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Local learning of inverse kinematics in human reaching movement

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Abstract

We have investigated how the paths of reaching movements improve with motor learning, and whether these improvements transfer to movements other than those in which subjects were trained. Planar reaching movements were recorded in three groups moving in diagonal and lateral directions using a digitising table. All subjects made a number of reaching movements in a pre-test session. In the subsequent training phase of the experiment, one group of subjects was instructed to make lateral movements with as straight a path as possible; a second group made similar lateral movements following a straight line marked on the table; while a third group made diagonal movements, also following a marked line. All three groups were then tested making lateral and diagonal movements, without the benefit of any marked lines. The straightness and variability of movement paths were analysed to investigate improvements in neural control following training. A significant group by direction interaction indicated that movement straightness improved locally for the directions which were trained. Movement variability, in contrast, improved equally for all directions of movement. The results are consistent with local learning of a neural inverse kinematics model used in movement planning and global learning of a neural forward kinematics model used in movement execution.

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Keywords: Reaching; Kinematics; Learning; Hand paths

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1. Introduction

The human arm is redundant for most reaching and pointing tasks. This means that a movement between any given start and target positions can be made with any one of an infinite set of joint rotations. The motor system therefore faces an inverse kinematics problem of choosing just one set of suitable joint rotations. Many studies have measured the paths of the joints and of the hand in multi-joint reaching movements, in order to establish how the motor system might solve this selection problem (Morasso, 1981; Atkeson and Hollerbach, 1985). The major argument used in such studies is an argument from invariance. If a particular kinematic feature of either joint or hand movement is found to recur with low variability under many different circumstances, and for many different classes of movement, then this parameter must reflect a preferred solution to the inverse kinematics problem, and must form part of the representation used by the motor system to plan and control movements.

Learning and adaptation experiments provide another obvious method for investigating the fundamental representations underlying human movement. If a given parameter is used in the planning and control of movement, its values should remain stable even when subjects are forced to make movements under unusual conditions (e.g., in adaptation experiments), and the value should become more stable with practice and experience (e.g. in learning experiments). Recent motor adaptation experiments have addressed precisely this question (Shadmehr and Mussa-Ivaldi, 1994; Lackner and DiZio, 1994).

A second kind of adaptation experiment inverts this argument. If the experimenter can deceive the subject as to the value of the control parameter that the subject seeks to keep invariant, changes in movement patterns should be observed as a function of the experimental manipulation. Using this approach, Wolpert et al. (1995) have suggested that the visual perception of a straight hand path plays an important role in motor representation. Their experiment involved giving subjects distorted visual feedback of their finger position during the course of movement. They found that subjects adjusted the actual movement path so as to produce a perceptually straight path. That is, the actual movement path was adapted while the underlying representation of the visually-perceived straight path was invariant.

This kind of adaptation could be achieved in two ways. First, the motor system could alter the entries in a stored internal lookup table specifying the motor commands required to produce a visually perceived straight movement. In this case, the adaptation should affect only the class of movements, or the entries in the table, for which the adapting stimulus (e.g. displaced visual feedback) was given. This can be called local adaptation. Second, the motor system might form a general model of the relation between motor commands and visually perceived paths throughout the workspace. Visuomotor adaptation would then involve adjusting the coefficients of this global model. The argument from invariance would suggest that parameters which contribute to the representations used to control movement should be adapted globally and systematically, rather than in a piecemeal fashion.

Few studies have investigated whether normal learning of a movement pattern through motor practice leads to stabilisation of invariant kinematic parameters in the same way as does adaptation to an external environment. The extensive early literature on motor learning (e.g. Schmidt, 1975) did not consider the inverse kinematics problem explicitly, while many recent studies of inverse kinematics have assumed that the reaching movements studied were 'overlearned', and already at a ceiling level of motor control. Other studies have found evidence for stabilisation of invariant kinematic parameters in learning movement trajectories (Darling and Cooke, 1987). However, it remains unclear whether this stabilisation is specific to the movement performed, or involves a global change in the way the motor system represents a whole range of movements, for example due to adjustment of a neural model of the arm's inverse kinematics (Kawato and Gomi, 1992).

