeys, of practice-dependent changes in the functional topography of area M1 (Nudo et al. 1996). After a few weeks of training, on a task that required skilled manipulation, new task-related movement combinations came to be represented in M1—representations that were not found in non-trained brains. It is not clear, however, whether practice results in the implementation of novel, sequence-specific, syntactic elements in low-level motor representations or whether, in advanced stages of skill acquisition, a more profound qualitative change can be induced in the representation of the trained sequence of movements replacing one strategy of movement with another.

In the current study, we sought to determine whether the effects of extensive practice on a sequence of planar hand trajectories would result in distinct learning stages (Karni et al. 1998; Hikosaka et al. 1999), as defined by specific learning stage indicators. Moreover, using kinematic analysis, we examined the possibility that the task may be performed at different stages of practice using different movement strategies, i.e., that different kinematic parameters are optimized in the different stages of training, presumably reflecting a transformation in the internal representation of the task. Finally, we tested whether the process of co-articulation and the emergence of new movement elements could result from a constraint of minimizing total movement jerk (minimum jerk).

Materials and methods

Behavioral data

In order to study the evolution of skilled performance and to unravel to what extent motor primitives are subject to modification by training in adults we used a handwriting-like task. Twenty-three healthy individuals (14 males and 9 females, aged 17–35 years) participated in the study. Participants were trained for 5–15 sessions (days), spaced 1–3 days apart (participants who showed no co-articulation by the ninth session were given six additional practice sessions in order to explore whether they would subsequently co-articulate). A training session was composed of 15–20 training blocks, each of 20 trials. Participants were placed in a supine posture on a bed and looked through a double mirror system at the workspace (digitizing table) (Fig. 1A). The digitizing table (Wacom Intuos; 616×446×37 mm, resolution 100 ppi, maximum data rate 200 pps, accuracy ±0.25 mm) was mounted on the scaffold above the participant's hip level in the vertical plane at a convenient distance for the subject to reach the table with a pen (cordless, 13 g weight). A convenient drawing distance was further guaranteed by adjusting the height of the digitizing table for each subject individually. To minimize shoulder movements and prevent head movements a head restraint was used. In order to minimize friction, targets (black crosses of 10×10 mm) were printed on commercial transparencies that were attached to the surface of the digitizing table. Digital data were streamed to computer disk for offline analysis.

The task consisted of a sequence of point-to-point movements for which participants were asked to connect four target points (ABCDA) with their dominant hand, "as rapidly and as accurately as possible", upon hearing an auditory cue (tone).

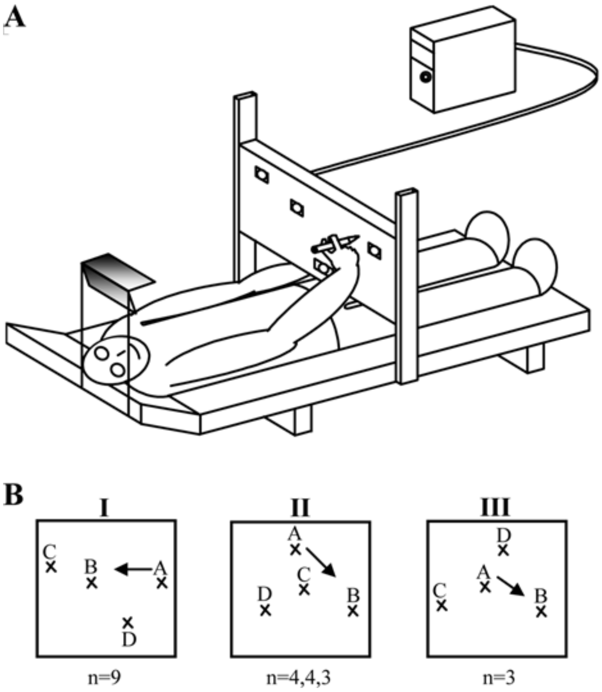

Fig. 1 **A** Experimental set-up. **B** Target configurations. *Arrows* depict movement direction

Participants were separated into three groups that practiced different target configurations, denoted I, II and III (Fig. 1B). Each participant practiced only one target configuration. Nine participants trained on target configuration I, which had two pairs of highly spatially co-aligned segments ($\overline{AB}$;$\overline{BC}$ and $\overline{CD}$;$\overline{DA}$). Eleven participants trained on target configuration II, which had just one pair of highly spatially co-aligned segments ($\overline{BC}$;$\overline{CD}$). Three participants trained on target configuration III, which had none.

Each of the eleven participants who practiced target configuration II was tested for the ability to transfer the performance gain to other training conditions (transfer experiments). The transfer conditions tested were: changing the starting and ending points, reversing movement direction, performance on size-scaled configurations, and performance on a partial configuration. Each transfer condition consisted of one training block (20 trials). The eleven participants were separated into three groups. Four participants performed the transfer conditions only in the first and last training session. Four participants were tested on the transfer conditions immediately after a single block of the trained condition, at the beginning of every training session. A control group, of three participants, practiced only the transfer conditions (one block per session) for seven training sessions.

Global planning model

The actual data was compared with the predictions of the minimum jerk model (Flash and Hogan 1985). The minimum jerk model assumes that given a starting point, end-point and one or more via-points (the position in the path where a local minimum velocity is attained, corresponding to the point of local maximum curvature), the system preplans an entire hand trajectory that passes through all these points with the smoothest possible (minimum jerk) trajectory. The objective cost function (Cost) to be minimized is the square of the magnitude of the jerk (rate of change of acceleration) of the hand integrated over the entire movement.

$$\text{Cost} = \frac{1}{2} * \int_0^{t_f} \left(\left(\frac{d^3x}{dt^3} \right)^2 + \left(\frac{d^3y}{dt^3} \right)^2 \right) dt$$

where x and y are the Cartesian coordinates, and t_f is movement duration. The model output is the position coordinates for each time bin. The model also predicts that the durations of individual parts of the trajectory are dictated by the locations of the start point, end point and the via-point position, and are not independently specified (Flash et al. 1992). In our study, it was assumed that repeated practice leads to the global minimization of jerk, and therefore the curved trajectories that have emerged were modeled by deriving the end-point locations for these strokes from the data and by assuming that the via-point corresponds to the point of minimum velocity [which was found in our data to always correspond to the point of local maximum curvature (see also Jacobs et al. 2003)]. This was done similarly to the approach used by Flash and Hogan (1985) to model obstacle-avoidance movements whereby the via-point location did not correspond to any actual target but was inferred from the data. As in the Flash and Hogan (1985) study, no velocity constraints were imposed at the via-points in the current paper.

With the assumption that neighboring segments were co-planned, the "global-planning" model was applied to a single pair of movement elements in configuration II ($\overline{BC}$;$\overline{CD}$) and to two pairs of movement elements in configuration I ($\overline{AB}$;$\overline{BC}$ and $\overline{CD}$;$\overline{DA}$) (Fig. 1B) assuming a single via-point for each pair.

For configuration I, we also tested a more "global" variation of the model, which included the use of three via-points for describing the entire task—the four segment trajectory (from point A through targets B, C, D and back to A); these attempts did not produce satisfactory results as far as the match between the predictions to the model and the actual data. Hence, the results for two pairs of successive movement segments ($\overline{ABC}$ and $\overline{CDA}$) are separately described.

The study was approved by the WIS Ethics Committee.

Results

Evolution of co-articulated trajectories

There were very robust changes in performance as a function of practice in all participants. Figure 2 depicts representative paths of target configuration I from days 1 and 5 of training for one representative participant. Hand paths generated during a block of trials at a late training stage (day 5) were clearly longer and more curved than those generated early on in training (day 1). Figure 3A depicts the evolution of typical hand trajectories in an individual training on target configuration I. On day 1, the four targets were connected with four straight paths, each generated with a bell-shaped velocity profile (Fig. 3A, *Day 1*). However, following 3 days of practice, the trajectories connecting the first and second pairs of segments ($\overline{AB}$;$\overline{BC}$ and $\overline{CD}$;$\overline{DA}$, respectively) became partially curvilinear with double-peaked velocity profiles. The complete stops at targets B and D were abolished (Fig. 3A, *Day 3*). By the end of the fifth training day, the prototypical straight paths disappeared and two curved paths have emerged, the first with a bell-shaped velocity profile and the second with a double-peaked velocity profile (Fig. 3A, *Day 5*). Seven participants (of nine) who practiced this target configuration replaced the straight paths by curved ones by the end of the ninth training day. We extend the term co-articulation for designating the emergence of such curved movement elements. Co-articulation was characterized by an average decrease of 57% in total movement duration as opposed to the two non-co-articulating participants who decreased their total movement duration only by 41%. Participants co-articulated when there was a relatively high degree of co-alignment between the lines connecting consecutive target pairs (e.g., $\overline{AB}$ and $\overline{BC}$ or $\overline{CD}$ and $\overline{DA}$), but did not co-articulate when there was a relatively low spatial alignment (e.g., $\overline{BC}$ and $\overline{CD}$). No co-articulation occurred when participants practiced target configuration III with a relatively low alignment between the lines connecting all consecutive target pairs (Fig. 3B). In the latter case, the average total movement duration decreased only by 37%. Thus, the acquisition of the co-articulation movement strategy, which was configuration dependent, was accompanied by increased reduction in movement duration (Table 1).

