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RESEARCH ARTICLE

The acquisition and implementation of the smoothness maximization motion strategy is dependent on spatial accuracy demands

Ronen Sosnik · Tamar Flash · Bjoern Hauptmann · Avi Karni

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Abstract We recently showed 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) (Sosnik et al. in Exp Brain Res 156(4):422–438, 2004). Reduction in movement duration was accompanied by the gradual replacing of a piecewise combination of rectilinear trajectories with a single, longer curved one, the latter affording the maximization of movement smoothness (“global motion planning”). The results from transfer experiments, conducted by the end of the last training session, have suggested that the participants have acquired movement elements whose attributes were solely dictated by the figural (i.e., geometrical) form of the path, rather than by both path geometry and its time derivatives. Here we show that the acquired movement generation strategy (“global motion planning”) was not specific to the trained configuration or total movement duration. Performance gain (i.e., movement smoothness, defined by the fit of the data to the behavior, predicted by the “global planning” model) transferred to non-trained configurations in which the targets were spatially co-aligned or when participants were instructed to perform the task in a definite amount of time. Surprisingly, stringent accuracy demands, in transfer conditions, resulted not only in an increased movement duration but also in reverting to the straight trajectories (loss of co-articulation), implying that the performance gain was dependent on accuracy constraints. Only 28.5% of the participants (two out of seven) who were trained in the absence of visual feedback from the hand (dark condition) co-articulated by the end of the last training session compared to 75% (six out of eight) who were trained in the light, and none of them has acquired a geometrical motion primitive. Furthermore, six naïve participants who trained in dark condition on large size targets have all co-articulated by the end of the last training session, still, none of them has acquired a geometrical motion primitive. Taken together, our results indicate that the acquisition of a geometrical motion primitive is dependent on the existence of visual feedback from the hand and that the implementation of the smoothness-maximization motion strategy is dependent on spatial accuracy demands. These findings imply that the specific features of the training experience (i.e., temporal or spatial task demands) determine the attributes of an acquired motion planning strategy and primitive.

Keywords Co-articulation · Motion primitives · Visual feedback · Spatial accuracy

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R. Sosnik (✉) · T. Flash
Weizmann Institute of Science, Rehovot 71600, Israel
e-mail: ronen.sosnik@weizmann.ac.il

B. Hauptmann
Department of Neurology, Charité, 10098 Berlin, Germany

A. Karni
The Brain, Behavior Research Center, University of Haifa,
Mt. Carmel 31905, Israel

Present Address:
B. Hauptmann
Neurological Centre, Segeberger Kliniken, Hamdorfer Weg,
323795 Bad Segeberg, Germany

Introduction

A well-known phenomenon in the motor behavior of adult humans and non-human primates is their tendency to generate straight paths when reaching toward visual targets in a two-dimensional plane (Morasso and Mussa-Ivaldi 1982; Flash and Hogan 1985). The prototypical straight paths are generated with a single-peaked, bell-shaped velocity profile and are invariant to rotation, translation, amplitude and time 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). The tendency to gradually return to the generation of straight paths after dynamic perturbations (Flash and Gurevich 1992; Shadmehr and Mussa-Ivaldi 1994) or the application of optical distortions (Flanagan and Rao 1995; Wolpert et al. 1995; Ghahramani and Wolpert 1997) implied that the paths are planned in extrinsic coordinates and might be implemented later by brain circuits that code movements in intrinsic coordinates. The invariants of the movements expressed in terms of extrinsic coordinates have led to the notion that straight paths are basic elements (primitives) that might serve as building blocks for the generation of more complex movements. It was shown that complex movements can be generated by combining together basic elements, not all necessarily straight (e.g., by superposition) (Flash and Henis 1991; Roher et al. 2002). 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 generation of a basic unit is influenced by the anticipated adjacent unit, resulting in their spatial and temporal overlap, hence, creating a new entity that is different from the sum of the elements which comprise it. This was shown to occur both in speech (Kent and Minifie 1977; MacNeilage 1980; Hardcastle and Marchal 1990; Blackburn and Young 2000), piano playing (Engel et al. 1997), fluent finger spelling and sequence tapping (Jerde et al. 2003; Karni et al. 1998) and recently in sequential drawing-like movements (Sosnik et al. 2004). The latter observation was based on our previous findings (Sosnik et al. 2004) where it was shown that co-articulation evolved slowly throughout training and that a new motion planning strategy was acquired, possibly reflecting a change in the internal representation of the task.

Recent studies on spinalised frogs and rats have suggested that the premotor circuits within the spinal cord are organized into a set of discrete modules. Each module, when activated, induces a specific force field and the simultaneous activation of multiple modules leads to the vectorial combination of the corresponding fields (Santello et al. 1998; Mussa-Ivaldi and Bizzi 2000; Bizzi et al. 2000; Saltiel et al. 2001; d'Avella et al. 2003; Weiss and Flanders 2004). Moreover, the non-linearity of muscles (their low-pass filtering properties) and the spinal reflex loop have been suggested to play a major role in generating the observed smooth bell shaped speed profiles (Gribble et al. 1998; Karniel and Inbar 1997, 1999; Krylow and Rymer 1997).

It was previously shown that hand trajectories of infants in their first year of life are jerky and are composed of many accelerative/decelerative strokes (Hofsten 1991; Konczak et al. 1995; Berthier 1996) but with motor development and practice, the movements become smoother. Studies in subjects that underwent hemiplegic stroke have also shown that following the stroke the patients reverted to generating jerky movements which could be decomposed into separate units (sub movements) (Krebs et al. 1999). These findings imply that these high-level and low-level basic elements are not hard-wired from birth but instead may evolve as a solution to the problem of redundancy and high dimensionality inherent in the motor system. The primitives being selected and their tuning properties might reflect a learning process that involves optimization, formalized as the minimization of different kinematic and dynamic costs such as total hand jerk (minimum jerk) (Flash and Hogan 1985), muscular energy (Cruse 1986; Alexander 1997), effort (Hasan 1986; Lan 1997), rate of change of joint torques (Uno et al. 1989), kinetic energy (Soechting et al. 1995) and position variance (Harris and Wolpert 1998).

It was suggested that smooth, straight trajectories do not only minimize the total hand jerk of planar hand movements but also minimize the end-point variance of repeated movements generated from one target to another (Harris and Wolpert 1998). This was accounted for by the suggestion that smooth hand movements minimize the signal dependent noise that is inherent in the neural motor commands, and thus increasing the end-point accuracy. The sources of the noise can arise from the planning process (Gordon et al. 1994; McIntyre et al. 1997; Vindras and Viviani 1998; van den Dobbelsteen et al. 2001) or in the course of motor execution (Van Beers et al. 2004). The observation that rapid movements are generated by increased activations of wider pools of motor units may explain the finding that faster movements come at the expense of decreased position accuracy. This phenomenon was described by Fitts law, which formulated the speed-accuracy tradeoff (Fitts 1954). Analysis of the position variance of movements generated between two targets, in participants trained with visual feedback of the arm, has shown that the maximum and minimum position variance was found to reside between and on the targets, respectively (Todorov and Jordan 2002; Sosnik et al. 2004). An explanation for this pattern of variance was based on stochastic optimal control theory arguing that the optimal feedback control laws for typical motor tasks obey a ‘‘minimal intervention’’ principle: deviations from the average trajectory are only corrected if they interfere with the task goals (Todorov and Jordan 2002, 2003).

Movement corrections are based both on visual feedback and on propioceptive information and can be derived by an internal model that calculates predicted hand position from efference copies of motor commands. It was postulated that the internal model generates an error signal that reflects the discrepancy between the on-line and desired future positions (e.g., end-point position). This allows correcting the movement more rapidly without waiting for the delayed information based on feedback. When visual feedback from the hand is absent, as in the dark or while training with the eyes closed, the position variance of the hand was shown to gradually increase with the amplitude of the movement (Messier and Kalaska 1997, 1999). This finding suggests that the information emerging from the visual system may have a central role in the process of reducing the end-point variance in reaching movements towards visual targets.

A recent study (Sosnik et al. 2004) has shown that prolonged training on a drawing-like sequential task (connecting four target points ‘‘as rapidly and as accurately as possible’’ on a digitizing tablet) leads to the co-articulation of consecutive movement segments generated between a series of targets. Moreover, prolonged practice resulted in a novel curved trajectory, which although corresponding to a longer hand path, afforded smooth and rapid performance with no loss in accuracy. This was shown to agree with a model that assumes a motor planning strategy, which is based on the use of globally optimal smooth trajectories (‘‘Global planning’’ model, Sosnik et al. 2004). It was further suggested that the ‘‘global planning’’ strategy leads to the emergence of new, modifiable motion primitives that are used instead of the concatenation of discrete movement elements. The attributes of the newly acquired co-articulated motion primitives seemed to be dictated solely by the geometrical shape of the path, rather than by both path geometry and its time dependent velocity profile, and were termed ‘‘geometrical primitives’’. The emergence of such geometrical motion primitives supported the notion that the shape of the path traveled by the hand and its time dependent kinematic attributes (i.e., velocity, acceleration) are separately represented, as was earlier suggested on the basis of a study of drawing movements (Viviani and Flash 1995) and three-dimensional reaching movements (Torres and Zipser 2002). A recent study focusing on the analysis of monkey scribbling movements revealed the emergence of geometrically identified parabolic strokes, following a period of extensive practice (Polyakov et al. 2001). These findings have indicated the possibility that geometric motion primitives (e.g., parabolic segments) may have a special significance in both motor learning and production. Transfer experiments, which were conducted by the end of the practice experiments and examined the performance of the participants on untrained, large scale configuration, suggested that the implementation of the co-articulation strategy did not rely on whether participants use only their wrist in order to generate the task (as in the training sessions) or whether the entire arm participated in the task (Sosnik et al. 2004). Furthermore, performance gain was transferred to other conditions in which different joint rotations, amplitude or reversals, not previously practiced, were used. However, it was not clear whether the new motion strategy would be implemented when a new target configuration is presented, i.e., to what extent can the performance gain be transferred to unvisited target configurations in which the alignment between consecutive targets is different from the trained configuration.