We have therefore studied the spatial patterns of reaching movements as a function of motor learning due to training, rather than as a function of adaptation to an altered external environment. We asked subjects to make straight hand paths during planar multi-joint reaching movements. We hypothesised that training a particular class of movement might lead either to a local change in the form of that particular class of movements, or to a global change in the kinematic patterns of all reaching movements, including those which were not trained. The former result would suggest that subjects produce straight hand paths by learning local solutions to the inverse kinematics of their arms, while the latter result would suggest that training allows subjects to learn a complete and comprehensive internal model of the inverse kinematics. Our analyses of average shape of spatial paths suggested local learning of inverse kinematics, while our analyses of variability of repeated spatial paths suggested global learning of forward kinematics.

2. Methods

Eighteen right-handed subjects from the academic community of Oxford University participated in this experiment. Subjects sat at a digitising table located in a plane just below the shoulder (GTCO Ltd.) and held a stylus in their right hand. Pointing movements were recorded by sampling the x and y stylus position at 133 Hz while the hand moved from start to target. Two movement conditions, lateral and diagonal, were studied. The lateral condition involved a movement of 50 cm amplitude in the fronto-parallel plane, crossing in front of the right shoulder approximately halfway through the movement. The diagonal condition involved 50 cm movements from proximal left to distal right, again approximately symmetrical about the right shoulder. Start and target positions for each movement were 1 cm squares marked on the table surface. An auditory signal was used to indicate when the stylus was within the start and target zones. Each trial began with the subject holding the stylus in the start zone. Following a signal from the experimenter the subject made a movement at a comfortable speed to the target position designated for that block. The start and target positions were selected so that the subjects made reaching movements involving the shoulder and elbow joints to displace the hand in the horizontal plane of the shoulder. The setup for the experiment is shown in Fig. 1.

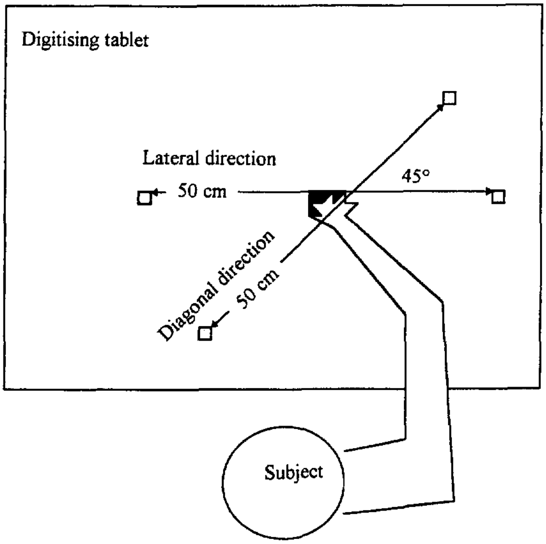

Fig. 1. Experimental setup.

Table 1
Details of movements performed by subjects in each group

PRE-TEST: "move between the two target positions"		
	ALL GROUPS 16 lateral movements 16 diagonal movements 16 lateral movements 16 diagonal movements	
Training: "make as straight a path as possible"		
GROUP A	GROUP B	GROUP C
60 lateral movements (unmarked worksurface)	60 lateral movements (marked on worksurface)	60 diagonal movements (marked on worksurface)
Testing: "make as straight a path as possible"		
GROUP A	GROUP B	GROUP C
30 diagonal movements	30 diagonal movements	30 lateral movements
30 lateral movements	30 lateral movements	30 diagonal movements
30 diagonal movements	30 diagonal movements	30 lateral movements
30 lateral movements	30 lateral movements	30 diagonal movements

Subjects were allocated randomly to three experimental groups. The arrangement of conditions for each group is shown in Table 1.

