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Motor adaptation to different dynamic environments is facilitated by indicative context stimuli

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Abstract When humans are exposed to external forces while performing arm movements, they adapt by compensating for these novel forces. The basis of this learning process is thought to be a neural representation that models the relation between all forces acting upon the system and the kinematic effects they produce, called inverse dynamic model (IDM). The present study investigated whether and how the predictability of a given external force affects the selection of an appropriate motor response to compensate for such force. Adult human subjects ($N=32$) held a handle that could rotate around the elbow joint and learned to perform goal-directed forearm flexion movements, while an external velocity-dependent negative damping force was applied that assisted forearm movement. Subjects were randomly assigned to two groups. In the *associative group*, the applied damping force was always associated with a specific initial position. Thus, after initial learning, the force application became predictable. In the *non-associative group*, where the same movements were performed, the applied force was independent of the initial position, so that no association between force and location could be formed. We found that only the *associative group* significantly reduced target error when damping was present. That is, the location cue aided these subjects in generating dynamic responses in the

appropriate limb. Our results indicate that motor adaptation to different dynamic environments can be facilitated by indicative stimuli.

Introduction

Recent evidence suggests that the control process underlying rapid arm movements is based on neural representations of the limb dynamics, called internal motor models. There are two types of internal motor models, forward and inverse dynamic models (IDM). Forward models can serve a predictive function, i.e., they transform efferent motor commands specifying limb dynamics into a set of joint kinematics. Limb dynamics refers to the muscular and nonmuscular forces causing the movement, joint kinematics to the resulting changes in joint angles. IDMs function as controllers by transforming planned kinematic trajectories into appropriate patterns of muscle activation (Jordan & Rumelhart, 1992; Wolpert, Ghahramani, & Jordan, 1995; Kalveram, 1998; Wolpert & Kawato, 1998). We use the term “dynamic model” here strictly in its mechanical sense, implying a model that computes forces according to desired kinematic trajectories. This explanation is important since other authors use the term “dynamic” when referring to the adaptability of IDMs. Shadmehr and Holcomb (1997), for example, differentiate between dynamic (adaptable) and static (non-adaptable) inverse models.

IDMs are thought to contain an abstract rule of the limb dynamics, rather than a look-up table containing associations between an experienced force and planned kinematic trajectories. Empirical evidence for this concept comes from experiments in which humans executed goal-directed arm movements under unknown dynamic conditions. It was shown that humans are capable of performing accurate movements to targets that they had not learned in the training phase. This ability to extrapolate dynamics into previously unvisited portions

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of the workspace is indicative of an underlying neural internal model (Shadmehr & Mussa-Ivaldi, 1994; Gandolfo, Mussa-Ivaldi, & Bizzi, 1996; Conditt, Gandolfo, & Mussa-Ivaldi, 1997). Furthermore, after removal of the damping force, subjects exhibited kinematic after-effects, typically a target error in the opposite direction of that found when first introducing the damping force. These after-effects were found in the trained regions of workspace, but also when moving to new targets in previously unvisited workspace (transferred after-effects). Such behavior is typical of an inverse model compensating for the arm's dynamics plus the external force that no longer exists.

In addition, subjects were found to be able to adapt to various dynamic conditions when the different force fields were presented in blocks and learning was separated in time by at least 5 h to avoid interference (Shadmehr & Holcomb, 1997, 1999; Vetter & Wolpert, 2000). The finding that learning one model interferes with the learning of another IDM, but that two motor maps can be learned and retained, if the training sessions for each task are separated by an appropriate time interval (Shadmehr & Holcomb, 1997, 1999), favors a modular IDM structure. Modularity of IDMs means that the brain builds a separate model for each force field, or that one IDM is provided with two input channels, where each channel specifies distinct values of the present dynamics (Kalveram, 1991, 1998, 2000). It is also possible, however, that an existing dynamic model is continuously adapted according to the prevailing dynamic conditions (Karniel & Mussa-Ivaldi, 2002).