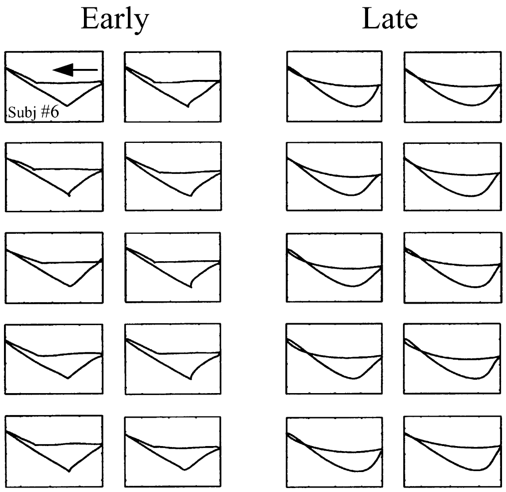

Fig. 2 Representative trials from the first (*Early*) and last (*Late*) training blocks. The *left* ten plots and the *right* ten plots depict trajectories generated in the first training day and last training day, respectively. *Arrow* indicates movement direction

Via-point position, isochronicity index and the global-planning model

The transition from discrete prototypical segments (four straight hand-paths, each with a bell- shaped velocity

Table 1 Dependency of the reduction in total movement duration on the acquisition of co-articulation motion strategy

	Subject	First block (mean ±SD)	Last block (mean ±SD)	Mean decrease (%)
Configuration I				
Co-articulating	1	2.52±0.45	0.87±0.05	65.4
	2	2.09±0.18	1.12±0.12	46.4
	3	1.85±0.15	1.01±0.05	45.4
	4	2.32±0.22	0.92±0.06	60.3
	6	1.95±0.15	0.90±0.04	53.6
	7	1.82±0.12	0.93±0.07	48.6
	9	2.65±0.54	0.52±0.02	80.1
Non-co-articulating	5	2.3±0.16	1.33±0.18	42.2
	8	2.76±0.45	1.63±0.12	40.8
Configuration III				
Non-co-articulating	14	1.36±0.12	0.85±0.03	37.5
	15	1.45±0.16	0.86±0.05	40.6
	16	1.41±0.16	0.88±0.05	37.5

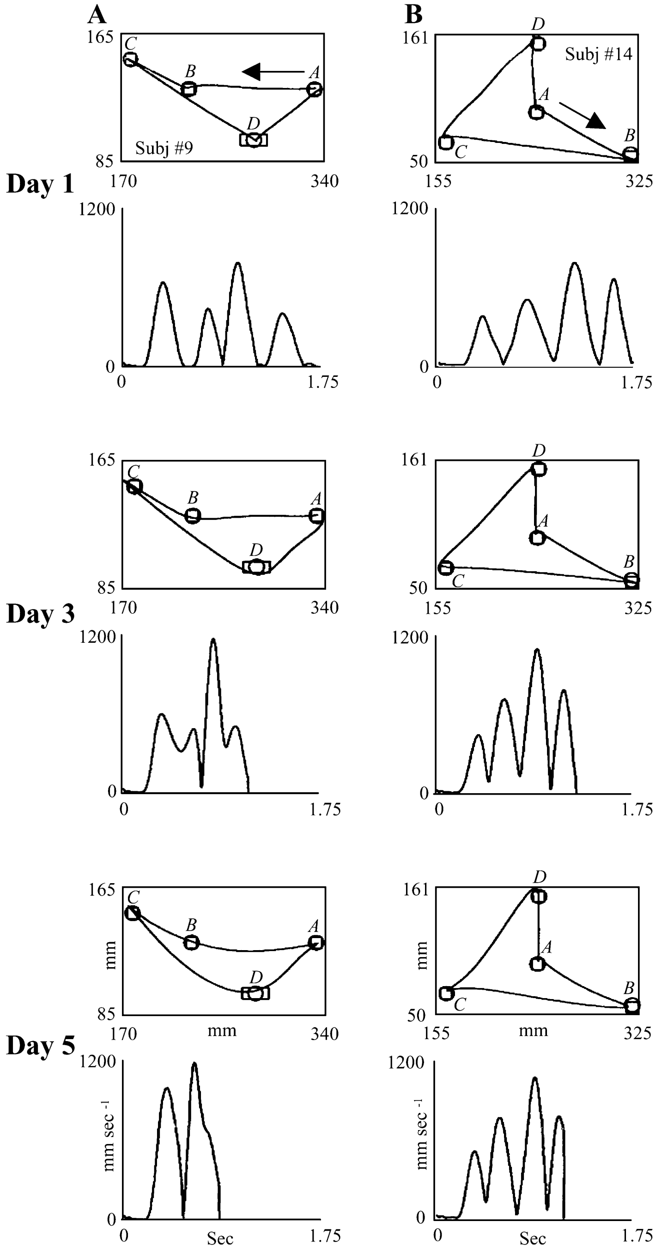

Fig. 3A, B The dependence of co-articulation on the spatial co-alignment between the lines connecting consecutive target pairs. **A** Relatively high spatial alignment (obtuse angle) between the lines connecting target pairs $\overline{AB}$ and $\overline{BC}$, or $\overline{CD}$ and $\overline{DA}$. For each training day, *upper* and *lower* plots denote trajectories and velocity profiles, respectively. **B** Relatively low spatial alignment (acute angle) between the lines connecting all consecutive target pairs (notations as in **A**). No co-articulation evolved throughout training

profile) to co-articulated ones (two curved paths, with their respective velocity profiles) suggested that participants were planning the first and last pairs of segments each in its entirety (global-planning). To test this conjecture we tested the fit between the predictions of the minimum jerk model and actual performance data. The minimum jerk model predicts that for a movement with a given start and end position and one via-point, the durations of the motion from the initial position to the via-point (t1) and from the via-point to the final position (t2) are roughly equal, except for cases in which the via-point is very close to either one of the two movement end-points (Flash and Hogan 1985). The latter observation was referred to as the isochrony principle (Viviani and Terzuolo 1982)—the phenomenon that movement durations of large and small segments of a trajectory are roughly equal. For such a two-segment sequence an isochronicity index can be derived by dividing the first segment duration (t1) by the total duration of the two segments (t1+t2.) In the case of isochronicity the value of the index will be 0.5.

We looked at the evolving changes in both the position of the via-point and in the isochronicity index throughout practice. In the first training day, when participants connected the four targets with four straight paths, the first via-point was found to lie on the first target (target B) (Fig. 4A, *Day 1* left panel) with marked isochronicity between the first two segments (isochronicity index 0.536), i.e., each of the two segments, although having a different length, was generated within a roughly equal movement duration (Fig. 4A, *Day 1* right panel). At day 2, a semi-curvilinear path was generated between target pairs $\overline{AB}$ and $\overline{BC}$. The via-point location (i.e., minimum velocity) gradually shifted from target B toward target C, thus no longer coinciding with the location of target B (Fig. 4A, *Day 2* left panel), and the isochronicity between the two movement segments was lost (isochronicity index of 0.645) (Fig. 4A, *Day 2* right panel). Thus, more time was devoted to the movement between point A and the via-point than to the movement from the via-point to target C. By the third day of practice, targets A, B and C were connected with a curved path $\overline{ABC}$ (Fig. 4A, *Day 3* left panel), the via-point position shifted further towards target C and the isochronicity index increased to 0.689 (Fig. 4A, lower right panel).

The model predicts that the two segments should have roughly equal durations except when the via-point is quite close to the initial or final targets (Fig. 4B). We tested whether the measured values of the isochronicity index followed the trend dictated by the minimum jerk model according to the location of the via-point, i.e., according to the value of the ratio of distances (d1/d1+d2) (see Fig. 4B for the definitions of d1 and d2). This analysis has shown that on the second training day, when the first via-point began shifting toward the second target (target C), the measured isochronicity index did not match the minimum jerk model's predicted value of the ratio of distances (Fig. 4B, lower panel). On the following days of training, however, a closer match between the predicted and measured values of the isochronicity index was obtained, and the variance of the data around the model's predicted curve decreased. The fit to the model's predicted curve improved with practice, and was almost perfect by day 5, suggesting that with progressive training, participants' performance converged on a strategy of movement fluency as reflected by the minimum jerk model. In contrast, there was no change, throughout training, in the position of the second via-point (which resided on target D). The difference in the behavior of these two via-points during training presumably relates to the fact that the angle between segments $\overline{CD}$ and $\overline{DA}$ (point D position) was too acute, enforcing a significant slowing down at point D and preventing a shift in the via-point position.