The finding that co-articulation was correlated with increased reduction in total movement duration (as opposed to participants who did not co-articulate) implied that the new motion planning strategy has evolved as a mean to reduce the total movement duration. In the current experiments, we investigated whether the new motion planning strategy is velocity and/or accuracy dependent, i.e., we tested whether, given the trained target configuration, different accuracy or temporal constraints will result in deterioration in the performance gain accrued in practice. Since it was found that motion smoothness (defined by the fit of the data to the prediction of the minimum-jerk model, Sosnik et al. 2004) could serve as an indicator of the level of skill acquisition, we used this index to assess the performance at the different tested conditions. Finally, we tested whether visual feedback plays a role in the acquisition of the co-articulation movement strategy and whether geometrical motion primitives could evolve in the absence of visual feedback from the moving hand when only the targets are seen.

All the experiments presented in this study were conducted in a sitting posture in front of a table on which there was a digitizing tablet. Some of the experiments that were conducted in the previous study were also repeated in this study in order to verify that the findings were not an artifact of the ‘‘unnatural’’ supine posture.

Materials and methods

Nineteen healthy right-handed individuals (13 males and 6 females, aged 18–42 years) participated in the study. The only criterion used to determine which hand is dominant was the hand they reported using for writing. Participants were trained for 5–8 sessions (days), spaced 1–3 days apart (participants who showed no co-articulation by the fifth session were given three additional practice sessions in order to explore whether they would subsequently co-articulate). A training session was composed of 10–15 training blocks each consisting of 15 trials. There was a 2 s rest between two consecutive trials and 1-min rest between two consecutive blocks. Participants were seated in front of a digitizing tablet (WACOM INTUOS, 616 × 446 × 37 mm, resolution 100 ppi, max. data rate 200 pps, accuracy ± 0.25 mm) and the height of the chair was individually adjusted at a convenient distance for the participants to reach the table with a pen (Cordless, 13 g weight). 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 tablet. Digital data were streamed to computer disk for off-line analysis. Since the sampling rates of the digitizing tablet were irregular and in order to remove the high frequency, small jerky movements caused by physiological tremor, we smoothed the data with a fifth order Butterworth filter, cut off frequency 15 Hz.

The participants were divided into two groups. Six participants practiced in full light conditions whereas thirteen participants trained only in the dark (seven participants training on 10 × 10 mm targets and six participants training on 12 × 12 mm targets). The targets that were used in the dark condition were made of thin fluorescent stickers and placed between two thick commercial transparencies, preventing their detection based on propioceptive cues. The participants who practiced in the dark were unable to see their hand moving throughout the experiment and the tip of the pen was detectable only when it was close to one of the four glowing targets.

The task consisted of a sequence of point-to-point movements where participants were instructed to connect four target points (ABCDA) ‘‘as rapidly and as accurately as possible’’ with their dominant hand. The participants were instructed to begin moving following the hearing of an auditory cue (tone). All participants (i.e., both in the light and in the dark conditions) practiced a target configuration that had one pair of relatively highly spatially co-aligned segments (i.e., obtuse angle in Cartesian coordinates) $\overline{BC}$;$\overline{CD}$ (Fig. 1, configuration I). Each participant was also tested for his/her ability to transfer the acquired performance gain to other target configurations (transfer conditions). The transfer conditions tested were: (a) ‘‘Full mirror translation’’, wherein the targets depicted in target configuration I were transferred to their mirror image locations with respect to the symmetry line (denoted as a dotted line, configuration II), (b) ‘‘Partial mirror translation’’, wherein target C was transferred to its mirror image location (C’) with respect to the symmetry line $\overline{BD}$ (configuration III) and (c) ‘‘90° rotation’’, in which all the targets in target configuration I were clockwise rotated by 90° (configuration IV). Each transfer condition was tested in a single block (15 trials), conducted at the beginning of the first training session and at the end of the last training session.

Participants who practiced in the light condition were tested on the last training day on two additional transfer conditions: a ‘‘strict accuracy’’ task and a ‘‘slow-pace’’ task. In the ‘‘strict accuracy’’ task, participants were instructed to pass through the center of the targets (rather than anywhere within the targets’

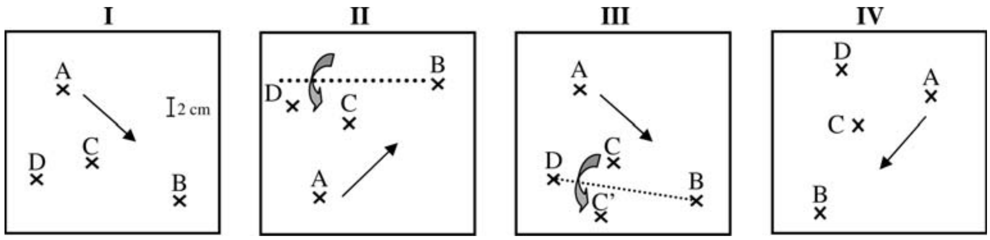


Fig. 1 Target configurations. The *black arrows* depict movement starting position and direction. The *dashed horizontal line* between targets B and D (configurations II and III) depicts the symmetry line. Target C’ (in configurations III) is the image mirror location of target C with respect to the symmetry line $\overline{BD}$

area), thus, increasing the required accuracy demand. In the "slow-pace" task, the participants were allowed to pass anywhere within the targets' area (as in the training condition) but to generate the movements at a pace similar to the average pace in which they generated the "strict accuracy" task. The participants were asked to start moving upon the hearing of a first tone (a "GO" tone) and reach the final target upon the hearing of a second tone (an "END" tone). In order to familiarize them with the new pace the participants were given a preliminary practice block of five trials. Table 1 summarizes the different transfer conditions tested in the light and in the dark in the different training days.

Assessing similarity between paths generated in the training and transfer conditions

In order to test whether the paths generated in the transfer conditions were not significantly different from the paths generated in the training condition the following procedure was performed:

1. The durations of the training paths and the transfer paths were stretched (by spline interpolation) to have a duration of 800 time bins (8 s), which was substantially longer than the trial with the longest duration. Later, the amplitude of each velocity profile was scaled by the ratio of its original duration and the longest duration (in order to prevent deformation of the new path with respect to the actual path**).** This was done separately for the x and y components of the velocity profile (V_x and V_y) for each trajectory.
2. The stretched training paths and transfer paths were constructed (by integration) from the stretched V_x and V_y velocity profiles and an average training path and transfer path were constructed.
3. The area between each normalized training/transfer path and the average normalized training path was computed.
4. The two area distributions were tested for a significant difference in their means (2-tail *t-test*).

Global planning model

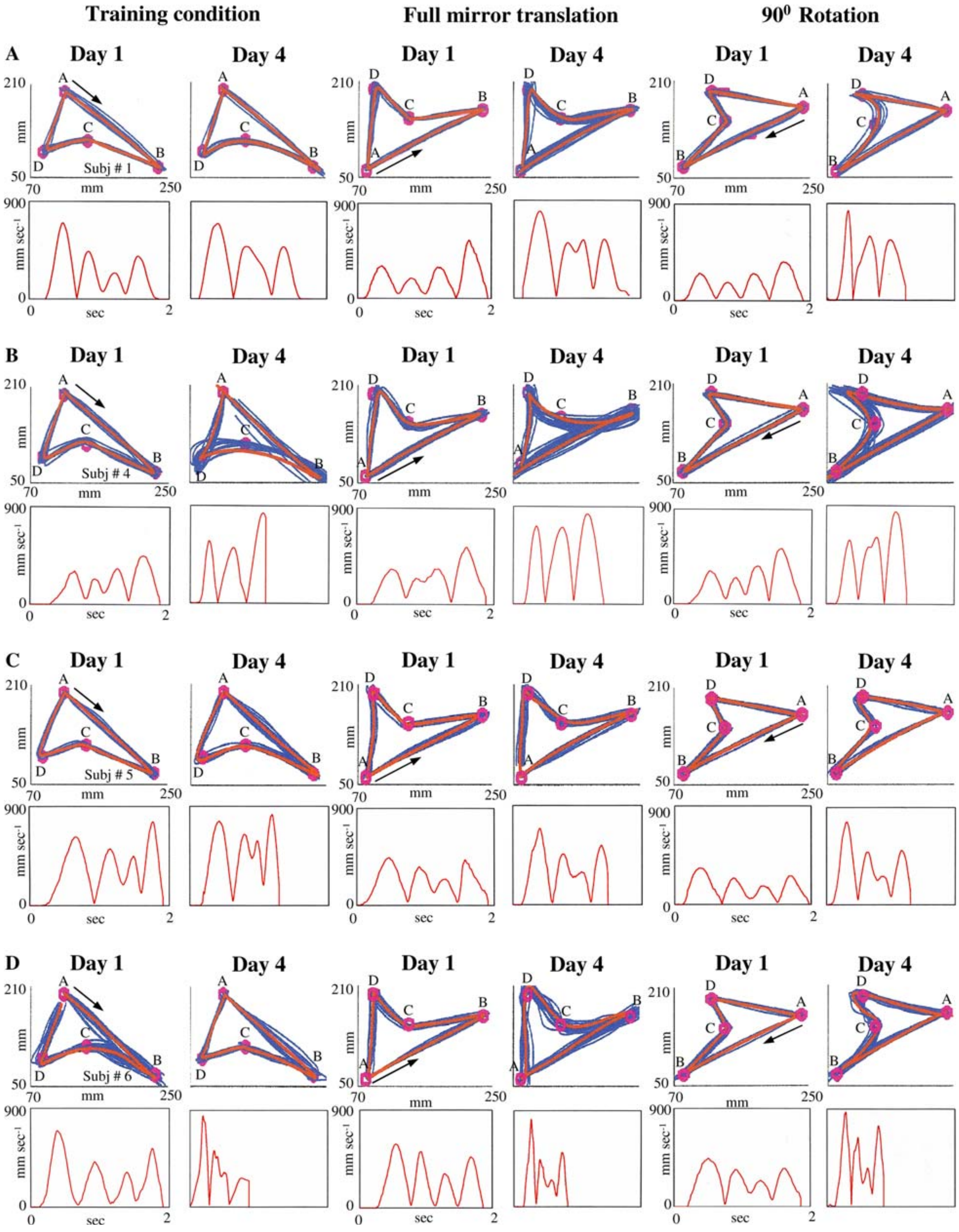
The actual data were compared to the predictions of the minimum jerk model (Flash and Hogan 1985; Sosnik et al. 2004). The minimum jerk model assumes that given a starting point, end-point and one or more via-points (the position in the path where a local minimum velocity is attained, corresponding to 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.