All groups made 64 movements, alternately in flexion and in extension, in the pre-test phase of the experiment. These were divided into four blocks each containing 16 movements (i.e., 8 flexions interspersed with 8 extensions); subjects were instructed to make the pre-test movements at a natural and comfortable speed, but were given no explicit instructions about the spatial path to follow in this phase. This phase was necessary to ensure equivalent behaviour in each group of subjects. It was followed by a training phase of 60 movements, again alternating between flexions and extensions. All subjects were instructed to follow as straight a path as possible between start and target during the training phase. For subjects in group A, the training phase involved lateral movements between the same start and target positions as before. Group B subjects moved between the same target positions as group A, but, in addition, a straight line was drawn on the table surface between the start and target positions to indicate the straight path precisely. Group C subjects followed a similarly marked diagonal line between the same start and target positions used for diagonal movements in the pre-test phase. After training, the marked lines were erased from the table surface. All subjects then made 120 movements in the testing phase, divided into 4 alternating blocks of 30 lateral and 30 diagonal movements each. Subjects were again instructed to make their movements as straight as possible in the testing phase. To avoid diluting any transfer of learning effects, and to ensure that training and testing phases were distinct, the first block of the testing phase always involved the movement direction that was not used in training. Thus, groups A and B made diagonal movements in the first block of the training phase, while group C made lateral movements. The entire experiment was carried out in a single experimental session, lasting approximately 1 hour. The pauses between the different blocks of movements and the different phases of the experiment were made as brief as possible.

The spatial path of each movement was obtained by interpolating the time series of x and y positions along a straight line between start and target positions. The spatial paths of all the movements in each condition (pre-test diagonal, pre-test lateral, training, testing diagonal, testing lateral) were analysed to quantify their straightness and their variability in shape. We used Generalised Procrustes Analysis (GPA; Gower, 1975) to determine the mean spatial path and the variability about the mean for each subject's movement in each condition. GPA is an iterative procedure which finds the mean and variability of a set of shapes, by attempting to translate and rotate the shapes so as to minimise the sum of least-squared distances between corresponding points in the shapes. The average and variability determined by GPA differ from conventional movement averages (e.g. Darling and Cooke, 1987) because they discard differences in the extrinsic location and orientation of repeated movements, retaining only differences in shape. The application of GPA to movement paths has been discussed in detail elsewhere (Haggard and Richardson, 1996; Haggard et al., 1995a). Briefly, we suggest that the average path calculated by GPA corresponds to the underlying shape of movement planned by the motor system. It could thus reflect the output of a neural inverse kinematic model. The variability of repeated movements around that average is the variability in the shape of the paths produced, irrespective of their extrinsic location. This variability arises when the shape of each individual path is modulated during movement execution, and reflects the difficulty of implementing the pre-planned representation. It could therefore reflect the accuracy of a neural forward model.

The straightness of movements was calculated as the root mean square residual from a line of best fit to the GPA average path, while the variability of movements was calculated as the root mean square residual of the translated and rotated paths from the GPA average path. These straightness and variability measures were compared across groups and conditions using repeated measures

ANOVA, with additional planned comparisons being used for specific pairs of conditions.

3. Results

All subjects made movements between the start and target positions in all conditions without difficulty. The movements typically lasted around 500–700 ms. Inspection of the data showed very similar spatial paths for flexion and extension movements in each condition, so pooled GPAs of both flexion and extension movements in each condition and phase of the experiment were used. Fig. 2 shows typical spatial paths in each condition from a range of different subjects. Within each plot the spatial paths after GPA are shown just above the raw data and the GPA straightness and variability measures following GPA are shown above the paths.

Means and standard deviations across subjects of GPA straightness and variability measures in each condition are shown in Table 2. The results were analysed by a series of repeated-measures ANOVAs, using group as a between-subjects factor and movement direction and phase of the experiment as within-subjects factors. The results for the straightness measure will be discussed first.