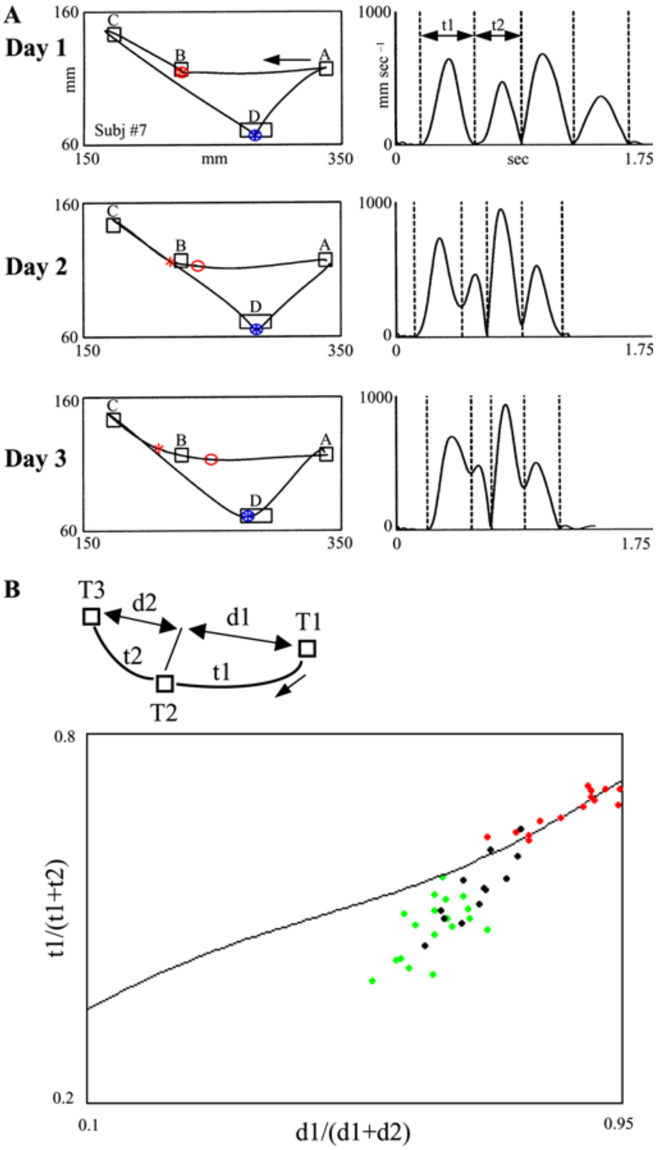

Fig. 4A, B Via-point position and isochronicity index as possible indicators of the learning stages. **A** *Left panels* represent hand paths. *Red* and *blue circles* denote isochronicity positions for the first and second pairs of segments, respectively. *Red* and *blue asterisks* denote the positions of the first and second via-points, respectively. *Right panels* represent velocity profiles. *Dashed vertical lines* denote time points where minimum velocities were attained, with *t1* and *t2* denoting the first and second segment durations, respectively, computed from minimum to minimum velocity. **B** Measured versus predicted isochronicity index for different via-point positions throughout training. In *upper panel*, movement end-points (*T1* and *T3*) are connected by a straight line. The perpendicular to this line, which passes through the via-point (*T2*), is drawn—dividing the line connecting the two end-points into two segments of length *d1* and *d2*. *Lower panel* represents a plot of predicted *t1/(t1+t2)* versus *d1/(d1+d2)* (*solid line*). Superimposed are measured t1/(t1+t2) values, with *green*, *black* and *red dots* representing measured values from the second, third and fifth training days, respectively

Altogether, our data show that isochronicity, characterizing the initial performance on the two segments $\overline{AB};\overline{BC}$, was breaking down as the via-point was shifting toward target C, as predicted by the minimum-jerk model.

The model's predicted trajectories

As the task required the generation of the complete set of trajectories on each trial, to what degree were neighboring segments co-planned? Figure 5A depicts the qualitative fit between typical actual trajectories and the global planning model's predicted trajectories (assuming that neighboring segments were co-planned) for target configuration I for different training days. The model's fit to the data was poor on day 1 suggesting that participants did not connect targets A, B and C with a smooth trajectory. Rather, the two segments were planned independently, each as a straight path with a bell-shaped velocity profile (Fig. 5A, *Day 1*). The model's fit to the data, however, improved from day 1 to day 3, with an almost perfect fit by day 8, indicating that the trajectories became smoother with practice (Fig. 5A, *Days 3–8*). The same qualitative results were attained from participants training on target configuration II (Fig. 5B), again indicating that participants switched from independently planning two straight trajectories ($\overline{BC}$ and $\overline{CD}$) to a smooth curved trajectory ($\overline{BCD}$). Figure 5C,D quantitatively depicts the difference between the model's prediction and the actual data, for both path and velocity, for target configurations I and II, respectively, for each block throughout training. The fit of the model's predicted trajectory to the data increased substantially from day 1 to day 3 ($p<0.01$, two-tailed *t*-test), and continued to increase from day 3 to day 5 ($p<0.05$, two-tailed *t*-test), although at a decreased rate. There was no significant change in the model's fit to the data between day 5 and day 8 ($p>0.1$, two-tailed *t*-test), indicating that learning attained an asymptote, whereas the magnitude of the standard deviation of the errors between the data and the model's predictions continued to decrease, indicating that participants continued to converge on the novel movement strategy. There was a significant change in the model's fit to the data between the first and last training session for all co-articulating participants (Fig. 6A). The two participants who practiced target configuration I and did not co-articulate (i.e., continued to generate a series of straight paths between the consecutive segment pairs) showed no significant change in the data's fit to the model between days 1 and 8 ($p>0.1$, two-tailed *t*-test), indicating no implementation of a global planning strategy even in the highly co-aligned pairs of segments (Fig. 6B). There was also no significant change in the model's fit to the data for the three non-co-articulating participants who practiced the relatively low alignment target configuration III.