Beyond that, Wolpert and Kawato (1998) proposed the existence of multiple paired forward and inverse dynamic models that are specific for a given environment and can be addressed through context stimuli. Context identification is realized through a "responsibility predictor" estimating the responsibility of a certain module for the present context by way of environmental stimuli. In addition, a responsibility signal is proposed, which is based on the prediction error of the paired forward model. In a study by Rao and Shadmehr (2001) it was shown that spatial cues aided the switching between perturbations after extensive training.

In contrast, a recent study by Karniel and Mussa-Ivaldi (2002) showed that even after extensive training subjects showed no signs of improved performance with alternating force fields. The indicative stimulus used in that study was the movement sequence, as the two force fields investigated were applied in alternation. Analysis of directional errors and modeling of the motor behavior found led the authors to the conclusion that the subjects tried to learn a single inverse dynamic model whose parameters were continuously updated according to the existing force field.

The question remains whether the lack of adaptation to the different dynamic environments was due to specific details of the motor task investigated in the study of Karniel and Mussa-Ivaldi (2002). The force field alternated, while six different movements to three targets

were randomly varied. Subjects might have been overcharged with the task to extract and address different dynamic systems while the kinematics required changed.

The picture emerging from previous research is that subjects are able to cope with different dynamic environments if force fields are learned in blocks (Shadmehr & Holcomb, 1997, 1999; Vetter & Wolpert, 2000). This adaptation seems to be further facilitated by context cues (Wolpert & Kawato, 1998; Rao & Shadmehr, 2001). The purpose of the present study was to supply further evidence that adaptation to two different dynamic conditions is possible and assisted by an indicative stimulus such as initial position of the movement. To this end, we investigated single-joint forearm-flexion movements in two groups. In the first group, the application of an external force was indicated by the starting position of the movement, while in the other group, who performed exactly the same movements as far as direction and amplitude were concerned, force application was independent of starting position.

Material and methods

Subjects

Thirty-two right-handed subjects (15 female, 17 male) participated in the study. Subjects' ages ranged between 21 and 40 years (mean = 28). The subjects were randomly assigned to four groups (see below). All participants gave written informed consent to take part in the study. The preparatory procedure took about 10 min including instruction. The subsequent experimental procedure took about 20 min for each individual subject. The local ethics committee approved the experimental procedures.

Apparatus

Participants sat in an adjustable chair facing a concave screen about 1.5 m in front of them. Their right forearms were inserted into an orthosis that was attached to a lever of a robot manipulator. It allowed only flexion-extension movements of the forearm in the horizontal plane. The size of the orthosis was adjusted to each subject's arm anthropometrics to ensure a secure and tight fit. Subjects viewed two illuminated arrows on the concave screen. The "target arrow" indicated the required target position and a "hand arrow" specified the actual angular position of the forearm. In our set-up, 0° angular position corresponded to 90° elbow flexion (see Fig. 1). Both arrows had the same triangular form. The triangle apex of the hand arrow was directed downward and that of the target arrow upward.

Procedure

Prior to movement onset, the subject actively aligned the hand arrow to the position of the target arrow, i.e., at 20° or -10°, depending on the respective experimental block. Subsequently, the target arrow jumped either to a position of 0° (initial position 20°) or -30° (initial position -10°) on the screen. Subjects were instructed to perform a goal-directed forearm flexion movement to the respective target position (see Fig. 1) and told to move accurately and at a quick pace.

During specific trials the torque motor generated a damping force with the amplitude being proportional to the angular velocity of the subject's arm movement (negative damping). The force was

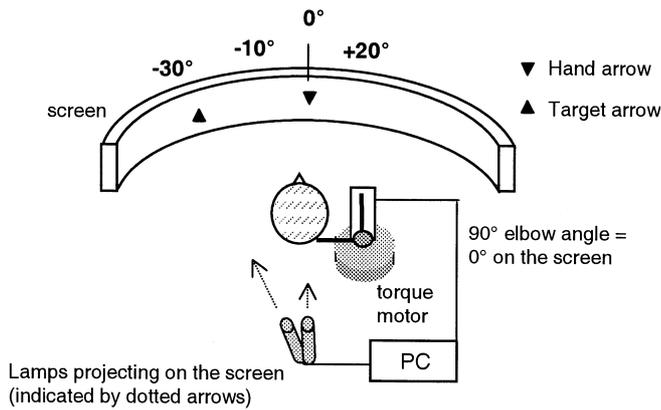


Fig. 1 Experimental apparatus. Subjects sat on a chair facing a concave screen 1.5 m in front of them. The forearm lay on a horizontal manipulandum, whose pivot point was located underneath the elbow joint's axis of rotation. The shoulder assumed an angle of approximately 90°. For further details see Materials and methods section