$$\mathrm{Cost} = \frac{1}{2}\int_0^{t_f}\left(\left(\frac{\mathrm{d}^3x}{\mathrm{d}t^3}\right)^2 + \left(\frac{\mathrm{d}^3y}{\mathrm{d}t^3}\right)^2\right)\mathrm{d}t,$$

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

Table 1 Transfer conditions tested in the light and in the dark on different training days. The " + " and "–" signs denote tested and untested conditions, respectively

Tested condition	Day 1	Day 2	Day 3	Day 4	Day 5
Light					
Training ABCDA	+	+	+	+	+
Transfer CDABC	+	+	+	+	+
Transfer 90° rotation ABCDA	+	–	–	–	+
Transfer 90° rotation CDABC	–	–	–	–	+
Transfer full mirror translation ABCDA	+	–	–	–	+
Transfer full mirror translation CDABC	–	–	–	–	+
Strict accuracy task	–	–	–	–	+
Slow pace	–	–	–	–	+
Dark					
Training ABCDA	+	+	+	+	+
Transfer CDABC	+	–	–	–	+
Transfer reverse ADCBA	+	–	–	–	+
Transfer 90° rotation ABCDA	+	–	–	–	+
Transfer full mirror translation ABCDA	+	–	–	–	+



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

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Fig. 2 Performance gain was transferred to other target configurations. **a** Trajectories generated by one representative co-articulating participant. *Upper panels*, paths. *Lower panels*, velocity profiles. The left two panels depict trajectories generated in the first (Day 1) and last (Day 4) training blocks. The *two central panels* and *rightmost panels* depict trajectories generated in the Full mirror translation and the 90° rotation conditions, respectively. The *black arrow* depicts movement starting position and direction. *Blue curves*, training trajectories. *Red curve*, average training trajectory. **b–d** Trajectories generated in the training condition and in the two transfer conditions by the other three co-articulating participants

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 in 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. In the current work, as in Flash and Hogan (1985), no velocity constraints were imposed on the via-point positions.

With the assumption that neighboring segments were co-planned, the "global-planning" model was applied to a single pair of movement elements in configuration I ($\overline{BC}$;$\overline{CD}$) assuming a single via-point.

Results

Light conditions

Performance gain is transferred to untrained target configurations

In order to verify that our previous findings, obtained while lying in a bed, were not an artifact of the "unnatural" posture, we asked six naïve participants to train on a target configuration that was previously trained in the supine posture (Fig. 1, target configuration I) but to generate the task while sitting (see also the Materials and methods section). Figure 2a depicts the evolution of typical hand trajectories of a representative individual training on target configuration I. In day one, the four targets were connected with four straight paths, each generated with a bell-shaped velocity profile (Training condition—Day 1). However, following 4 days of practice, the trajectories connecting segments $\overline{BC}$;$\overline{CD}$ became curved and were generated by a bell-shaped velocity profile (Training condition—Day 4). Four (out of six) participants co-articulated by the end of the last training session. The shapes of the paths were not significantly different from the shapes of the paths obtained on the same target configuration while training in the supine posture ($P < 0.01$) (for the comparison procedure see "Assessment of position variance" in the Materials and methods section). This finding, suggests that the transition from generating straight paths to generating curved, smooth paths was not a by-product of the supine posture.

In order to test whether the performance gain (co-articulation) is configuration specific, the four co-articulating participants were asked to perform on the "Full mirror" configuration and "90° Rotation" configuration both in the first and last training day. In the first training day, the four targets were connected with four straight paths, each generated roughly with a bell-shaped velocity profile (Fig. 2a, "Full mirror translation" and "90° Rotation"—Day 1). However, in the last training day (Day 4), the two highly co-aligned segments $\overline{BC}$;$\overline{CD}$ were co-articulated ("Full mirror translation" and "90° Rotation"—Day 4). The same qualitative findings were obtained for the other three co-articulating participants (Fig. 2b–d). In order to test whether the paths generated in the two transfer conditions were not significantly different from those generated in the training condition we compared the area between each transfer path or training path and the average training path both for the first and last training days. The analysis was done after rotating the paths by 90° (for the "90° Rotation" comparison) or after a vertical flip (for the "Full-mirror translation" comparison), where the imaginary line connecting targets B and D is the symmetry line. The shape of the paths both in the training and transfer conditions was significantly affected by performance time (first or last block) but were not affected by the task condition (training or transfer) (two-way ANOVA, $P < 0.01$ and $P > 0.1$, respectively, for each of the four participants). Thus, the paths generated in the "90° Rotation" configuration and in the "Full mirror translation" configuration were not significantly different from those generated in the training condition in the same day indicating that the newly acquired motion strategy was not configuration specific.

Performance gain is not transferred when strict spatial accuracy demands are imposed

For each of the four co-articulating participants, mean total movement duration in the last training block was significantly shorter than the mean total movement duration observed in the first training block ($P < 0.01$).

Co-articulation was characterized by an average decrease of 26.5% in the total movement duration as opposed to the non co-articulating participants who decreased their average total movement duration only by 13.5%.

In order to study whether the implementation of the new movement strategy is dependent on the total movement duration and/or spatial accuracy demands, we conducted in the last training day a ‘‘strict accuracy’’ task in which the co-articulating participants were asked to connect the four targets ‘‘as rapidly and as accurately as possible’’ while passing through the center of the targets (i.e., being very accurate). Most of the minimum velocity positions (93%) were found to reside within a radius of 2 mm around the targets, i.e., participants generated the ‘‘strict accuracy’’ task successfully. The mean total motion duration in the ‘‘strict accuracy’’ task was longer by 144% than the mean total motion duration in the training condition, generated in the same training day, and it was longer by 77% than the mean motion duration generated in the first training block in the first training day (Table 2). The longer motion durations in the ‘‘strict accuracy’’ condition were well predicted by Fitts’ law ($\mathrm{MT} = a + b \times \mathrm{ID}$, Index of Difficulty) (Fig. 3a).

Surprisingly, performance on the ‘‘strict accuracy’’ task did not result merely in a substantial increase in the movement duration. The co-articulating individuals promptly reverted to generating four straight point-to-point paths that were not significantly different from the paths generated in the first training block ($P > 0.3$, two-tailed t test) (Fig. 3a–d).

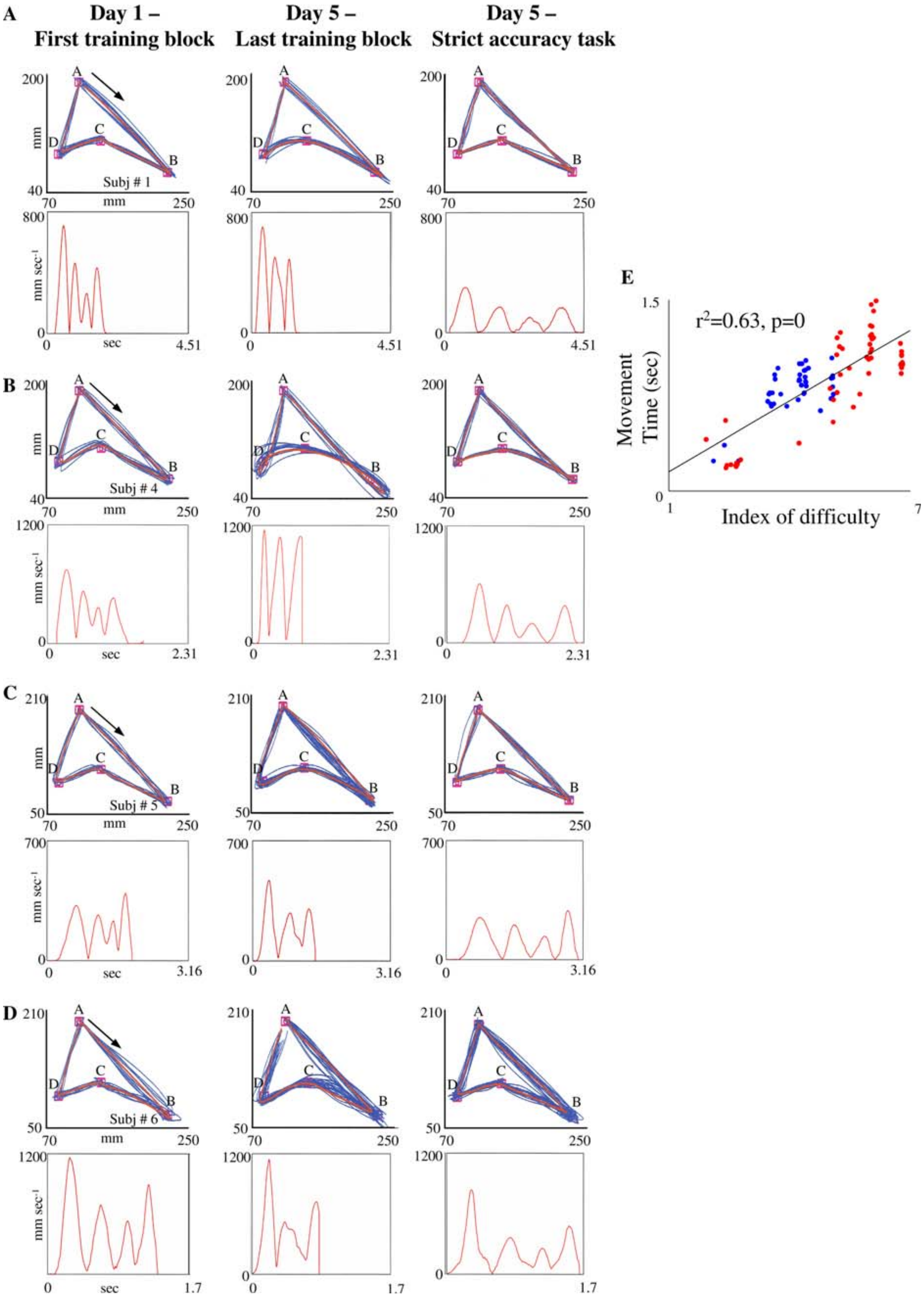
In order to explore whether the shift from the co-articulation motion planning strategy to generating straight paths was caused by the increase in the total movement duration (and reduction in mean motion velocity) we asked the four participants to perform on the over-trained task (i.e., allowing to pass anywhere within the targets’ area) but to generate the task at a slow pace, similar to the pace in which they generated the ‘‘strict accuracy’’ task (i.e., four, two, three and two seconds for the first, second, third and fourth participant, respectively). The total movement durations in which the four participants generated the task (3.99 ± 0.34, 2.21 ± 0.23, 2.93 ± 0.61 and 2.11 ± 0.53 s, respectively) were not significantly different from the instructed total movement durations ($P < 0.05$ for all participants). All the participants co-articulated the segments pair $\overline{\mathrm{BC}}$ and $\overline{\mathrm{CD}}$, although the curved path $\overline{\mathrm{BCD}}$ was jerky, probably due to the slow, unnatural hand movement (Fig. 4). The paths were not significantly different from those generated in the training condition on that day ($P > 0.15$) but were significantly different from the paths generated in the ‘‘strict accuracy’’ task ($P < 0.05$). The finding that participants continued to co-articulate even when a constraint was imposed on the total movement duration suggests that the slipping back to straight paths in the ‘‘strict accuracy’’ task resulted from the stringent spatial accuracy demands.