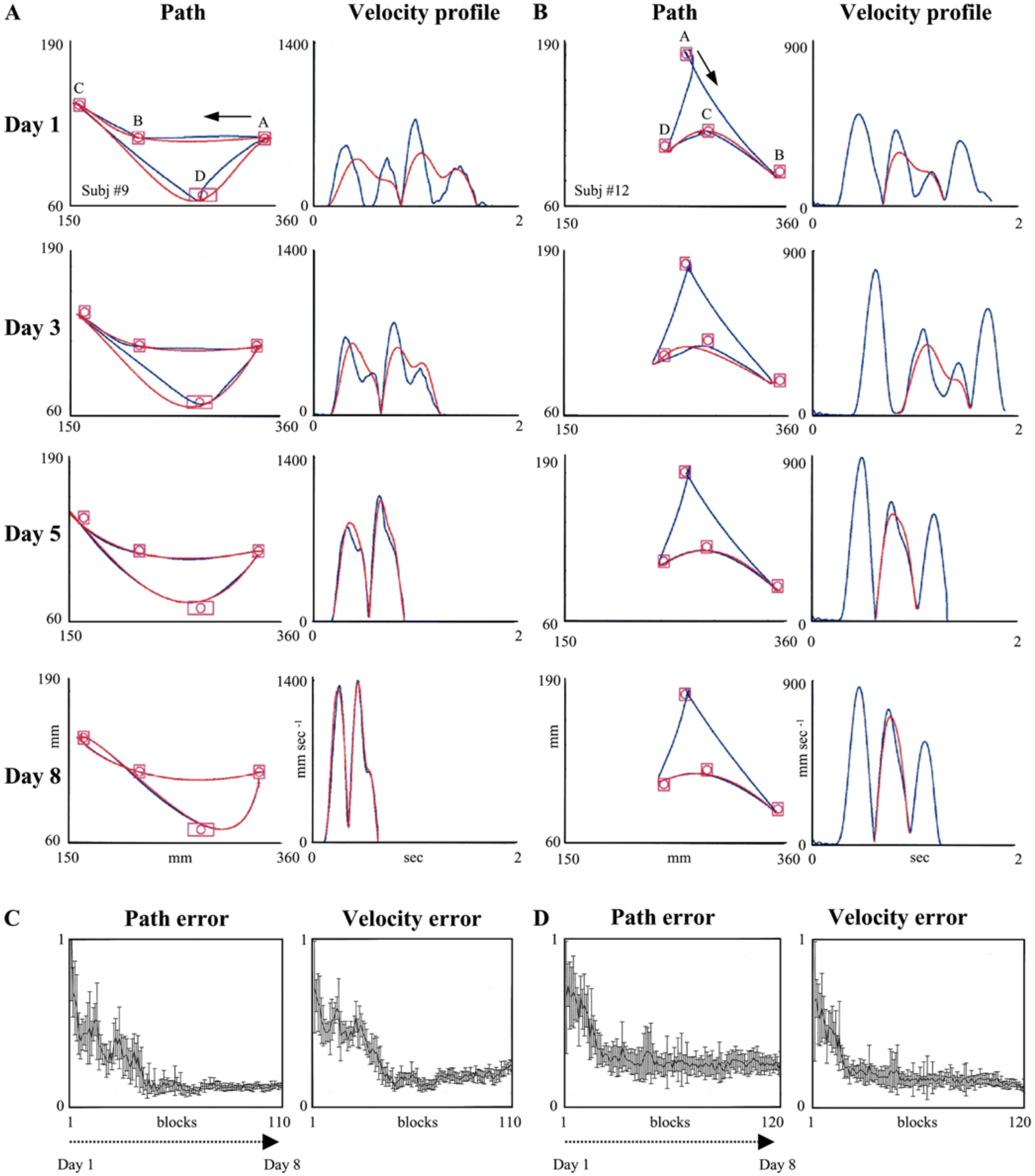

Fig. 5A–D Global planning model predictions versus measured data. **A, B** Two different target configurations (I and II) are shown. *Left* and *right panels* depict path and velocity profiles, respectively, for one representative participant (of seven) who co-articulated. *Red* and *blue curves* indicate model predicted and actual trajectories, respectively. **C, D** Error assessment for model versus measured data. The model's fit to the data was estimated by comparing both the normalized path area difference (area between the measured path and the model's predicted path divided by the measured path length) and the normalized velocity area difference (area between the measured velocity profile and the model's predicted velocity profile divided by the area under the measured velocity curve). For each target configuration, *left* and *right panels* depict the path and velocity mean (±SD) errors, respectively, for every training block. Errors were normalized by the maximum error

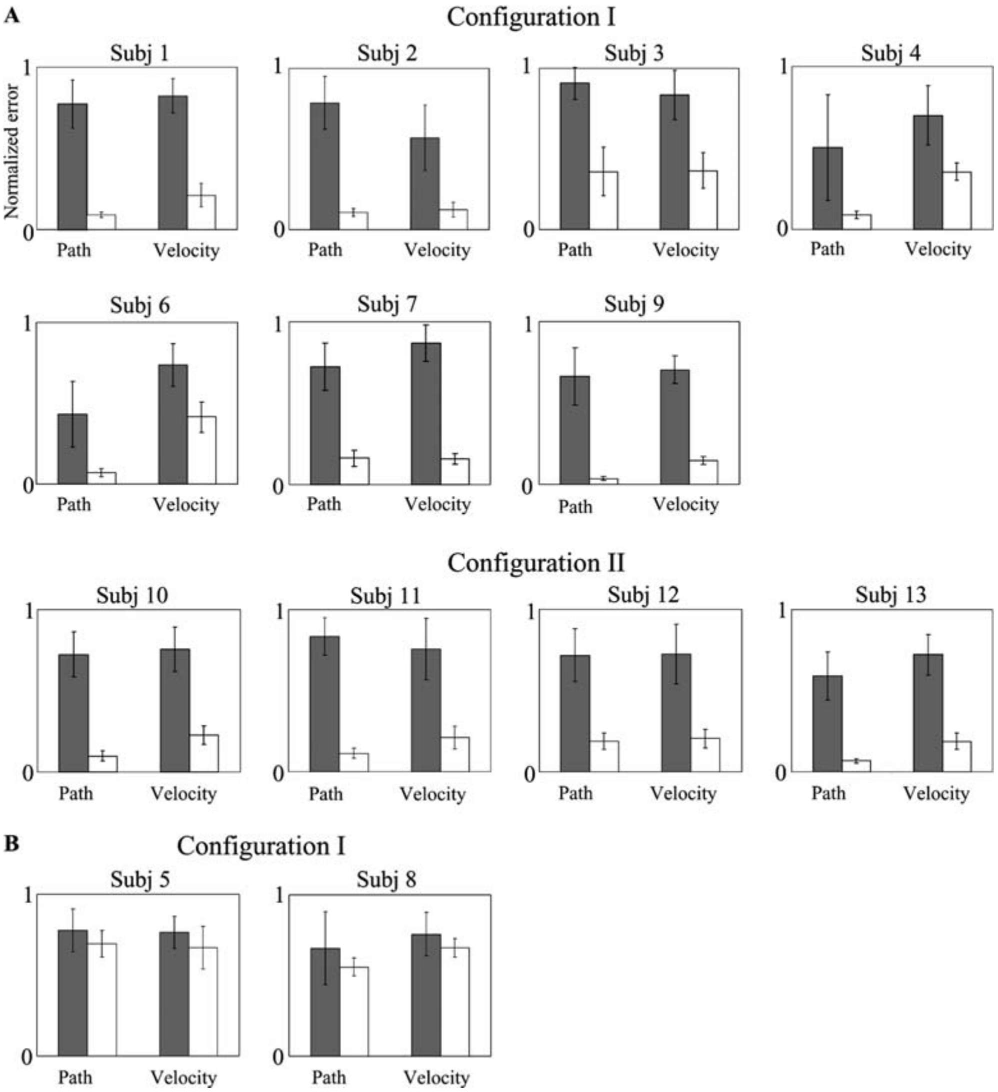

Fig. 6A, B Model's fit to the data for all participants. **A** Co-articulating participants. **B** Non-co-articulating participants. In each panel, the *left pair* of bargraphs depict the error between predicted and actual path; the *right pair* of bargraphs depict the error between predicted and actual velocity. *Filled bars* represent first training block, first training day; *Open bars* represent last training block, final training day

Position variance

Another possible indicator for the progress of learning with training (learning stage indicator) may be position variance. On day 1, participants generated stereotyped straight point-to-point movements (Fig. 7A, *Day 1* left panel) and had a total of four points at which the position variance reached either a maximum or minimum (Fig. 7A, *Day 1* inset). The maximum variance positions were found to reside between the targets (red ellipses in Fig. 7A), whereas the minimum variance positions were located on the targets (*Day 1* right panel). At day 3, participants did not reach full co-articulation and the path was semi-curvilinear (Fig. 7A, *Day 3* left panel). As can be seen (Fig. 7, *Day 3* right panel), the position variance represented an intermediate stage between the stereotyped point-to-point movements of day 1, and the fully co-articulated curvilinear movement generated at day 8. The first minimum variance ellipse did not reside on target B but was shifted towards target C, in relation to the shift in the via-point location (Fig. 4), indicating that the via-point was the location wherein maximal accuracy was imposed on. By training day 8, participants co-articulated the two segment pairs ($\overline{ABC}$ and $\overline{CDA}$) (Fig. 7, *Day 8* left panel) and had two maximum and minimum variance points (Fig. 7, *Day 8* inset). The maximum variance position of the first new co-articulated segment (segment $\overline{ABC}$) was found to reside on target B (wherein previously minimum variance was attained), whereas the minimum variance position resided on target C (Fig. 7, *Day 8* right panel).

The change in the position variance configuration was correlated with the implementation of the co-articulation motion strategy. For two (of nine) participants who did not co-articulate by the end of training, no change took place in the location of the points at which the position variance