present during the complete movement, that is, during the target movement from the starting point to the target and during the reverse movement from the target back to the starting point.

The damping coefficient was $-1.5 \text{ nm}^\circ/\text{s}$, which in our set-up translated into the generation of a velocity-dependent force that *assisted* forearm motion. Participants experienced negative damping as if the arm was pushed from behind during flexion. As the force was velocity-dependent, each time arm velocity was zero (as, for example, at trial onset), no force was acting on the forearm. The torque motor received its input from a workstation computer. Control software to drive the torque motor was developed based on MATLAB technical computing language.

Each experimental block consisted of 10 trials. Subjects were not allowed to take a break between blocks. Maximum time allowed for each trial was 3 s. In other words, every 3 s, the target arrow jumped from the starting position to the target position and back. Reacting as quickly as possible was not emphasized in the instruction, as it was not crucial to the question of association of initial position, and thus reaction time was not analyzed.

We applied blocks alternately with and without damping force, starting with a null-damping block. Eight blocks were administered leading to a total of 80 trials. The experimental procedure is depicted in Fig. 2 and explained in detail below.

Subjects were randomly assigned to two groups. In the *associative group* the presence of the damping force was linked either to movements starting from 20° or to movements starting from -10°. In the *non-associative group* external force was not linked to starting position of the movement. Subjects in both groups were then assigned to two subgroups—one subgroup started the experiment on the left (-10° starting position), the other on the right (20° starting position). The formation of these subgroups allowed us to control the possible effects of the side of starting position: in one associative subgroup, force application was always on the left side, while in the other associative subgroup, force application was always on the right side. Analogous to these “mirror” associative subgroups there were two non-associative subgroups (see Fig. 2).

The crucial difference between the two groups was that in the associative group, the force was applied when the movement started on the left (associative subgroup 1) or when they started on the right (associative subgroup 2). In both non-associative subgroups, the force was either applied when the movement started on the left (1st and 3rd damping block in non-associative subgroup 1 and 2nd and 4th damping block in non-associative subgroup 2) or on the right (1st and 3rd damping block in non-associative subgroup 2 and 2nd and 4th damping block in non-associative subgroup 1). Thus, the initial position of the movement was a cue indicating the application of force in the associative, but not in the non-associative subgroups.

	Associative subgroups				Non-associative subgroups			
	left	right	left	right	left	right	left	right
Block 1		0	0			0	0	
Block 2	-1.5			-1.5	-1.5			-1.5
Block 3		0	0			0		0
Block 4	-1.5			-1.5		-1.5		-1.5
Block 5		0	0			0		0
Block 6	-1.5			-1.5	-1.5			-1.5
Block 7		0	0			0		0
Block 8	-1.5			-1.5		-1.5		-1.5
	Subgroup 1		Subgroup 2		Subgroup 1		Subgroup 2	

Fig. 2 Experimental design. All subjects moved alternately in a null-force ($0 \text{ nm}^\circ/\text{s}$) and a damping condition ($-1.5 \text{ nm}^\circ/\text{s}$). *Left side*: in associative subgroup 1, the damping force was applied only in movements starting on the left and in associative subgroup 2, in movements starting on the right. *Right side*: in both non-associative subgroups, damping force was either applied in movements starting on the left or on the right

Measurements

Angular position and velocity were measured by a potentiometer and tachometer at the motor shaft for each trial. The data were sampled at 520 Hz and digitized with a 12-bit analogue-to-digital converter (Meilhaus ME300). Digital data were stored on hard disk and then filtered offline with a 2nd order Butterworth filter with a cut-off frequency of 10 Hz.