A geometrical motion primitive is acquired in light conditions whenever the ‘‘global planning’’ motion strategy is implemented

We have previously shown that a geometrical motion primitive of the over-trained target configuration was acquired after the new motion planning strategy (‘‘global planning’’) was implemented (Sosnik et al. 2004, Fig. 10). In order to test whether these findings apply also to the sitting posture we asked the four co-articulating participants to perform on the ‘‘CDABC’’ transfer condition by the end of each training day and compared them to the training trajectories in that day. On the first training day, the paths generated in the training condition (Fig. 5, Day1, Training) were all straight and were not significantly different from those generated in the transfer condition ($P > 0.1$) (Fig. 5, Day1, Transfer). The global-planning model’s fit to the training data was poor (0.77 ± 0.14 and 0.82 ± 0.13 for path and velocity normalized errors, respectively). On the third training day, participants generated curved paths in the trained condition and the velocity profiles were double-peaked (Fig. 5, Day 3, 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. 5, Day 3, Transfer). The model’s fit to the data improved but was still poor (0.48 ± 0.05 and 0.46 ± 0.08 for path and velocity normalized errors, respectively). On training day four,

Table 2 Dependency of total movement duration on spatial accuracy demands. Data are means ± SD (s) obtained from 15 trials in the first and last training blocks and in the ‘‘strict accuracy’’ task

Participant #	First training block (sec)	Last training block (s)	Strict accuracy task (s)
1	1.71 ± 0.15	1.52 ± 0.06	4.51 ± 0.28
4	1.44 ± 0.31	0.88 ± 0.07	2.31 ± 0.20
5	2.02 ± 0.10	1.52 ± 0.04	3.16 ± 0.52
6	1.43 ± 0.17	0.86 ± 0.03	1.70 ± 0.19


A
Day 1 – First training block
Day 5 – Last training block
Day 5 – Strict accuracy task
A
B
C
D
Subj # 1
mm
200
40
70
250
mm sec-1
800
0
sec
4.51
B
Subj # 4
1200
2.31
C
Subj # 5
210
50
700
3.16
D
Subj # 6
1.7
E
r²=0.63, p=0
Movement Time (sec)
1.5
0
1
7
Index of difficulty

◀

Fig. 3 Effect of strict spatial accuracy demands on motion planning strategy. **a–d** For each participant, the *upper panels* and the *lower panels* depict paths and velocity profiles, respectively. The *blue curves* and the *red curve* depict training paths and average training path, respectively. **e** Movement time versus Index of Difficulty. The *blue dots* and *red dots* denote readings from the first training session and the "strict accuracy" task, respectively. The longer total movement durations in the "strict accuracy" task are well predicted by Fitts' law

participants fully co-articulated segments $\overline{BC}$ and $\overline{CD}$ in the trained condition (Fig. 5, Day 4, Training) and the model's fit to the data improved implying that the two segments were globally planned (0.21 ± 0.03 and 0.24 ± 0.02 for path and velocity normalized errors, respectively). The paths generated in the transfer condition resembled the paths generated in the training condition in that day ($P > 0.05$) (Fig. 5, Day 4, Transfer). Thus, as in the supine posture, participants have acquired a geometrical motion primitive only after the "global planning" model prediction fitted the data.

Given the following findings: (a) Participants who acquired the co-articulation motion strategy promptly co-articulated and implemented the "global planning" motion strategy on novel, untrained target configurations ("Full mirror CDABC" and "90° Rotation CDABC") (Fig. 2), and (b) A geometrical motion primitive of the trained configuration was acquired after the co-articulation motion strategy was obtained (and the "global planning" model was shown to fit the data) (Fig. 5), would participants who co-articulated on their first encounter with an untrained target configuration also promptly acquire a novel geometrical primitive?

To that end, the four co-articulating participants were asked on the last training day (Day 4) to perform

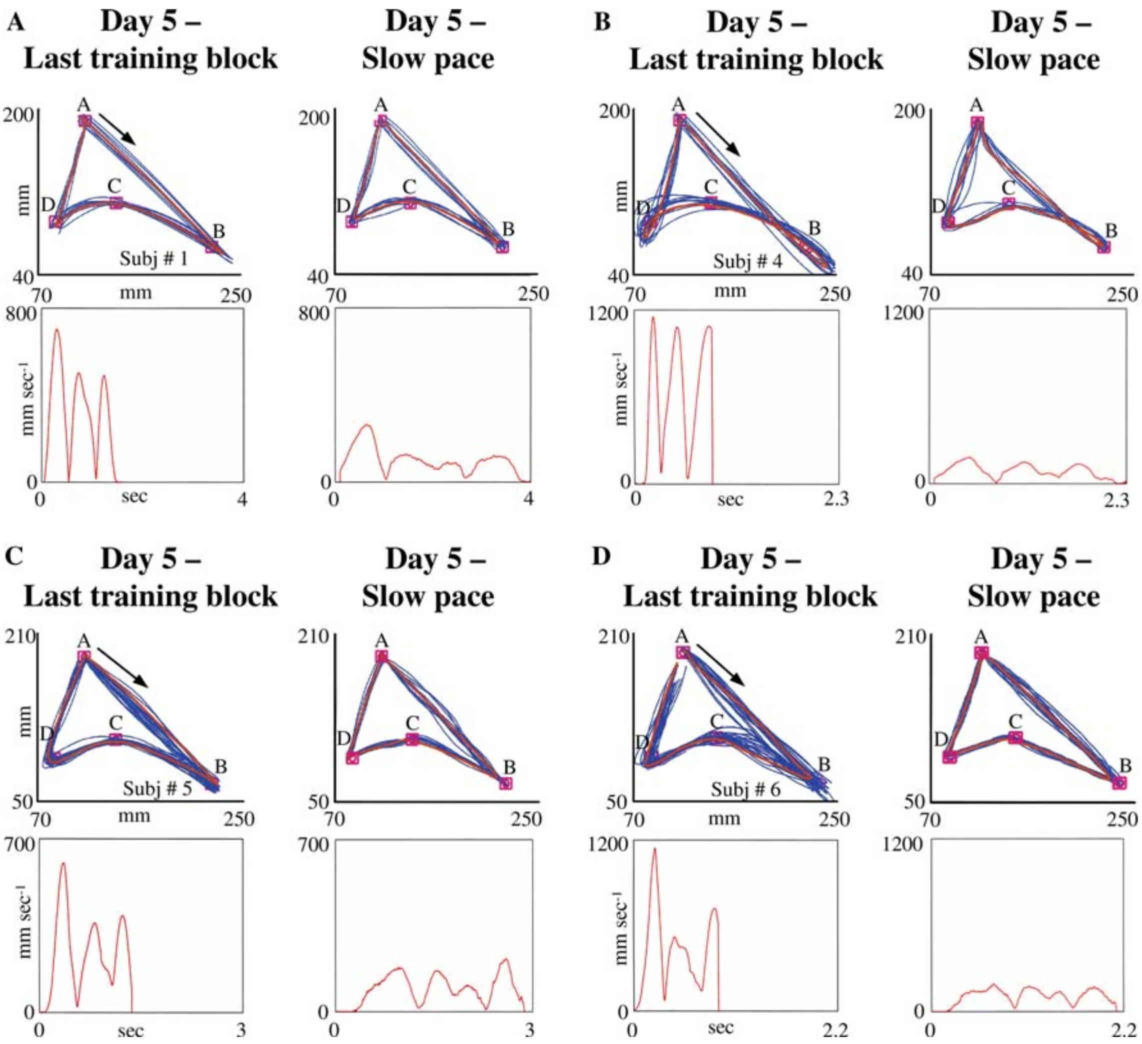


Fig. 4 Slow pace does not alter motion-planning strategy. Color-coding as in Fig. 3

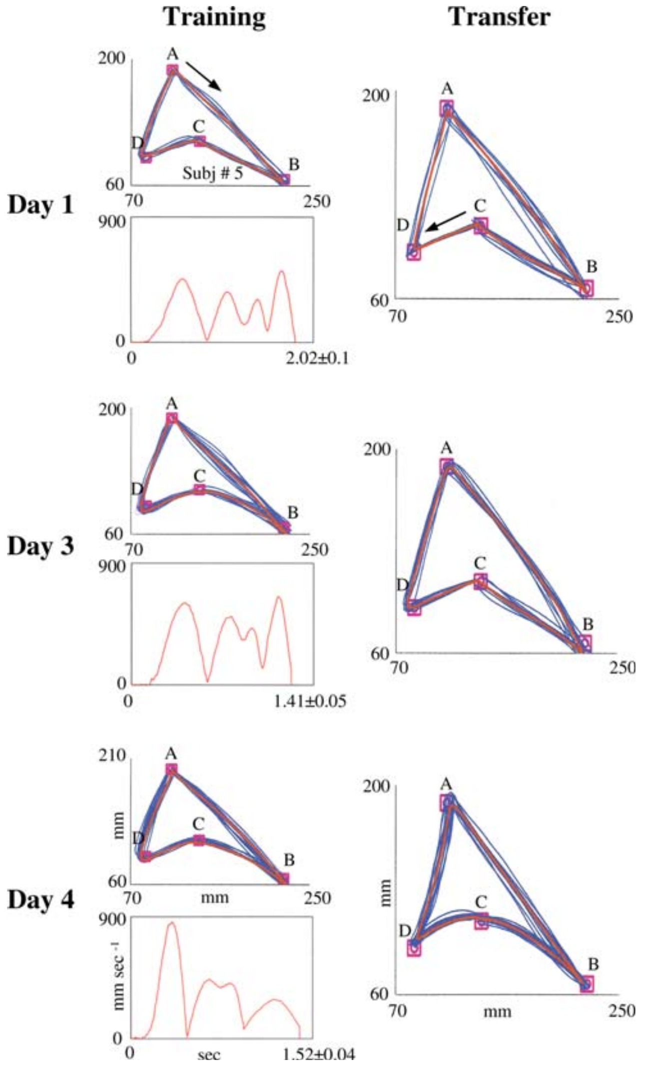


Fig. 5 The evolution of a geometrical "primitive". Depicted are training trajectories and transfer trajectories, generated on the same training day, by one representative participant. For each training day, the upper left plot denotes 15 training paths (*blue*) and average training path (*red*). The *lower left plot* denotes average velocity profile. The *plot on the right* denotes 15 transfer paths (*blue*) and average transfer path (*red*)

on the two untrained (transfer) target configurations (II and IV) but to start and end at a different target point (target C instead of target A). A curved path between targets C and D and between targets B and C was generated both in the "Full mirror CDABC" configuration and in the "90° rotation CDABC" configuration (Figs. 6a, b, respectively). For three participants (#1, 4 and 5) the shapes of the paths, generated in the "Full mirror CDABC" and "90° Rotation CDABC" condition were not significantly different from those generated in the "Full mirror ABCDA" and "90° rotation ABCDA" condition, respectively, in that day ($P > 0.1$ for all the three participants).