The mean straightness measure, and its standard deviation across subjects, are shown graphically in Fig. 3. There was no difference between the groups in the straightness of spatial paths in the pre-test phase: $F(2,15) = 0.02$, $p = 0.98$. Diagonal movements were significantly more curved than more lateral movements: $F(1,15) = 22.61$, $p = 0.001$. This replicates the findings of a previous study (Haggard et al., 1995a), in which this effect was attributed to the tendency to make diagonal movements largely using elbow rotations, without the associated movements at the other joints which would be necessary to produce a straight path. The interaction of group by direction in the pre-test phase was not significant: $F(2,15) = 0.895$, $p = 0.429$. There were no significant group or direction effects in an analysis of the variability in the pre-test phase, suggesting that the precision of motor execution was similar for all directions of movement and groups in the experiment.

As expected, all groups of subjects produced straighter hand paths overall in the training phase, in which they were instructed to move as straight as possible, than in the pre-test phase: $F(1,16) = 112.47$, $p < 0.001$ (pooling over groups and directions). The variability was also lower in the training phase ($F(1,16) = 49.16$, $p < 0.001$). Further, the spatial path of groups B and C, who followed a marked line on the work surface in the training phase, were straighter than those

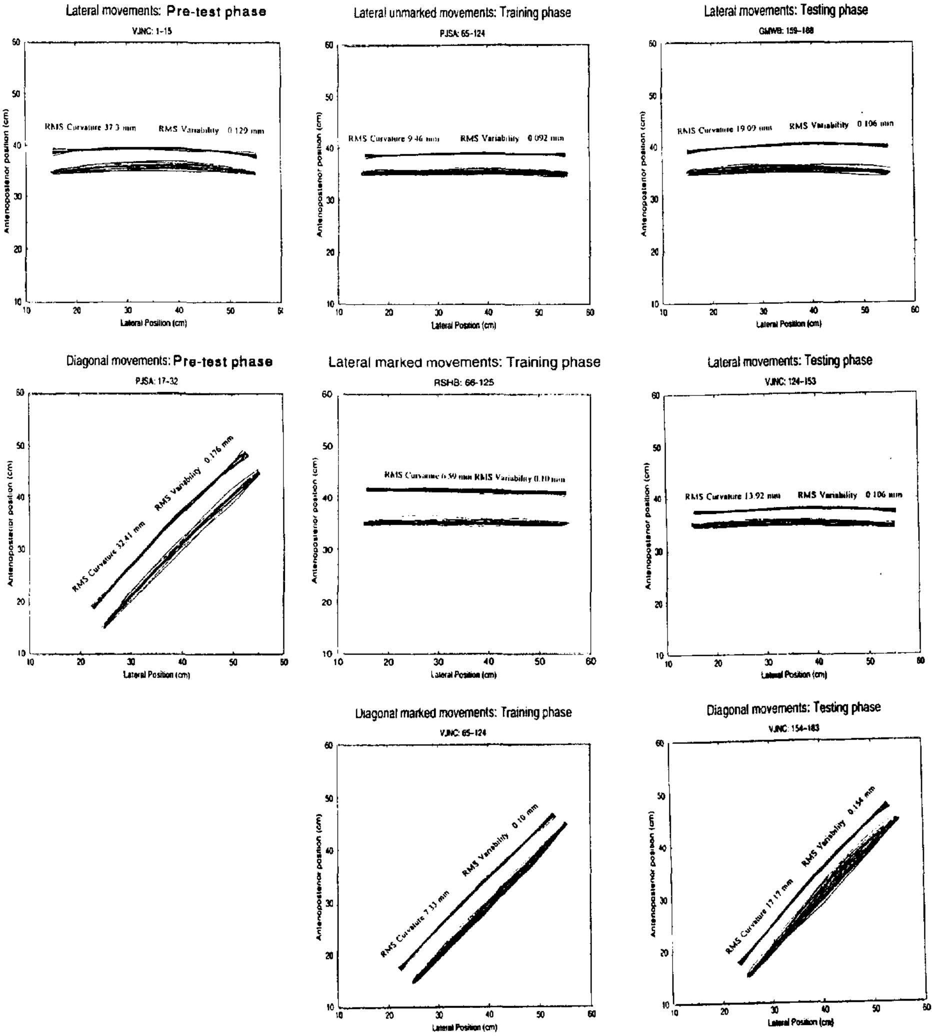