Positional difference score

For each subject, we determined the time of the second zero-crossing of the acceleration curve of the baseline trials (i.e., for the first block where no force was applied) and of the first trial in each following block (trials 11, 21, 31, 41, 51, 61, and 71). The second zero-crossing of the acceleration curve marks the end of the first acceleration and deceleration phase of the movement. After the first acceleration and deceleration phase, the transport phase of the reach has ended. It is thus the latest point in the trajectory, where we can reasonably assume that the observed kinematics were the result of feed-forward control and were not entirely influenced by the processing of afferent feedback (Konczak, Jansen-Osmann, & Kalveram, 2003). The angular position value at this time was computed. This does not mean, however, that subjects stopped movement at this point. We were just interested in the angular position subjects reach by way of the part of the movement-trajectory that is not feedback-driven. This angular position value was subtracted from the required target position to obtain a measure of target accuracy (*absolute target error*). For each subject we then subtracted the absolute target error of trial 11, 21, 31, 41, 51, 61, and 71 from the mean absolute target error of the baseline movements (trials 3–10 of block 1; the first and second trial were regarded as practice trials). That is, the so-called “positional difference score” (DS-p) was obtained by first subtracting actual position at the second zero-crossing of acceleration from target position (absolute target error) and then subtracting this absolute target error in each first trial of a block from the mean absolute target error in the first baseline block. This measure allowed us to normalize performance in the 2nd to 8th block to the baseline error. A negative value of DS-p implied a larger error than in the baseline block, a positive value a smaller error. A DS-p approximating zero showed equality of target error in baseline block and following blocks. Apart from the DS-p of the first trial of each block, no other trials were considered for statistical analysis.

Velocity difference score

The velocity difference score (DS-v) was computed in a similar way to the DS-p, but for the first trial of each damping block only. Maximum velocity in the first trial of each damping block (11, 31, 51, and 71) was subtracted from mean maximum velocity in the baseline block (trials 3–10). That is, the larger the DS-v, the slower the movement compared with the baseline, and the smaller the DS-v, the nearer the movement velocity of the first trial of each block to mean baseline velocity. A DS-v value approximating zero stands for equality of baseline velocity and the velocity in the first trial of the damping block. Negative values of DS-v show that velocity in the first trial of a block was larger than mean baseline velocity. This additional variable was conceived to look for differences in movement velocity between experimental groups, to trace velocity changes over the course of the experiment and to find out whether subjects reach baseline velocity by the end of the experiment. This was done since unpredictable and thus noncompensated application of an assisting damping force leads to an increase in movement velocity, and therefore adaptation capacity should also be evident in this velocity parameter.

Control analyses

For each block we tested if there was a difference in DS-p between the two non-associative and associative subgroups. Table 1 shows the DS-p in each damping and nondamping block and the *t*- and *p*-value testing the difference between the two associative and non-associative subgroups. The initial position of the movement (right, left) in the respective block is given too. It is evident that the side of force application had an influence on DS-p. When a force was applied, DS-p was larger when the movement started on the right than when it started on the left. This effect was most pronounced in non-associative group 1, but also found in non-associative group 2 and associative group 2. Though the within-group variability was increased due to this side effect, we averaged the DS-p of the two non-associative and associative subgroups for further analysis. This seemed reasonable since the side effect was present in both associative and non-associative subgroups and movements on both sides had an equal frequency in both groups.

Statistical analyses

The further analyses were performed on the first trial of each damping block (trials 11, 31, 51, and 71) as dependent variable. The positional difference score (DS-p) was analyzed using a univariate analysis of variance design with the factor GROUP (associative vs. non-associative). This was done separately for each damping block and merged across all damping blocks in which the associative group could build an expectation as to the application of an external force (2nd to 4th damping block). We additionally computed a repeated measures analysis of variance with the between-subjects factor GROUP and the within-subjects factor BLOCK for the velocity-difference score (DS-v). Finally, we tested separately for each experimental group if DS-v in the last damping block was significantly different from zero. We accounted for multiple testing by adjusting critical α to .01 (DS-p) and .025 (DS-v) using the Bonferroni method.