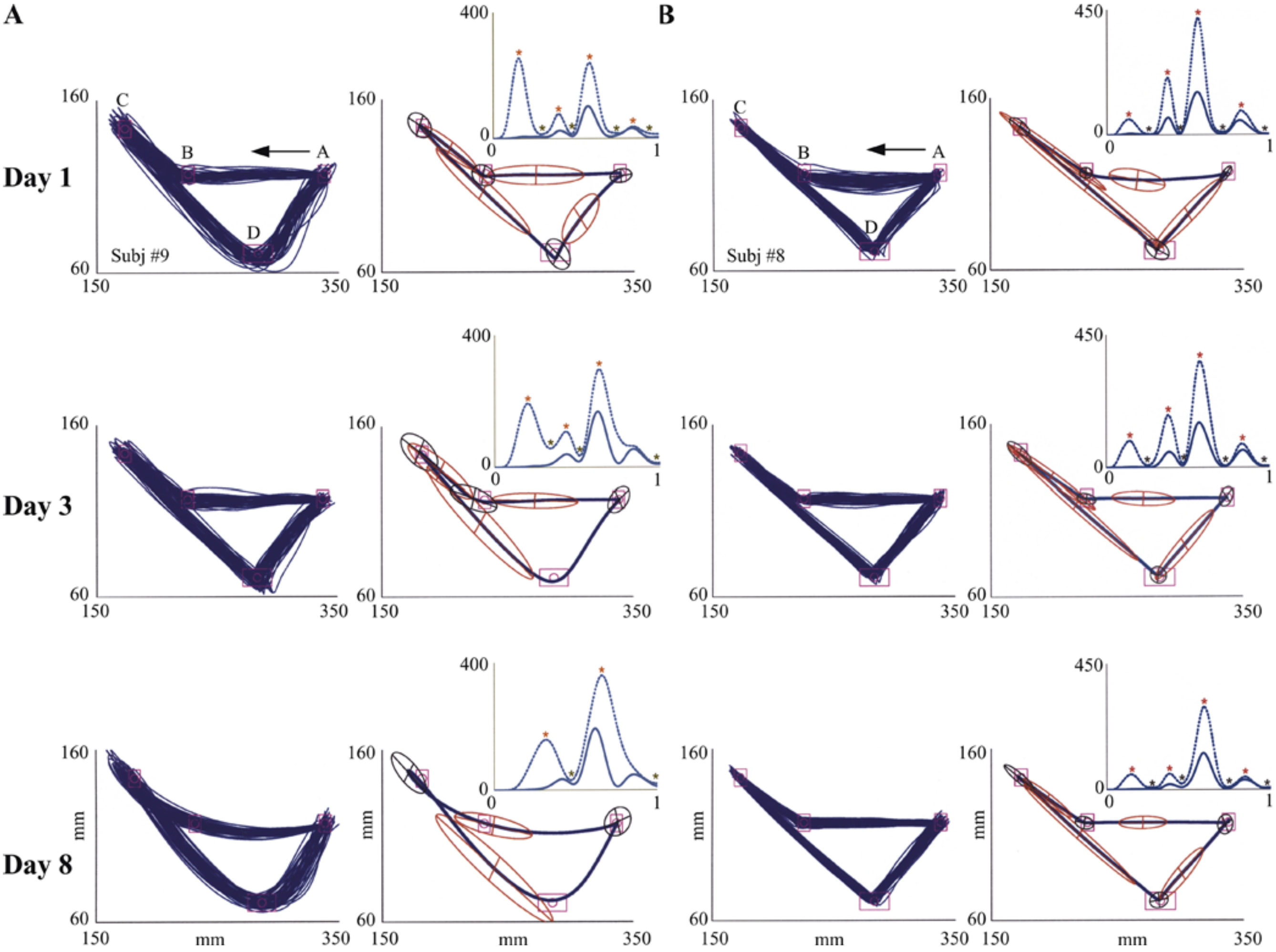

Fig. 7A, B Position variance as a possible indicator for learning stages. **A** Co-articulating, and **B** non-co-articulating representative participants. *Left panels* represent trajectories of the first training block (20 trials) in the day. In *right panels*, for each training block, all the trajectories were duration normalized by the trajectory with the longest duration in the block. Duration normalization was done separately for the *x* and *y* components of the velocity profile (Vx and Vy) for each trajectory. The normalized paths were constructed from the normalized Vx and Vy velocity profiles, and later *x* and *y* variances were computed for every time bin. Principal component analysis (PCA)-derived position ellipses were computed at time bins where maximum or minimum position variances were found. *Blue curve* denotes average trajectory. *Red* and *black ellipses* denote 95% of maximum and minimum position variance, respectively. In *insets*, *x-axis* is normalized duration, *y-axis* is variance, and *dotted lines* and *solid lines* represent *x*- and *y*- position variances, respectively. *Red asterisks* indicate maximum position variance; *black asterisks* indicate minimum position variance

reached either maxima or minima, and these subjects continued to generate four straight point-to-point movements throughout training (Fig. 7B, left panels). These participants had four maximum and minimum positions variance points throughout training (Fig. 7B insets), which resided between the targets and on the targets, respectively (Fig. 7B, right panels). When comparing the area of the variance ellipses in the first training day to the last training day, it was found that the area of the minimum variance ellipses ("on-target" accuracy) decreased by an average of 10%, while the area of the maximum variance ellipses ("inter-target" accuracy) decreased by an average of 30%. Thus, participants managed to increase their movement velocity and decrease their movement duration by 41% (Fig. 3) while substantially reducing inter-target position variance. They did not however reach the next performance stage, co-articulation.

Transfer experiments

The ability to generalize the new trajectories to novel conditions was also tested. The underlying rationale for this approach is that one can infer which task features are learned and under what conditions the task is regarded as new by comparing performance gains under different transfer conditions. Figure 8 depicts novel task conditions for which performance gains (co-articulation) attained in the trained condition were retained. Four (of the four participants tested) generated trajectories similar to those attained by the end of training (ABCDA) in all of the following conditions:

1. When they were asked to start from a different target point (*BCDAB* in Fig. 8, left upper panel)

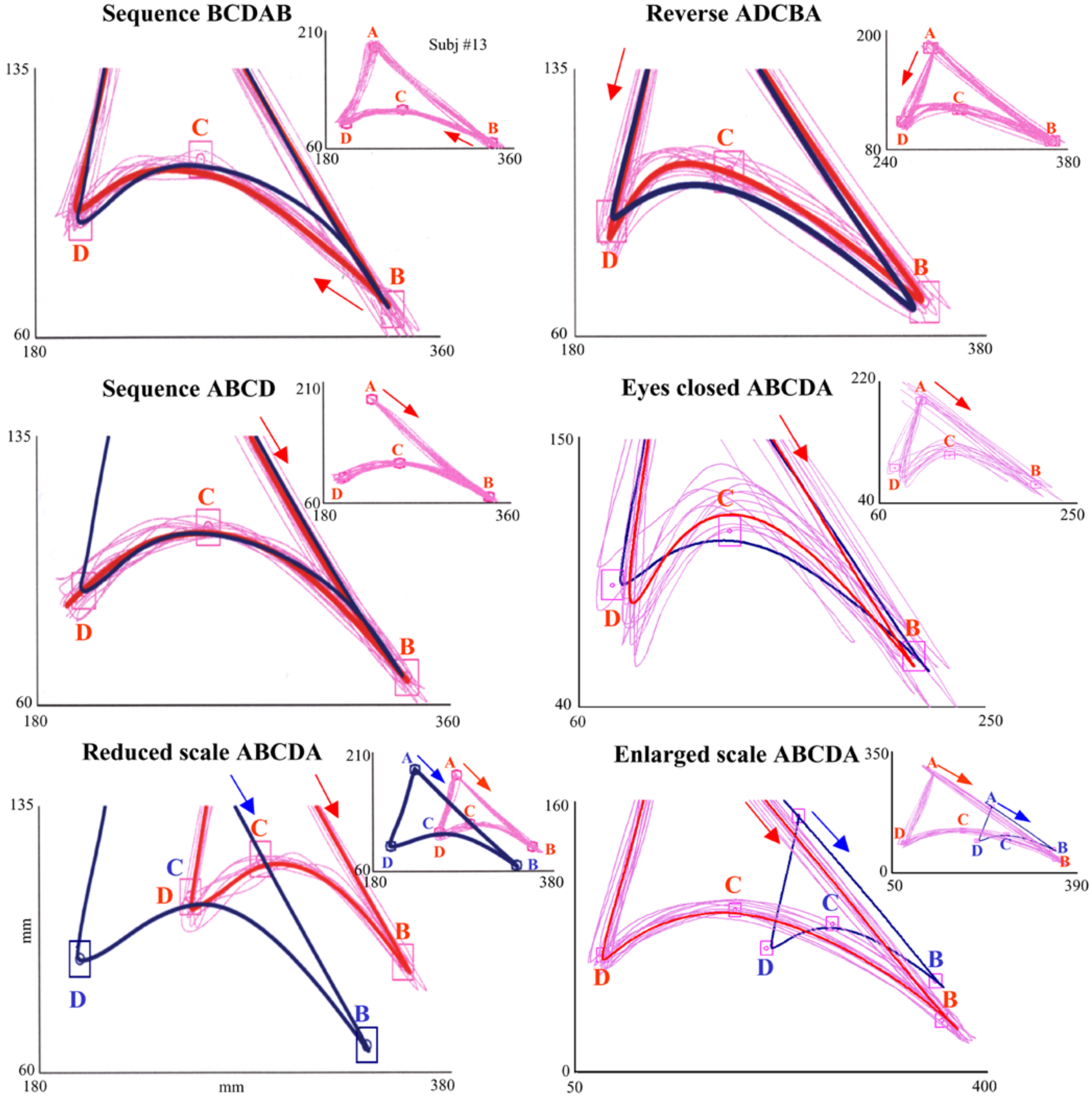

Fig. 8 Paths generated in the transfer conditions. *Insets* represent trajectories of 20 transfer trials (*pink*). *Red arrows* depict movement starting position and direction. *Main panels* show zoom-in on the lower half of the target configuration. *Pink curves* represent transfer trajectories, *red curves* average transfer trajectory, *blue curves* average training trajectory from the same day transfer was measured (ABCDA target configuration). Transfer conditions: *Sequence BCDAB* different start and end points, *Reverse ADCBA* reversed movement direction, *Sequence ABCD* a partial configuration performance; *Eyes closed ABCDA* trained sequence with eyes closed, *Reduced scale ABCDA* and *Enlarged scale ABCDA* are size-scaled trained target configuration