Fig. 2. Spatial paths from repeated movements from a range of subjects in each phase of the experiment. Within each plot the lower group of traces are the raw spatial paths, plotted in the coordinate system of the digitising table. The upper group of traces are the same paths after GPA. They have been positioned in approximately the same orientation as the original data. The curvature and variability measures taken from the data after GPA are shown immediately above.

of group A, who were asked to move in as straight a line as possible but did not have this visual guidance (Fig. 2). However, the group effect was not strongly significant: $F(2,15) = 2.854$, $p = 0.089$. A post hoc comparison showed no difference between the straightness of marked lateral movements of group B

Table 2
Straightness and RMS variability of movements in each condition

	Group A		Group B		Group C	
	Straightness	Variability	Straightness	Variability	Straightness	Variability
PRE-TEST						
Diagonal	55.93 (19.67)	0.18 (0.06)	61.57 (12.57)	0.16 (0.05)	57.82 (29.03)	0.15 (0.03)
Lateral	40.46 (18.01)	0.14 (0.03)	33.38 (12.41)	0.17 (0.05)	40.74 (10.06)	0.15 (0.02)
Training	15.59 (7.39) (lateral unmarked)	0.11 (0.03)	10.41 (4.95) (lateral marked)	0.12 (0.01)	8.60 (1.99) (diagonal marked)	0.12 (0.02)
Testing						
Diagonal	26.16 (16.26)	0.15 (0.04)	27.00 (13.24)	0.14 (0.02)	16.98 (3.79)	0.15 (0.02)
Lateral	16.40 (11.15)	0.11 (0.04)	14.06 (3.82)	0.12 (0.01)	17.48 (4.07)	0.12 (0.02)

Note: Numbers in parentheses indicate standard deviation across subjects.