The shapes of the paths generated by the fourth participant (#6) in the "Full mirror CDABC" condition were not significantly different from those generated in the "Full mirror ABCDA" condition in that day ($P < 0.03$). However, the shapes of the paths that were generated by this individual in the last training day, in the "90° Rotation CDABC" condition were significantly different from the shapes of the paths generated in the "90° Rotation ABCDA" condition. An excessively curved path was generated between targets C and D, which deviated from the average path generated in the training condition in that day. Overall, these transfer experiments indicate that the implementation of the "global planning" motion strategy on an untrained target configuration was interlinked with the acquisition of a geometrical motion primitive.

A geometrical concave motion primitive is acquired

We next investigated whether participants would implement the newly acquired motion strategy on an untrained target configuration in which the two co-aligned segments, $\overline{BC}$ and $\overline{CD}$, are positioned differently relative to the other segments. To that end, the four co-articulating participants were tested in the first and last training sessions on the "Partial mirror" configuration (Configuration III) wherein target C was transferred to its mirror location (C′) with respect to the symmetry line $\overline{BD}$, thus preserving the same angle between segments $\overline{BC}$ and $\overline{CD}$ as in the training sessions. The two highly spatially co-aligned segments in the "Partial mirror" configuration were *convex* with respect to the rest of the configuration whereas in all the other transfer conditions, as well as in the training condition, the two co-aligned segments were *concave* with respect to the rest of the configuration. Surprisingly, instead of connecting target pairs $\overline{BC}$ and $\overline{CD}$ with two straight paths or connecting them with a curved, convex path, two curved *concave* paths were generated: one between target B and an imaginary target located roughly below the original target C (C*), and a second one between the imaginary target C* and target D (Fig. 7a). These findings were found in three co-articulating participants (out of four). In order to quantify the curvature in each trial in the transfer condition, we computed the longest perpendicular line (d1) from the concave curve $\overline{BC*}$ to the straight-line connecting targets B and C* and the longest perpendicular line (d2) from the concave curve $\overline{C*D}$ to the straight-line connecting targets C* and D (Fig. 7b upper plot). We repeated the computation for segment $\overline{BD}$ (d3) in the last training day (Fig. 7b lower plot). Since the distances between the different target pairs

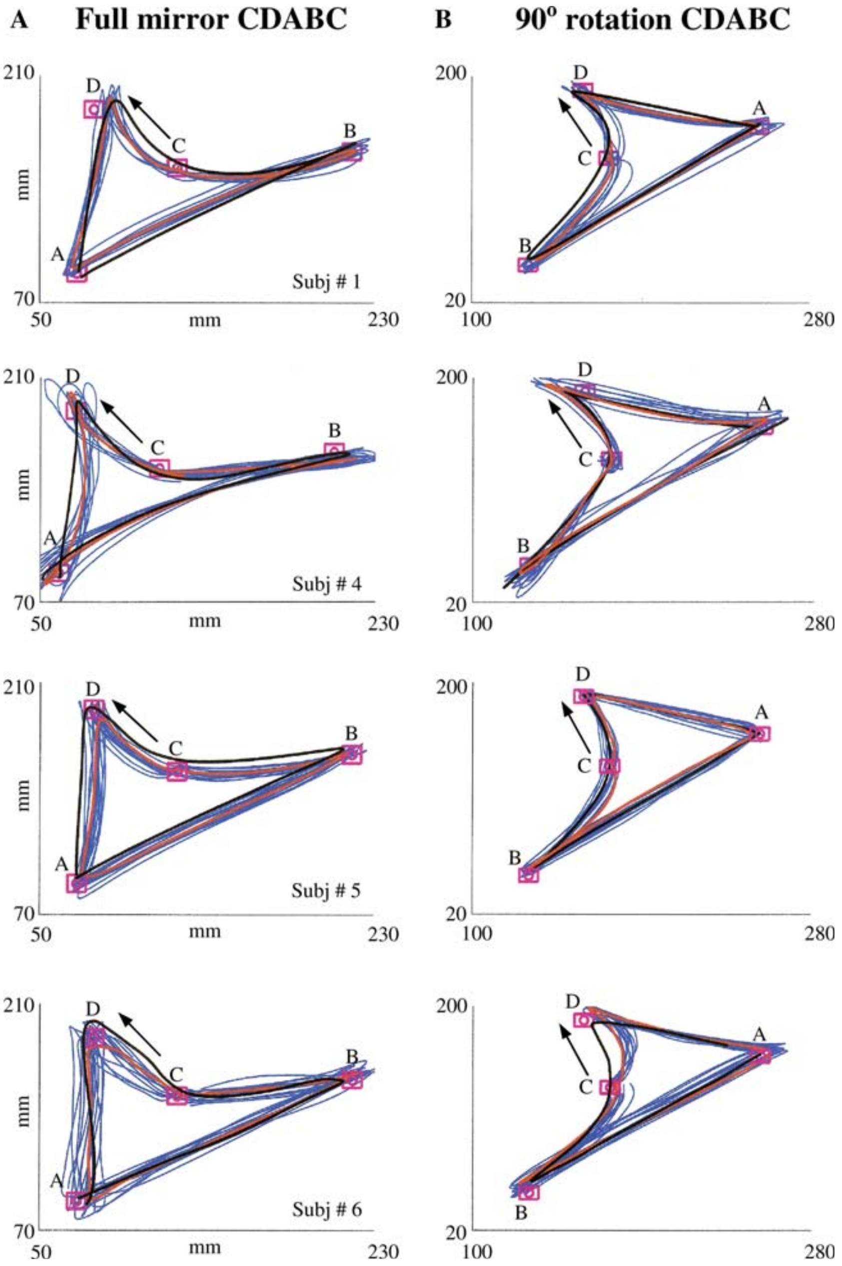


Fig. 6 A geometrical motion primitive was acquired when implementing the global planning motion strategy on an untrained target configuration. **a, b** paths generated in the two transfer conditions. The *blue curves* and the *red curve* depict transfer paths and average transfer path, respectively, starting and ending at point C ("Full mirror CDABC" and "90° rotation CDABC"). The *black curve* depicts average transfer path generated in that training session starting and ending at point A ("Full mirror ABCDA" and "90° rotation ABCDA")

were different we normalized d1, d2 and d3 by the distances $\overline{BC*}$, $\overline{C*D}$ and $\overline{BD}$, respectively. The average normalized curvature of segments $\overline{BC*}$ and $\overline{C*D}$ was 0.016 ± 0.014 and 0.021 ± 0.013, respectively, and was significantly different from the average curvature of segment $\overline{BCD}$ generated in the last training block in that day (0.085 ± 0.027) ($P < 0.01$). This pattern of results suggests that although the geometrical primitive was a concave curved path (the average curvature was significantly different from zero) the concavity of the acquired motion primitive was not specific to the curvature of the paths generated in the training condition. The remaining fourth co-articulating participant started off by generating two concave paths, one between target B and an imaginary target located roughly below the depicted target C (C*), and a second one between the imaginary target C* and target D. However, the paths connecting target pairs $\overline{BC}$ and $\overline{CD}$ gradually became less curved throughout the transfer block (Fig. 7c).

Training in the dark

The absence of visual feedback impedes the acquisition of the co-articulation motion strategy

In order to test whether visual feedback has a role in the acquisition of the global planning motion strategy