2. When asked to reverse movement direction (*Reverse ADCBA* in Fig. 8, right upper panel)
3. When asked to perform on a partial configuration (*Sequence ABCD* in Fig. 8, left middle panel)
4. When asked to perform with their eyes closed (*Eyes closed* in Fig. 8, right middle panel) or under size scaling conditions (bottom panels *Reduced scale* and *Enlarged scale*)

Surprisingly, in configuration ABC (Fig. 9A, *Sequence ABC*), participants generated a curved path between targets B and C rather than connecting them with a straight path, as was expected. Similarly, even in the CDABC configuration (Fig. 9A, *Sequence CDABC*), participants were generating a curved path between C and D and between B and C, although one would have expected them to generate straight paths because segments CD and BC were not produced consecutively in time (Fig. 9B). All the participants behaved in a similar manner (Fig. 9C). Quantitative comparisons of the paths generated in the training and transfer conditions in the first and last blocks (comparing the area between each path and the average transfer path) has shown that the shape of the paths were significantly affected by performance time (first or last block) but not by the task condition (training or transfer)

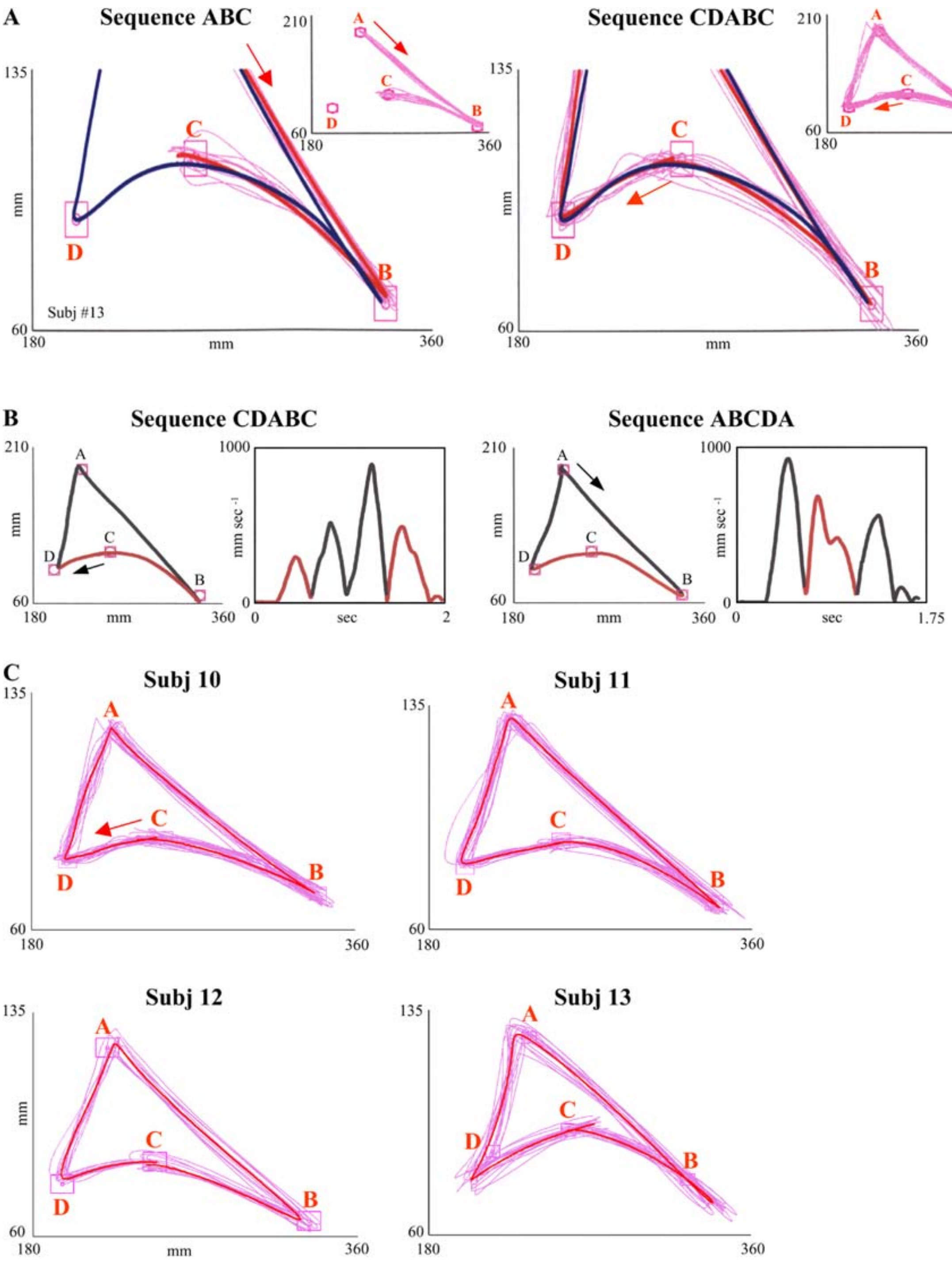

Fig. 9A–C The emergence of geometrical “primitives”. **A** Typical transfer paths. *Insets*: trajectories of 20 transfer trials (*pink*). *Red arrow* movement starting position and direction. *Main panels* show zoom-in on the lower half of the target configuration. *Color-coding* as in Fig. 8. Participants continued to generate a curved path between targets C and D (configuration CDABC) and between B and C (configuration CDABC and configuration ABC), indicating the acquisition of a geometrical primitive. **B** Curved path in neighboring segments in temporally non-consecutive execution. *Two leftmost panels* represent transfer sequence CDABC. *Two rightmost panels* represent training sequence ABCDA. For each series of targets, the path is shown to the left of the velocity profile. *Red lines* indicate segments of path and velocity for which participants generated a curved path. **C** Transfer trajectories (*pink curves*) and average transfer trajectory (*red curves*) for each of the four participants (final training day)

($p<0.01$ and $p>0.1$, respectively, two-way ANOVA). The paths generated in the CDABC and ABC transfer conditions were not significantly different from the co-articulated curves attained during the last training block but were significantly different from those attained during the first training block ($p>0.1$ and $p<0.001$, respectively, Sheffé post hoc test). Thus, the results suggest that participants have acquired a geometrically defined movement element. Indeed, it seems that this primitive was geometrically (or even abstractly) represented in a scalable and a direction invariant manner. The data do not however support the notion that the new movement element corresponded to specific temporal and spatial muscle activation pattern (as evidenced by the *Reverse ADCBA* configuration for which participants attained co-articulated curved paths although the generation of these movements required altered muscle activation patterns compared with those developed on training).