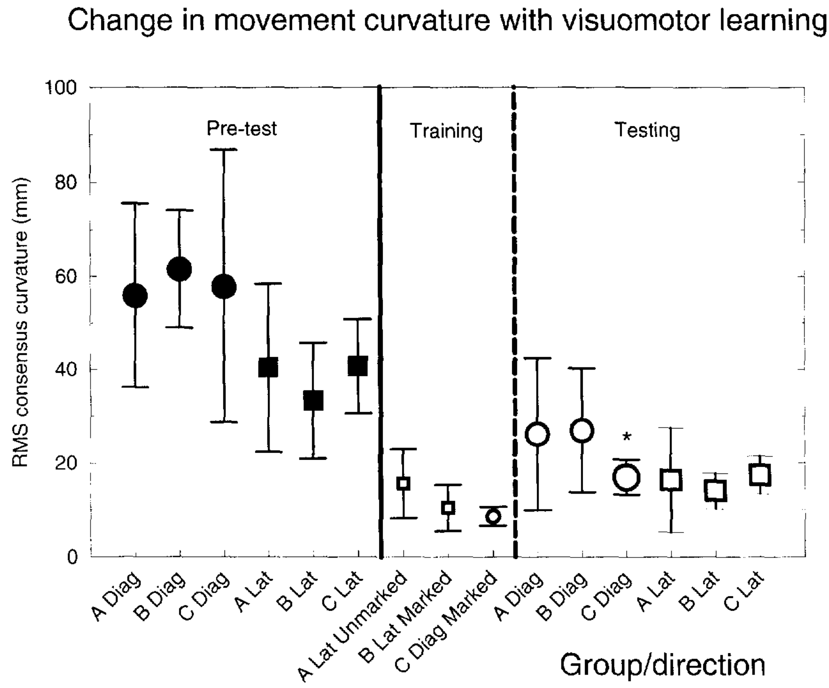

Fig. 3. Values of the GPA straightness measure for each group in each condition. Higher values indicate less straight movements. Cirles represent diagonal movement conditions, and squares represent lateral movement conditions. Pre-test data is shown using filled symbols. Note espcially the unusually straight movements in the diagonal direction for group C in the testing phase (asterisked). Error bars represent standard deviations across subjects.

subjects and marked diagonal movements of group C subjects ($F(1,10) = 0.692$, $p = 0.425$). Thus, the ability to reproduce a straight hand path was comparable for the two directions of movement studied. There were no significant differences between groups in the variability of repeated movements in the training phase.

Overall, movements in the testing phase were significantly straighter than in the pre-test phase ($F(1,16) = 67.84$, $p < 0.001$), but significantly less straight than in the training phase ($F(1,16) = 29.18$, $p < 0.001$) (pooling over groups and directions). Similarly, movements in the testing phase were less variable than in the pre-test phase ($F(1,16) = 13.27$, $p = 0.002$), but more variable than in the training phase ($F(1,16) = 13.68$, $p = 0.002$). Therefore, subjects' motor performance changed following training, but did not reach a ceiling level of performance. Within the testing phase, there was no significant effect of group on movement straightness: $F(2,15) = 0.326$, $p = 0.727$. Lateral movements were again significantly straighter than diagonal movements: $F(1,16) = 14.887$, $p = 0.020$. Most interestingly for the present study, the interaction of group and direction factors in the testing phase was significant: $F(2,15) = 4.461$, $p = 0.030$. Post hoc testing showed that this interaction was due to subjects in group C making particularly straight movements in the diagonal condition, and more curved movements in the lateral condition, compared to groups A and B (Fig. 3). There was no significant interaction between group and direction factors when considering only groups A and B. The straighter movements made by group C subjects in the diagonal condition appeared therefore to result from their experience of making diagonal movements during the testing phase.

Analysis of the variability of movements in the testing phase (see Fig. 4) showed that lateral movements were significantly less variable than diagonal movements: $F(1,15) = 54.278$, $p = 0.001$. This is consistent with previous results (Haggard et al., 1995a,b). Neither the group effect, nor the group by direction interaction approached significance.

The effects of training on straightness of the average path, and variability around the average path were then compared in a canonical MANOVA procedure (Krzanowski, 1988). This analysis produces standardised canonical coefficients (SCCs) which quantify how much each of several dependent variables contributes to the difference between the levels of a factor. An overall analysis of differences between the pre-test, training and testing phases, pooling over groups and directions, produced 1st SCCs accounting for 99.7% of inter-phase variance. These SCCs showed that the straightness of average movement changed more over the course of the experiment (SCC = 1.24) than did the variability of movements (SCC = 0.22). Note that this result is not inconsistent