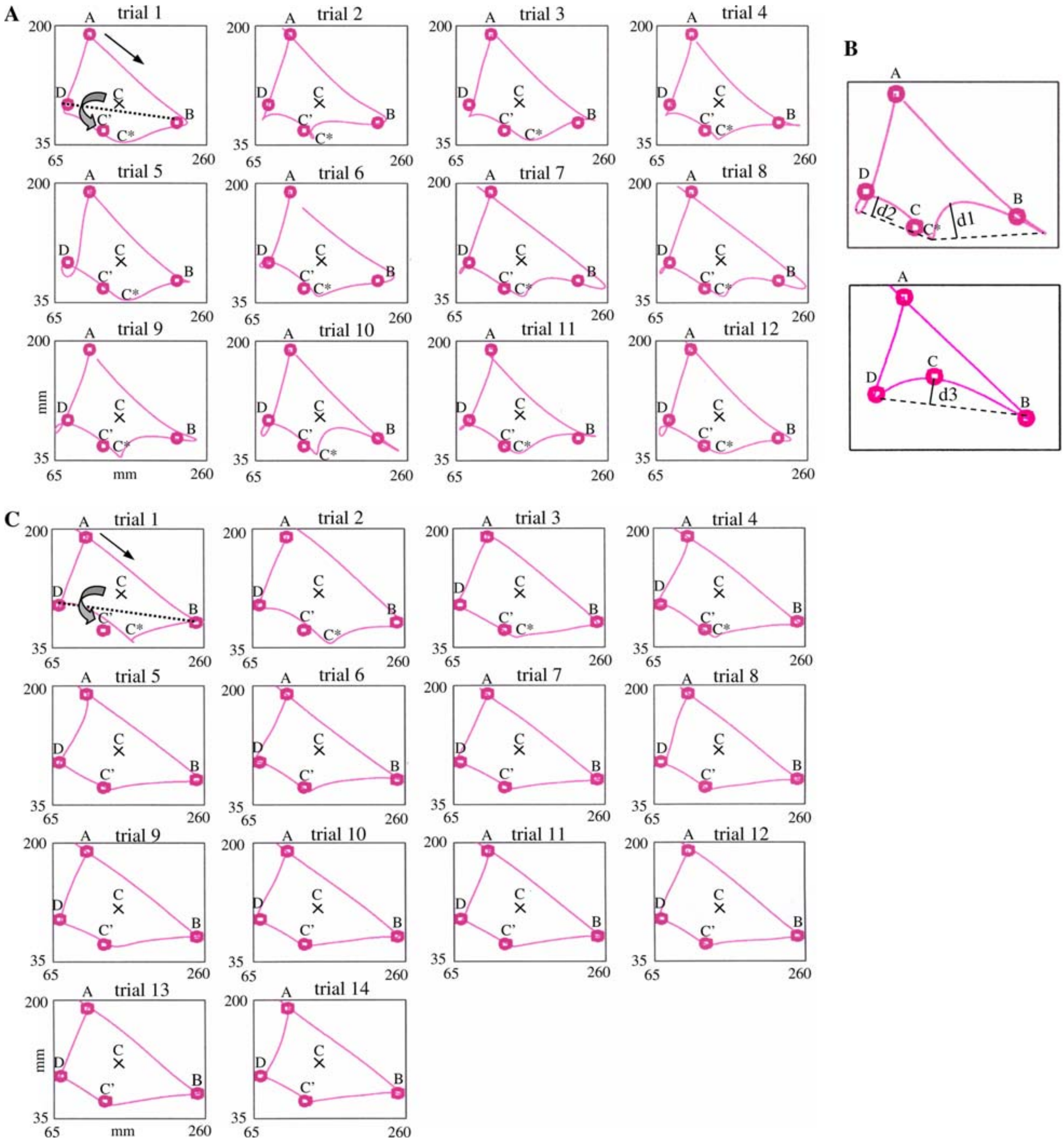


Fig. 7 A concave geometrical primitive was acquired. **a** concave paths generated in consecutive trials in the ''Partial mirror'' condition by one representative co-articulating participant (out of three). The *cross sign* denotes the previous location of target C (in the training configuration). The *asterisk* denotes the imaginary target where minimum local velocity was attained. The *black dashed line* connecting targets B and D denotes the symmetry line. **b** Curvature indices. *Upper plot d1* depicts the longest perpendicular line from the concave curve $\overline{BC*}$ to the straight line connecting targets B and C*. *d2* depicts the longest perpendicular line from the concave curve $\overline{CD*}$ to the straight line connecting targets C* and D. *Lower plot d3* depicts the longest perpendicular line from the concave curve $\overline{BD}$ to the straight line connecting targets B and D. **C** The evolution of the paths generated by the fourth co-articulating participant

we asked seven naïve participants to train for five daily sessions on target configuration I in the dark when only the targets were seen (i.e., participants could not see their hand. See Materials and methods section). Only two out of seven (28.5%) participants in this condition co-articulated by the end of the fifth training session as opposed to four out of six (67%) participants co-articulating in the light condition in the sitting posture

Table 3 Dependency of the reduction in total movement duration on the acquisition of co-articulation motion strategy. Data are means ± SD (s) obtained from 15 trials in the first and last training blocks

Participant #	Day 1—First block (s)	Day 5—Last block (s)	Mean decrease
Co-articulating			
8	1.62 ± 0.42	0.74 ± 0.03	54.21%
10	2.39 ± 0.29	1.31 ± 0.05	44.92%
Non co-articulating			
5	3.88 ± 0.53	2.85 ± 0.21	26.54%
7	2.82 ± 0.99	2.33 ± 0.18	17.37%
9	2.59 ± 0.51	1.82 ± 0.11	29.88%
11	5.70 ± 0.85	3.68 ± 1.36	35.43%
12	3.49 ± 1.29	2.26 ± 0.02	35.24%

[and eight of out ten (80%) co-articulating in the light condition in the supine posture]. Co-articulation was characterized by an average decrease of 49% in total movement duration as opposed to the five non co-articulating participants who decreased their total movement duration only by 28% (Table 3). The mean position variance at the targets and the mean total position variance along the paths, generated by the two participants who co-articulated in the dark condition, were not significantly different from those of the six participants who co-articulated in the light condition ($P < 0.1$) (Fig. 8). When the five participants, who were trained in the dark and have not co-articulated by the end of the last training session, were instructed to train for one session in light condition, four of them fully co-articulated after only three training blocks, indicating that visual feedback, although not essential, has an enhancing impact on the acquisition of the co-articulation motion planning strategy.

Performance gain is not transferred to untrained target configurations in the dark

In order to test whether the performance gain (co-articulation) acquired in the dark is configuration specific, the two co-articulating participants were asked to perform on a ‘‘Full mirror’’ configuration both in the first and the last training days. In the first training day, the two participants connected the four targets with four straight paths, each generated roughly with a bell-shaped velocity profile (Fig. 9a ‘‘Full mirror AB-CDA’’—Day 1). When tested on the last training day, the participants continued to generate four straight point-to-point trajectories and did no co-articulate (Full mirror ABCDA—Day 5). Hence, the performance gain was not transferred to the novel configuration. The same findings were obtained in the ‘‘90° Rotation’’ condition (Fig. 9b ‘‘90° Rotation’’—Days 1 and 5). In order to test whether the paths generated in the two transfer conditions were not significantly different from the paths generated in the first training block, we compared the area between each transfer path or training path and the average training path both in the first and last training day. The analysis was done after rotating the training paths by 90° (for the ‘‘90° Rotation’’ comparison) or after a vertical flip (for the ‘‘Full-mirror rotation’’ comparison). The shape of the paths, generated in the two transfer conditions, were not significantly affected by performance time (first or last block) but were significantly affected by the task condition (training or transfer) (two-way ANOVA, $P > 0.1$ and < 0.05, respectively). The paths generated in the ‘‘Reverse’’ condition on the last training session (Fig. 9c ‘‘Reverse ADCBA’’—Day 5) were significantly different from the paths generated on the last training day ($P < 0.05$) but were also significantly different from the paths generated on the first training day ($P < 0.05$). These findings may imply that participants have attempted to apply the co-articulation motion planning strategy on the well-rehearsed target configuration, although not successfully. Thus, the paths generated in the ‘‘90° Rotation’’ configuration, the ‘‘Full-mirror’’ configuration and ‘‘Reverse’’ configuration were significantly different from those generated in the training condition on the same day, indicating that the newly acquired motion strategy was configuration specific, as opposed to the non-configuration specific performance gain attained in the light condition (see Fig. 2).

A geometrical motion primitive was not acquired in the dark

We next aimed to test whether the visualization of the geometrical shape of the trajectory traveled by the hand and/or increased accuracy demands have a role in the acquisition of a geometrical motion primitive. The two participants who were trained in the dark and co-articulated by the end of the last training session (day 5) were asked to perform in the dark on the ‘‘CDABC’’ configuration. Both participants generated a straight path between targets C and D and between