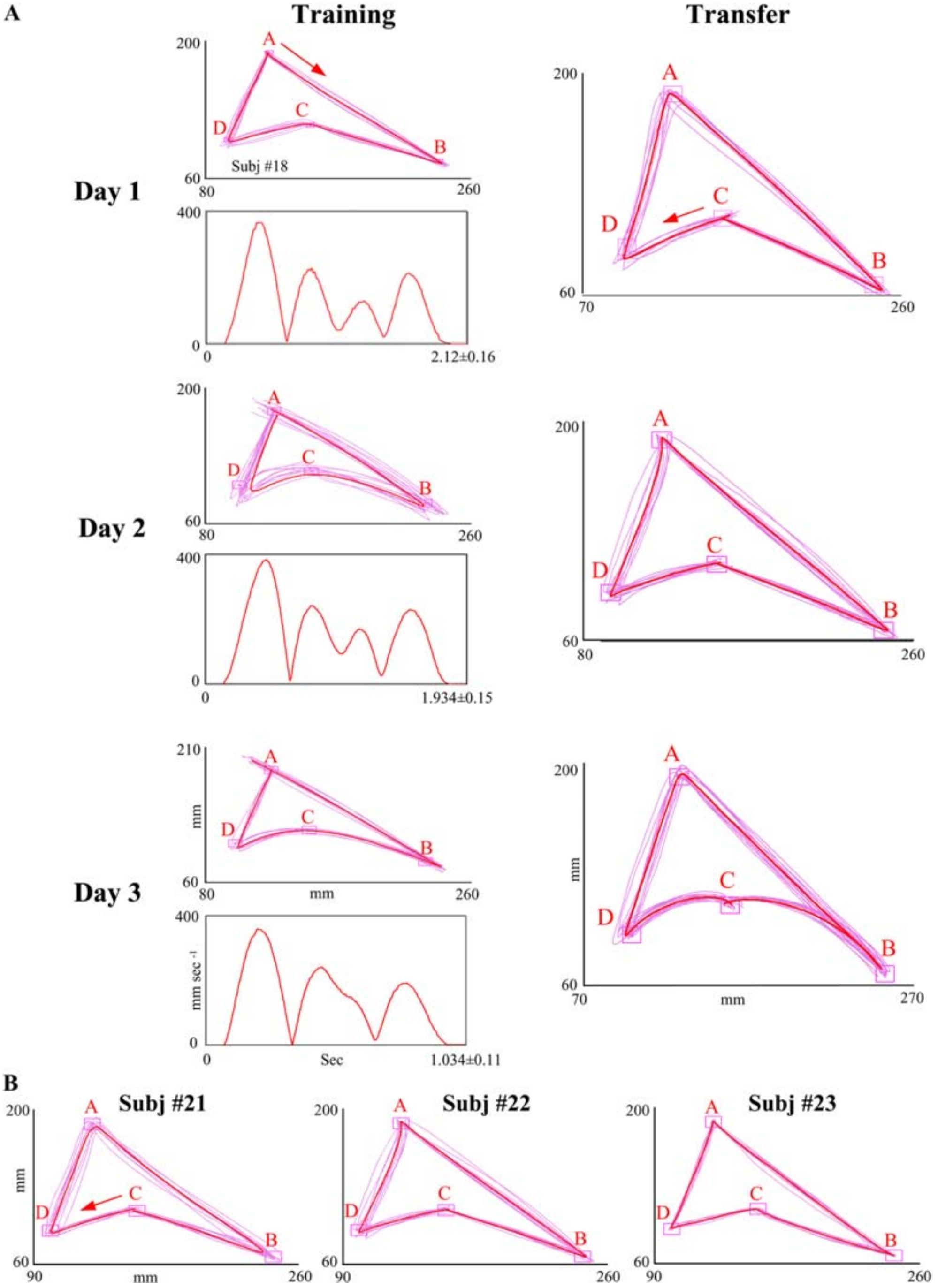

Fig. 10A, B The evolution of the geometrical "primitive". **A** Training trajectories and transfer trajectories, generated in the same training day, for one representative participant. For each training day, the *upper left plot* denotes 20 training paths (*pink*) and average training path (*red*); *lower left plot* denotes average velocity profile. The *rightmost plots* denote 20 transfer paths (*pink*) and average transfer path (*red*). **B** Transfer paths of three participants who practiced for 7 days only the transfer condition (single block each day)

In an attempt to test whether the new curved geometrical movement element was acquired at a specific learning stage, we tested four participants who were given training on configuration II to perform a transfer condition (sequence CDABC) in each training session (see Materials and methods section). In the first training day, participants generated four straight point-to-point movements with bell-shaped velocity profiles for the trained condition (Fig. 10A, *Day 1 Training*). These straight paths were not significantly different from those executed in the transfer condition (p>0.1) (Fig. 10A, *Day1 Transfer*). The global-planning model's fit to the data was poor (0.81±0.09 and 0.78±0.11 for path and velocity normalized errors, respectively). On training day 2, participants generated curved paths for the trained condition and the velocity profiles were double-peaked (Fig. 10A, *Day 2 Training*). However, the paths generated in the transfer condition, were straight and did not resemble those generated in the trained condition (p<0.05; Fig. 10A, *Day 2 Transfer*). The model's fit to the data improved but was still poor (0.36 ±0.03 and 0.52±0.06 for path and velocity normalized errors, respectively). On training day 3, participants fully co-articulated the two segments ($\overline{BC}$ and $\overline{CD}$) and generated curved paths (Fig. 10A, *Day 3 Training*) and the model's fit to the data improved implying that the two segments were globally planned (0.17±0.01 and 0.29±0.03 for path and velocity normalized errors, respectively). The paths generated in the transfer condition resembled the training paths (p>0.1) (Fig. 10A, *Day 3 Transfer*). All the participants behaved in a similar manner (Table 2). A control group of three subjects who practiced every day only on the transfer condition (only one training block) did not show any deviation from the prototypical straight trajectories (Fig. 10B). Thus, our findings suggest that the evolution of the curved path in the transfer condition was dependent on the (amount of) training in the trained condition. Moreover, the curved movement element (stroke) could not be implemented in the transfer condition, although it was in effect in the trained condition (day 2); rather, this could occur only after the global planning strategy was implemented for the trained condition (day 3).

Transfer of the skilled (co-articulated) movements, however, was not universal. In the configuration *Reverse CBA* of Fig. 11 (left panel), the path generated between targets C and B was straight, even though it was curved in the ABC configuration. Direction reversal alone could not explain the difference between the paths generated in the Reverse CBA and ABC conditions because paths in the ABCDA and Reverse ADCBA conditions were both curved. Assuming that the applicability of a learned movement path is context specific, changing several movement attributes at a time (new starting and ending positions and reversing the movement direction) may have caused the task to be regarded as a novel one resulting in the lack of implementation of the previously learned movement element.

Table 2 Test results of the significance between training trajectories and transfer trajectories (generated in the same day) for each participant

Subject	Training day				
	1	2	3	4	5
17	ns	*	**	ns	ns
18	ns	*	ns	ns	ns
19	ns	ns	**	ns	ns
20	ns	ns	*	ns	ns

*p<0.05, **p<0.01, *ns* not significant (two-tailed t-test)

There was also no transfer of the new trajectories to the untrained hand (Fig. 11, *Contralateral ABCDA*) suggesting that the newly acquired movement elements were effector-specific as was previously shown in both monkeys and humans (Hikosaka et al. 1995; Karni et al. 1995; Rand et al. 1998; Bapi et al. 2000) for different skilled movements. This finding is nevertheless puzzling if one considers the newly acquired movement primitives to be represented in terms of a geometrical path.

Discussion

Taken together, our results support the notion that motor planning as well as motor execution can be modulated to a large degree by experience, i.e., undergo a qualitative, rather than just a quantitative, change as a function of practice. We show that practice can lead to the co-articulation of consecutive segments of a given sequence of planar movements, generated between a series of target points. Moreover, we show that the outcome of prolonged training can be a novel, curved, trajectory, which although corresponding to a longer path, affords smooth and rapid performance with no loss in accuracy and which is effectively transferable to several untrained (transfer) conditions.

Our results suggest that different levels of performance may be associated with different internal representations of the task, and specifically, that new movement primitives, i.e., strokes, can evolve in the adult motor system as a result of prolonged practice on a sequence of movements. With accumulated experience, a qualitative change may occur in motor planning: from the generation of a sequence of individually planned component movements to the generation of globally planned movement units providing a highly effective solution to the challenge imposed by the double requirement to move "as rapidly and as accurately as possible" by affording reduced movement time and end-point variance. Rather than generating a complex movement sequence by combining existing, basic, movement elements, we show that adults have an effective means to achieve skilled motor fluency, through the addition of new movement elements to the basic movement vocabulary. Thus, we propose that a profound hierarchical change can occur in motor planning: from syntax dependent performance, to unitary (modular) globally planned movement. Depending on the operational definition of co-articulation, one may either consider this latter outcome (the replacement of two movements by a single new stroke) as a step superceding co-articulation or as the final stage of co-articulation.

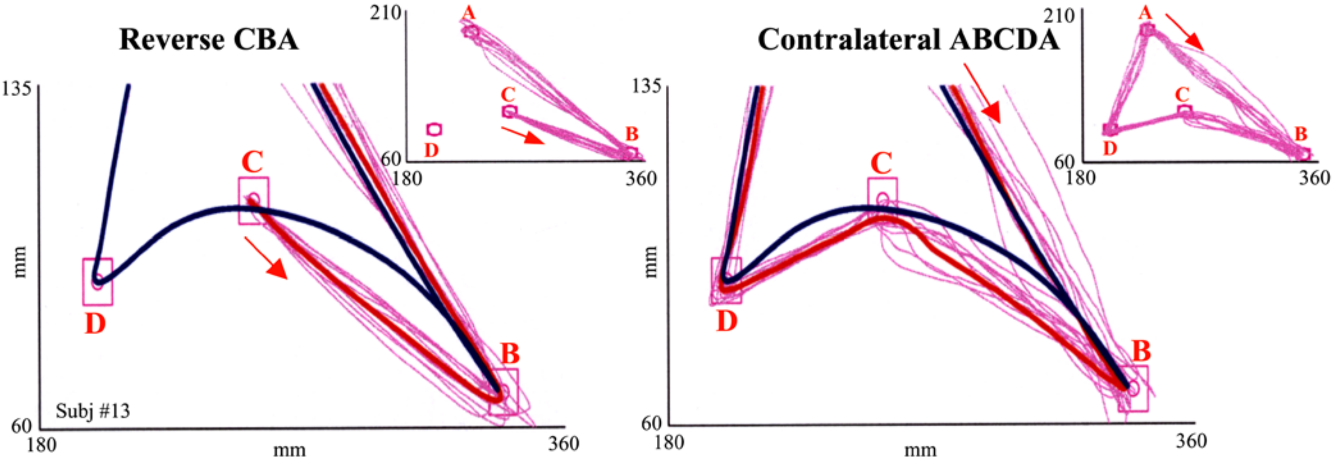

Fig. 11 Non-transfer conditions. *Reverse CBA* denotes no transfer to partial configuration with reversed movement direction; *Contralateral ABCDA* represents the trained sequence with the contralateral hand. *Color-coding* as in Fig. 8. The paths were not significantly different from those generated in the first training block and were significantly different from those generated in the last training block ($p>0.1$ and $p<0.001$, respectively, two-tailed t-test)

Learning stage indicators

The chronometric analysis clearly showed that, at initial stages of task performance, participants spent equal time on each individual segment of the sequence (isochronicity). Given that isochronicity, the metronome-like pacing of movement, indicates what the system considers to be independent segments, one might explain the loss of isochronicity when co-articulation develops as an indication that the system no longer regards the original segments as independent ones. Thus, the isochronicity of the naïve state was progressively lost, up to the moment when the two original segments completely co-articulated into a new unit that, from then on, was counted as a single entity within the context of the task. We propose that the isochronicity index and the via-point position can serve as indicators for the nature of the movement planning strategies and/or the internal representations of the component segments within the sequence. The possibility to identify a via-point and the gradual shift in its position suggest a transition from the planning of a series of separate straight point-to-point movements to that of co-articulated and more globally planned meta-segments.