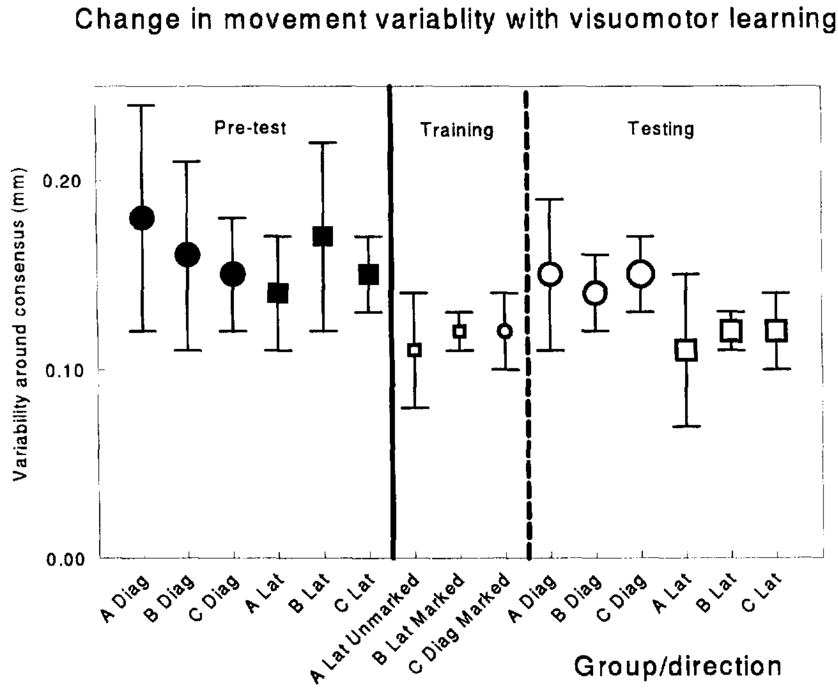

Fig. 4. Values of the GPA variability measure for each group in each condition. The symbol conventions are as for Fig. 3.

with a significant change in the variability of movement: it merely shows that the change in straightness was more marked than the change in variability. A second analysis of only the testing phase data produced 1st SCCs accounting for 92.1% of the group by direction interaction discussed above. These SCCs were also much greater for the straightness measure (SCC = 1.36) than for the variability measure (SCC = −0.44). These two analyses suggest that the overall motor learning was focused on the average movement shape rather than movement variability, and that the tendency for the groups' performance on different movement directions to depend on the direction of training was likewise focused on the average movement shape.

4. Discussion

This study investigated whether the improvement in motor performance resulting from training a movement would generalise to movements in another direction, or whether the improvement would be restricted to the specific condition in which training was given. To assess the effect of training, it was important to first assess the equivalence of movement across the 3 groups of subjects without this assessment influencing the subsequent training phase, or itself constituting part of their training experience. We therefore measured movement curvature and variability in a pre-test phase in which no instructions were given about movement path. Having established that the groups were equivalent in the baseline condition, we then compared movements during and after training in making straight line paths. This design does not conclusively rule out the possibility that the groups might have differed in their prior ability to produce straight hand paths. However, there is no evidence that they did so differ. Nor could the possibility have been tested without begging the question by giving the subjects an opportunity for motor learning, during the pre-test phase, of the very movement patterns that we sought to investigate in the training and testing phases. Our use of GPA allowed us to investigate these effects for both an average straightness measure, which we take to reflect the planning operations of a neural inverse kinematics model, and a movement variability measure, which we take to reflect the execution operations of a forward kinematics controller.

The most important result we observed was a significant group by direction interaction in the straightness of movements made during the testing phase immediatedly following training. This result is consistent with a local but not a global learning mechanism. Subjects in group C who were trained to follow a straight diagonal path, subsequently produced straighter diagonal movements in the testing phase than subjects who had been trained to follow a straight lateral path. There was no concomitant improvement in the lateral movements of these subjects. That is, the improvement in straightness was confined to the direction of movement which had been trained. In this sense our subjects learned the inverse kinematics of their own arms for the particular class of movements they performed in the training phase of this experiment. Since the relation between joint rotations and the hand translations they produce varies with workspace location and movement direction (Flash, 1990), a local mechanism of learning would seem to be appropriate when learning inverse kinematics.