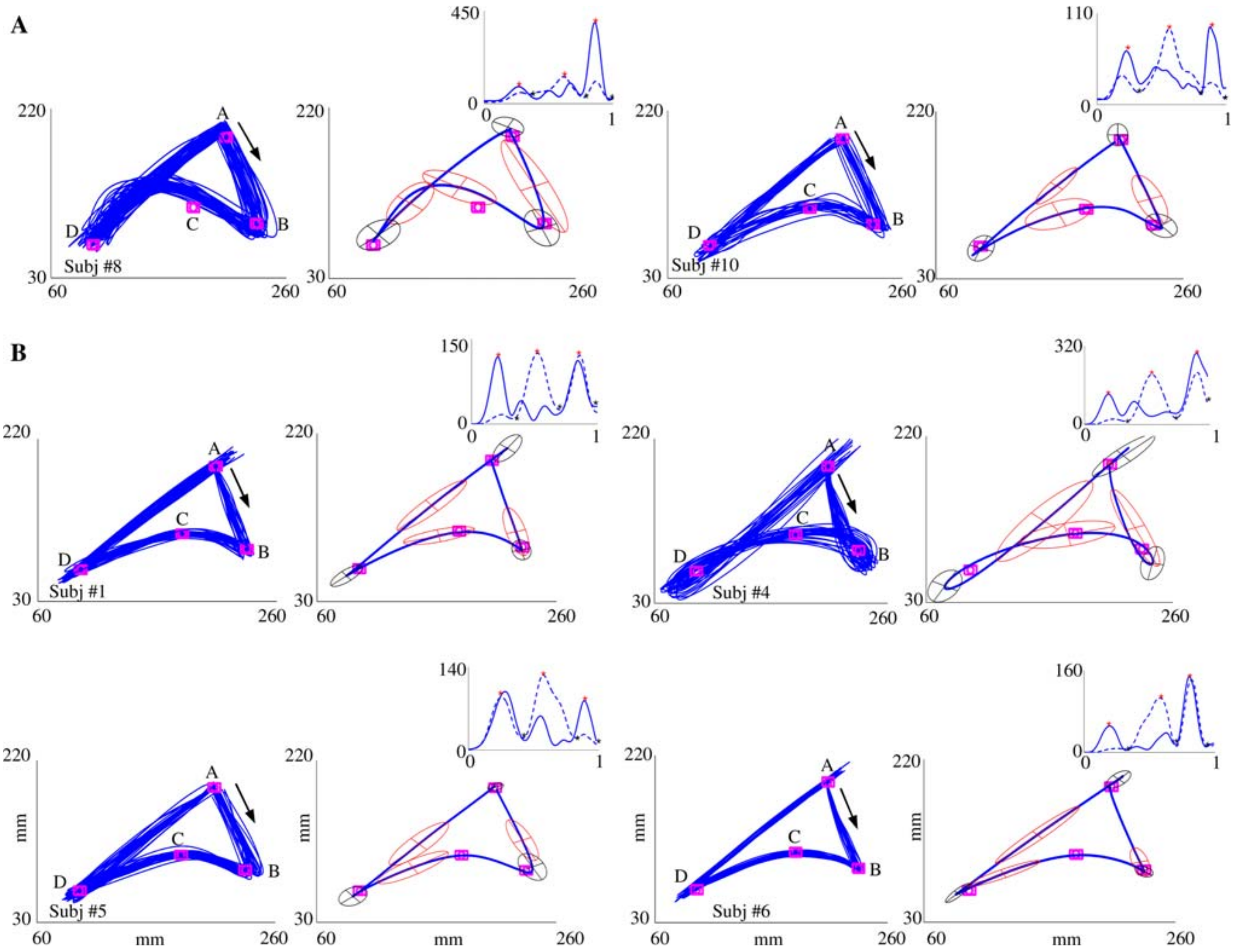


Fig. 8 Position variance while training in the dark and in the light. **a**, **b** Participants training in the dark and light conditions, respectively. *Left panels* trajectories generated in the last two training blocks (15 trials each). *Right panels* In each training block, all the trajectories were duration stretched (by spline interpolation) to have the same duration as the trajectory with the longest duration in the block. The interpolation was done separately for the x and y components of the velocity profile (V_x and V_y). Later, the amplitude of each velocity profile was scaled by the ratio of its original duration and the longest duration (in order to prevent deformation of the new path with respect to the actual path). The *stretched paths* were constructed from the stretched V_x and V_y 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. The *blue curve* denotes average trajectory. The *red* and *black ellipses* denote 95% of maximum and minimum position variance, respectively. *Insets x-axis*, normalized duration. *y-axis*, variance. *Dashed lines*, *solid lines*, x and y position variances, respectively. *Red asterisk* maximum position variance. *Black asterisk* minimum position variance

targets B and C (Fig. 10) implying that a geometrical primitive was not acquired, as opposed to the participants who were trained in the light and generated a curved concave path between these targets (see Fig. 5).

In order to examine whether a geometrical motion primitive was not acquired due to increased difficulty to meet with the accuracy demands while performing on an untrained condition or due the lack of visual feedback from the hand, we asked six naïve subjects to train on target configuration I in which the size of the targets (their area) was scaled by the ratio of standard deviations of the path variances, generated in the dark and light conditions (i.e., $\mathrm{STD}_{\mathrm{Path\_variance\_Dark}}/\mathrm{STD}_{\mathrm{Path\_Variance\_Light}} = 1.41$).

We also asked the subjects in the beginning of the first training session and in the end of the last training session to train on the “CDABC” transfer condition. All the six subjects co-articulated by the end of the last training session (Fig. 11a, b middle plots) indicating that the relaxed accuracy demands facilitated the acquisition of the co-articulation motion strategy. None of the subjects, however, has acquired a geometrical motion

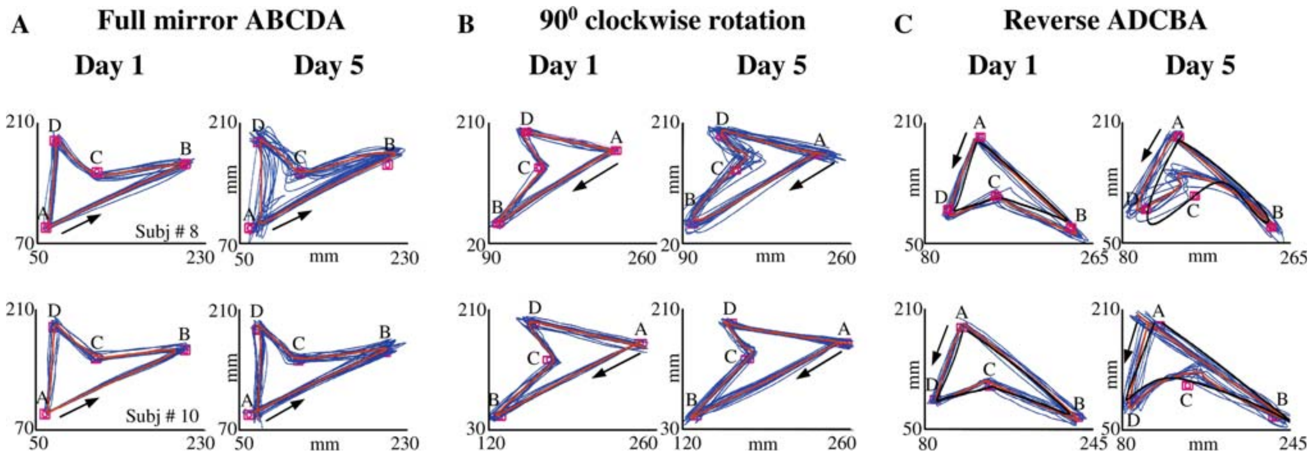


Fig. 9 Training in the dark—the performance gain was not transferred to other target configurations. **a–c** paths generated in the Full mirror configuration, 90° Rotation configuration and Reverse direction condition, respectively. In each panel, the *left plot* and *right plot* depict paths generated in the first training day (Day 1) and last training day (Day 5), respectively. *Blue curves*, transfer paths. *Red curve*, average transfer path. The black curve depicts average training path generated on the same training day

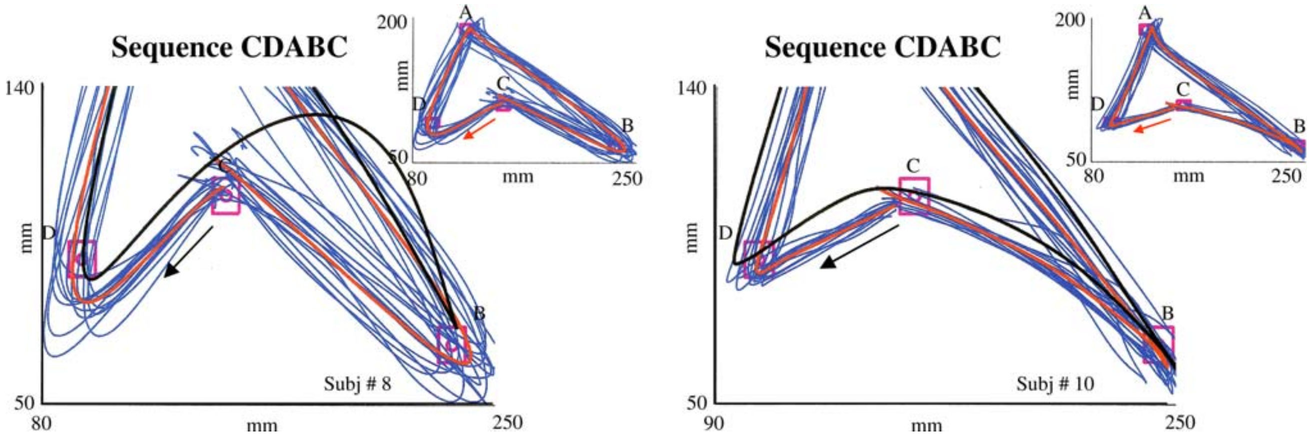
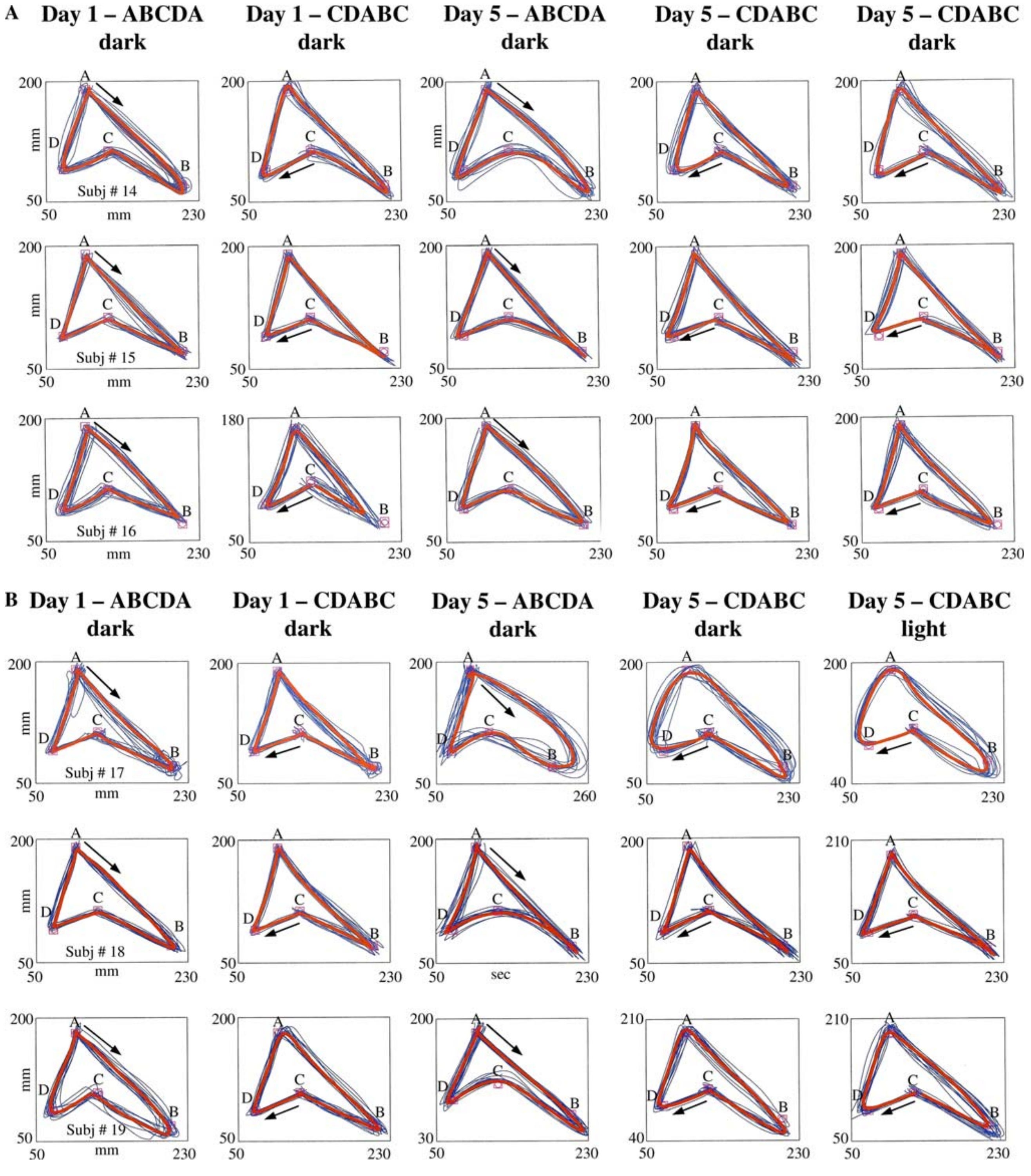