Another possible indicator for the change in the task's internal representation might be path variance. It was previously shown that participants increase path variance between targets in order to reduce position errors when passing through the targets (Todorov and Jordan 2002). This was accounted for by the "minimum intervention" theory, based on stochastic optimal feedback control. Similarly, Wolpert and Harris have shown that in the presence of signal-dependent noise, the shape of an arm trajectory is selected to minimize the variance of the final position (Wolpert and Harris 1998). Based on an analysis of the path variance during human hand trajectories, Todorov and Jordan (2002) suggested that the motor system aims to decrease position variance errors in places where maximum accuracy is required. Our observations concerning the locations of the points of maximum and minimum position variance may be indicative of the evolving internal representations of the targets and the via-points. Initially, the point of minimal position variance was located on target B. When participants started to co-articulate the first two segments of the sequence ($\overline{AB}$ and $\overline{BC}$) the via-point shifted from target B towards target C, and the position variance was no longer at minimum value at point B (Fig. 7A, *Day 3*). The new location at which the position variance reached a minimum was found to lie between targets B and C, in relation to the via-point location—indicating that point C and the via point were the locations wherein maximal accuracy was imposed on. Thus, with practice, participants seemed to be switching their aim from point B to a point between B and C, and thus no longer regarding point B as the "real" target. The change in the position variance configuration was correlated with the implementation of the co-articulated movement strategy. For participants who did not co-articulate, no change was found in the location of the points at which the position variance reached either maxima or minima throughout training, and these subjects continued to generate four straight point-to-point movements (Fig. 7B, left panels).

Curved versus straight paths

It was previously shown that when participants were asked either to move through an externally specified via-point or to avoid an obstacle, with no specific instructions concerning movement speed and/or accuracy, a curved trajectory was promptly and spontaneously generated (Flash and Hogan 1985). In the present study, the participants were instructed to move "as rapidly and as accurately as possible" and initially each and every participant produced straight trajectories. It is reasonable to assume that participants may have been unsure about their ability to meet both the accuracy and speed demands of the task, therefore, the kinematic solution chosen and implemented involved the generation of typical unconstrained point-to-point movements—straight hand paths with bell-shaped velocity profiles. Later on in training, when the end-point variance decreased, a new movement strategy, based on a more globally planned curved trajectory, may have been tested for the benefit of achieving higher movement velocity, thereby decreasing motion duration and resulting in a more smooth, fluent solution. Indeed, participants who switched to using curved trajectories were able to achieve higher gains in speed compared to those who maintained the straight path trajectories. Thus, it seems that the curved path was conducive to effective co-articulation as well as affording gains in both speed and accuracy.

Results to be reported in detail elsewhere (R. Sosnik, B. Hauptmann, T. Flash and A. Karni, unpublished data) suggest that relaxing the requirement for accuracy resulted in participants' achievement of curved co-articulated movements following significantly less practice, and vice versa, i.e., increasing the demands for accuracy made co-articulation the more difficult to attain. Nevertheless, even explicit instructions to perform the appropriate curved trajectories were ineffective in naïve subjects indicating that a critical amount of actual practice was necessary.

Geometrical movement primitives

The attributes of the newly acquired, co-articulated, movement elements seemed to be solely dictated by the geometrical shape of the path, rather than by both the path geometry and its dependent velocity profile. As shown in Fig. 9B, in the transfer test, participants generated a curved path for both neighboring segments that were not produced consecutively in time, although the velocity profile clearly indicated separate planning of the two segments. The transferred movement element was therefore a specifically shaped path, which was even executed with eyes closed. However, as can be seen in Fig. 10, the curved path could be transferred to novel conditions only after a global planning strategy was effectively applied to the trained condition. Hence, the spatial attributes of a given task (the spatial configuration of the targets in the current task) may have dictated the characteristics of the newly acquired strokes. While relatively few studies have addressed the question of whether geometrical and time-dependent kinematic attributes (i.e., velocity, acceleration) of movement are separately represented, there are some indications that this may be the case in the context of drawing movements (Viviani and Flash 1995) and of three-dimensional reaching movements (Torres and Zipser 2000). Our results support this notion and suggest that the attributes of the newly acquired co-articulated trajectory strokes seem to be dictated solely by the figural (i.e., geometrical) form of the path, rather than by both path geometry and its temporal-dependent velocity profile.

The finding that changing some task parameters or more than one movement parameter at a time (Fig. 11, *Reversed CBA*) resulted in reversion to the naïve, straight trajectories from the new, learned, trajectories indicates that the gained expertise (skilled performance) was *context* specific, i.e., strongly related to the specific attributes of the trained task. Thus, the generation of the novel acquired motion primitive in a new task configuration may depend on whether the new configuration was considered as a variation of the trained task by the motor system and perhaps reflect the ability to achieve non-degraded movement accuracy in the new task condition. Moreover, participants could not generate the new movement elements with the untrained hand, indicating that the products of extensive practice—the new curved movement elements, were *effector (hand)* specific. There are several indications from human and monkey studies that skilled motor sequences may be retained in long-term memory in an effector-dependent (lateralized) representation (e.g., Karni et al. 1995, 1998; Nudo et al. 1996; Hikosaka et al. 1999). The reversion to straight point-to-point trajectories on switching to the (non-dominant) untrained hand, clearly shown in the current study, can be explained as reflecting an attempt to achieve end-point accuracy with the untrained hand when, because the benefits of training were unavailable, the movement outcome could not be well predicted.

Optimization of sequence performance

Our global-planning model was based on the assumption that the motor system aims to maximize movement smoothness, which was equated with the minimization of the hand jerk. The fact that the trajectories generated following prolonged practice were well accounted for by the minimum-jerk model indicates that the maximization of movement smoothness might be a leading parameter optimized by repeated experience. Further work, however, is needed for identifying the underlying contributions of end-point variance constraints and effort for the increase in motion smoothness (Wolpert and Harris 1998; Todorov and Jordan 2002).

We do not believe that the term co-articulation should be confined to just simple addition or superposition of successive segments of a given sequence of movement (superposition) (Flash and Henis 1991). Our results support the notion that, with extensive experience, a new "movement element" can be generated and added to the basic movement repertoire of the adult motor system. We propose that these new elements (strokes) could be very different from the sum of the elements that initially comprised the sequence of movements, yet constitute an effective (or perhaps a more effective) means to perform the task at hand. They are a possible final product of a series of distinct, successive shifts in the internal representation of a sequence of movements as experience accumulates.

The finding that a new geometrical motion primitive, i.e., a stroke, is only learned after the system has reached optimal performance as dictated by the "global optimization" strategy, may indicate that the emergence of geometrical movement primitives is a byproduct of co-articulation—replacing different segments of a sequence by a tailor-made single unit in terms of motor planning. Thus, we propose that the working definition of co-articulation be extended to include the replacement of two (or more) consecutive basic movement units by an effective (in terms of task constraints) alternative movement unit. This new basic movement element can be conceptualized as a stroke. It does not abolish the previously available strokes but rather can be conceptualized as an additional module or unit especially suited for a specific set of task conditions and task contexts. This movement module may obviate the need for generating the target sequence of movements through the application of elaborate syntactic rules by the evolution of a basic primitive, which embodies the syntax for combining pairs or more of the movement elements comprising the sequence. Moreover, our results indicate that the new module may be of the nature of a "geometrical primitive"—a specific path that embodies the optimization of movement smoothness.

Altogether, our findings suggest that the perfection of performance with practice, which we suggest is equivalent to the optimization of a cost function, may lead to the emergence of new, versatile movement primitives that substitute for discrete movement elements. The evolution of these movement primitives, or strokes, may constitute the final product of a multi-stage process associated with qualitative changes in the internal representation of the task. These acquired strokes, may constitute an important substrate of motor memory for the skilled performance of motor sequences.

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