The localised aspect of motor learning we have described does contrast, however, with some models of learning in the motor control literature, which have often emphasised the generalisability of what is learned. Two examples will be used to illustrate this point. First, schema theory (Schmidt, 1975) proposes that people learn a single, global relationship between sensory initial conditions, movement parameters and sensory consequences. A well-formed schema can then be used in a very general way to adjust movement parameters according to initial sensory conditions throughout the range of possible movements. Second, the relative timing hypothesis for timing action sequences (e.g., Viviani and Laissard, 1996) posits that a generalised program for the occurrence of motor events can be scaled to run at any speed by adjusting a single multiplicative rate parameter. Both of these models suggest that people learn a single underlying representation of skilled actions, and generalise it across the whole range of possible movements by some simple transformations such as linear scaling. We suggest that complexity of multi-joint kinematics (Flash, 1990) would make this approach impractical in the case of producing straight hand paths by rotating several joints, as in the movements studied here. The transformations required to generalise a single underlying representation would undoubtedly be more complex than linear scaling, due to the redundancy and non-linearity of the human arm. We suggest a series of local solutions may be a more effective form of motor learning in such a system.

We now turn to the analysis of movement variability, as opposed to straightness. Our analysis of GPA measures of variability showed that movement variability decreased as a result of training. The GPA measure of variability quantifies differences between movements due to local modulations of the path, and ignores extrinsic differences such as the location and orientation of the movement. Therefore, we suggest this improvement arises from subjects' perfecting a mechanism for movement execution which is independent of the pre-planned representation or program for the movement. This result is therefore consistent with subjects' learning a forward kinematics model used during movement execution. Additional analyses of variability in the testing phase showed that the variability of a subject's movement in a particular direction in the testing phase was not influenced by whether or not the subject had been trained in that direction of movement. If path variability is interpreted as an index of a neural forward model, then the improvement of the forward model with learning is a generalised one. Whereas the path straightness is increased locally for a particular class of movement, the movement variability is reduced globally in a way that transfers to classes of movement other than those that were trained. Good transfer of learning would be expected if the forward model were implemented in a general purpose neural circuit such as the cerebellum. Indeed, many strands of evidence point to this possibility (Keele and Ivry, 1990; Kawato and Gomi, 1992; Haggard et al., 1994; Haggard et al., 1995a,b).

Further, we found no significant difference between groups A and B in the shape or variability of diagonal or lateral paths in the testing phase, despite the fact that group B had been trained at lateral movements with an explicitly marked straight path, while group A had not benefited from this explicit visual cue. This suggests that perceptual learning of straightness does not form an important component of our subjects' visuomotor learning process. (Perceptual learning may however play an important role in the larger-scale visuomotor recalibrations required under conditions of altered visual feedback [Wolpert et al., 1995] and the denial of visual information certainly influences the kinematic patterns observed in blind subjects suggesting the perception does influence hand path [Miall and Haggard, 1995]). Rather, our results indicate that visuomotor learning involves perfecting a transformation between the rotations of multiple joints and the resulting path of the hand. This study has examined changes in movement patterns attributable to training, and thus differs from many previous motor learning studies, which have investigated adaptation to altered external environments. Many of these perceptuomotor adaptation studies, beginning with Helmholtz's displacing prism experiments have found evidence of global perceptuomotor learning. The perceptuomotor learning in these cases may involve a further transformation between an exteroceptive representation of the location of the hand in Cartesian space, and the internal representation of hand position used in the motor system's neural kinematic models (Kawato and Gomi, 1992).

There is considerable evidence that the motor system represents reaching movements as straight hand paths (Hogan, 1984; Atkeson and Hollerbach, 1985). However, it is unclear precisely how the motor system achieves straight hand paths. We suggest that making a straight path may involve three distinct neural components. The first would provide a global mapping between egocentric sensory systems such as vision (Wolpert et al., 1995) and an internal coordinate system for representing hand position. The second would provide more local solutions to the inverse kinematics problem of relating Cartesian hand position to joint angles. We have shown that this second component can involve a learned process which does not generalise to movements other than those for which it was learned. The third component involves monitoring the joint angles during the execution of movement, presumably in order to compare the actual movement pattern with the intended pattern. Our results indicate that improvement of this execution process can transfer to movements other than those for which it was learned.

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