Fig. 10 Training in the dark—a geometrical primitive was not acquired. *Inset* Trajectories of 15 transfer trials. *Red arrow* movement starting position and direction. *Main panel* Zoom-in on the lower half of the target configuration. Color-coding as in Fig. 9

primitive (Fig. 11a, b fourth plot from the left). This finding suggests that the vision of the moving hand is crucial for the acquisition of the geometrical primitive. Since, still, there was a possibility that subjects have acquired a geometrical primitive but have chosen (explicitly or implicitly) not to generate it because of the difficulty to meet with the accuracy demands, we split the six subjects into two groups of three subjects each and asked them to train on the “CDABC” transfer condition in the end of the last training session. One group was trained in the dark while the other group was trained in the light, hence, relaxing the difficulty to meet with the accuracy demand. The group who was trained in the dark condition served as a control group to rule out the possibility that two consecutive training blocks on the “CDABC” transfer condition may be sufficient to acquire a geometrical motion primitive. Both groups have generated straight paths between targets C and D and between targets B and C (Fig. 11a, b leftmost plots), which were not significantly different from the paths generated in the training condition in the first training day. This finding suggests that visual feedback from the moving hand is crucial for the acquisition of a geometrical motion primitive.

Discussion

We previously showed that prolonged practice could lead to the co-articulation of consecutive segments of a given sequence of planar movements, generated between a series of target points (Sosnik et al. 2004). The outcome of the prolonged training was a novel curved trajectory, which although constituting to a longer



A Day 1 – ABCDA dark; Day 1 – CDABC dark; Day 5 – ABCDA dark; Day 5 – CDABC dark; Day 5 – CDABC dark

B Day 1 – ABCDA dark; Day 1 – CDABC dark; Day 5 – ABCDA dark; Day 5 – CDABC dark; Day 5 – CDABC light

Fig. 11 Training in the dark on enlarged targets. **a**, **b** paths generated by six subjects in the training and transfer condition in the first and last training day**.** In **a**, three subjects trained on the training and transfer conditions only in the dark while in **b**, three subjects trained on transfer condition "CDABC" by the end of the last training session in the dark and later in the light

path, afforded smooth and rapid performance with no loss in accuracy. This new trajectory was effectively transferable to several untrained (transfer) conditions. Moreover, our results were in line with the notion that different levels of experience might be associated with different internal representations of the task (Karni et al. 1998; Korman et al. 2003), and specifically, that new ‘‘movement primitives’’, i.e., strokes, could evolve in the adult motor system as a result of prolonged practice on a sequence of movements. 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 path geometry and its dependent velocity profiles. These results were replicated in the current study in the sitting posture. Furthermore, we show that the performance gain, acquired throughout training, is not restricted to the over-trained target configuration but can be swiftly transferred to other, untrained target configurations which consist of highly spatially co-aligned pairs of targets (Fig. 2).

The implementation of the acquired performance gain is dependent on spatial accuracy demands

When the participants, who co-articulated by the end of the last training session, were asked to perform on the ‘‘strict accuracy’’ task, they promptly reverted to generating four straight point-to-point movements and the total movement duration was substantially increased (Fig. 3a–d, Table 2). The increase in total movement duration while enhancing the accuracy demands is well predicted by Fitts law (Fitts 1954) (Fig. 3e), however, this was not the reason for the slipping back to the generation of straight point-to-point trajectories. When the participants were asked to perform on the over-trained task (i.e., relaxed accuracy demands) at a slow pace, similar to the pace in which they performed on the ‘‘strict accuracy’’ task, they all co-articulated (Fig. 4). These findings suggest that the turning back to the pre-training trajectories was not caused by the increase in the total motion duration but resulted from the increased accuracy demands. Had the newly acquired motion strategy been applicable on every combination of accuracy and speed values (as dictated by the speed-accuracy tradeoff), one would have expected the participants in the ‘‘strict accuracy’’ task to increase the total movement duration but continue to generate a curved path. Another cause for the deterioration in the performance gain in the ‘‘strict accuracy’’ task might be that the new instructions represent a sufficiently large change of context, and thus prevent generalization (as was shown in to occur in the ‘‘CBA’’ configuration, Sosnik et al. 2004). However, the current finding (Fig. 11), showing that enlarging the targets’ size while training in dark conditions resulted in all the six subjects co-articulating by the end of the last training session (as opposed to two subjects (out of seven) who trained in dark conditions on the smaller targets’ size) does not support this hypothesis. We therefore suggest that the acquisition and implementation of the co-articulation motion strategy depend on spatial accuracy demands per se. When new accuracy constraints are imposed, participants can no longer meet with the accuracy demands while applying the co-articulation strategy and they revert to the straight point-to-point motion strategy. It might be that given more practice on the ‘‘strict accuracy’’ task, participants would co-articulate the segments as in the trained (relaxed accuracy) task condition.

We previously showed that participants could not generate the new movement elements with the untrained hand, indicating that the products of the extensive practice—the new curved movement elements, were *effector (hand)* specific (Sosnik et al. 2004). This does not necessarily imply that the representation of the geometrical hand path is altogether lateralized and effector (hand) specific. The inability to transfer to the untrained hand might result from the uncertainty of the participants about their ability to meet with the accuracy demands (as might have happened in the ‘‘strict accuracy’’ task and in the dark condition) which resulted in slipping back to the generation of straight point-to-point trajectories.

The inability to transfer to untrained target configurations in dark conditions may result from a difficulty to meet with accuracy demands

Only 30% (two out of seven) of the participants who practiced in the dark on the 10 × 10 mm target size configuration have co-articulated by the end of the last training session as opposed to 100% (six out of six) who were trained on the 12 × 12 mm target size configuration. This finding suggests that visual feedback of the moving hand enhances the acquisition of the co-articulation motion strategy, presumably by facilitating the reduction of the end-point variance and meeting with the accuracy demands. The dependency of the implementation of the co-articulation motion strategy on spatial accuracy may explain the finding that the performance gain obtained in the dark was configuration specific, i.e., did not transfer to any untrained target configuration (as opposed to the light condition). The finding that two participants *have* manage to co-articulate while training in the dark further supports the notion that the co-articulated trajectory is globally planned before motion initiation and is not a product of on-line monitoring the hand position (Sosnik et al. 2004).

The acquisition of a geometrical motion primitive is dependent on the implementation of the co-articulation motion strategy and on the visualization of the path traveled by the hand

In our previous study, which was conducted in light conditions (Sosnik et al. 2004), we have shown that in the context of our drawing-like task, participants have acquired a motion element—‘‘primitive’’, whose attributes are dictated solely by the task geometry. We have argued in support of the notion that the representation of the hand position and its time derivatives are separately represented. We further showed that the new acquired geometrical motion primitive is only learned after the system has reached optimal performance, as dictated by the ‘‘global optimization’’ motion strategy, i.e., the global planning of two segments as a single, maximally smooth segment. The findings of the current study further support that notion and show that in light conditions, the instant co-articulation on a novel, unvisited target configuration is accompanied with the acquisition of a geometrical motion primitive (Fig. 6). Specifically we show that the above finding is valid only if a visual feedback from the moving hand is available.

The lack of a geometrical motion primitive acquisition in dark conditions (Fig. 10) was not due to increased difficulty meeting with accuracy demands (hence reverting to generating straight paths) since six naïve subjects, who trained in the dark on the increased target size, have continued to generate four straight paths in the ‘‘CDABC’’ transfer condition. In order to verify that the reason for not generating a geometrical primitive was the lack of its acquisition and not merely a conscious (or unconscious) decision not to express it, we applied a ‘‘boost’’ in the form of an additional transfer block, performed in light conditions. Still, participants generated four straight point-to-point paths, which were not significantly different from the paths generated in the first training block in the first training day.

Thus, we speculate that the inability to acquire a geometrical motion primitive in the absence of vision may result from the difficulty to form in memory a trace of the generated curved hand path. This memory trace of the hand path might be crucial for the construction and representation of a geometrical primitive. Although it is not known yet how a geometrical motion primitive is constructed, it might be that the visualization of the geometry of the path is crucial for its evolution through the learning process. This notion does not contradict the finding that the emergence of the geometrical motion primitive is dependent and interlinked with the acquisition of the co-articulation motion strategy. A possible framework to accommodate together the two findings is that in order to acquire a geometrical primitive one has to see the path, traveled by the hand and the geometrical form of the path must be repeatedly reproduced for some minimal amount of time (which is task specific) in order to facilitate processing and memorization of the geometrical form. When tested on the transfer condition in the intermediate learning stage (e.g., Fig. 5, day 3), the paths were constantly changing until a stable motion planning strategy, i.e., co-articulation, was maintained, thus, no trace of the path was acquired and subjects generated the ultimate choice—straight point-to-point movements.

An additional finding of the current study is that participants who practiced the ‘‘Partial mirror’’ configuration task connected target pairs $\overline{\mathrm{BC}}$ and $\overline{\mathrm{CD}}$ with two *concave* curved paths rather than connecting them with two straight paths or co-articulating them into one, convex path (Fig. 7a). The shape of the trajectories suggests that the shape of the geometrical motion primitive, which was added to the existing repertoire of primitives, was *concave*. Based on the results, we first hypothesized that when the participants were presented with the new target configuration they first took off from target B, as if they were still aiming at target C, and later made a correction movement toward target C’. The findings show, however, that target C’ was not hit even after 20 trials suggesting that the reason for generating the two concave paths could possibly be the acquisition of a geometrical curved, concave path. We are currently developing a model to account for the kinematic features of the movements generated through the learning process, which is based on this notion.

Altogether, our findings suggest that the implementation of a new motion generation strategy (namely, co-articulation) depends on spatial accuracy demands and that the acquisition of a geometrical motion primitive depends on the implementation of the co-articulation motion strategy and the existence of visual feedback from the moving hand. These results strengthen our previously suggested proposition that the characteristics of the task dictate the attributes of the acquired motion planning strategy and primitive and hint at the tremendous versatility, sophistication and adaptability of the motor system.

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