Results

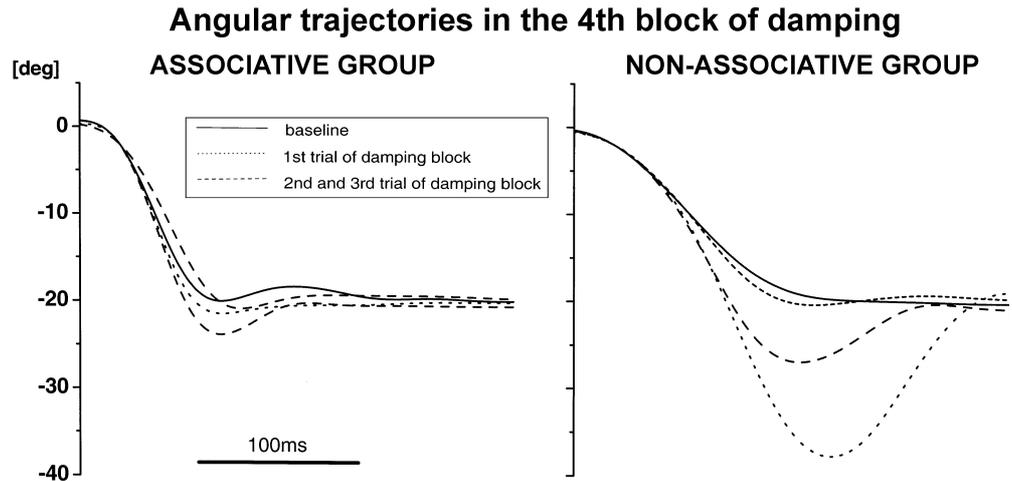
Effects of associating location to external force application

After experiencing damping for the first time, subjects of the associative group generally showed smaller deviations in the first trial of each damping block to the mean baseline trajectory than members of the non-associative group. Figure 3 illustrates how the application of a damping force differentially influenced associative and non-associative groups' subjects in the fourth damping block. The mean baseline trajectories and the first and two following trials of the block of one subject of each group are shown. For the purpose of clarity of graphical display, the curves were aligned to movement onset, which was determined as the time when angular path differed more than two degrees from starting position (i.e., 18° or -12°). All data preceding the movement

Table 1. Mean positional difference score (DS-p) and standard error (°) in the two non-associative and associative subgroups for each damping and non-damping block. The side of the initial position of the movement (right, left) and the *t*- and *p*-values testing the difference in DS-p between the two groups are given

	Subgroup				
	Non-associative 1		Non-associative 2		
	Initial position	DS-p (°)	Initial position	DS-p (°)	
Trial 11—damping	Left	-.52 (.98)	Right	-5.39 (2.18)	<i>t</i> = 2.034, <i>p</i> = .061
Trial 21	Left	.39 (.39)	Right	-.32 (.31)	<i>t</i> = 1.421, <i>p</i> = .177
Trial 31—damping	Right	-14.20 (2.09)	Left	-1.93 (.84)	<i>t</i> = -5.452, <i>p</i> < .0001
Trial 41	Right	.37 (.47)	Left	.35 (.37)	<i>t</i> = .030, <i>p</i> = .976
Trial 51—damping	Left	.13 (.75)	Right	-7.64 (.92)	<i>t</i> = 6.535, <i>p</i> < .0001
Trial 61	Left	.38 (.41)	Right	-.65 (.47)	<i>t</i> = 1.652, <i>p</i> = .121
Trial 71—damping	Right	-14.13 (2.15)	Left	-1.45 (.76)	<i>t</i> = -5.572, <i>p</i> < .0001
	Associative 1		Associative 2		
	Initial position	DS-p (°)	Initial position	DS-p (°)	
Trial 11—damping	Left	-1.38 (1.37)	Right	-5.31 (1.36)	<i>t</i> = 2.031, <i>p</i> = .062
Trial 21	Right	-.24 (.62)	Left	.72 (.55)	<i>t</i> = -1.158, <i>p</i> = .266
Trial 31—damping	Left	.03 (.87)	Right	-4.80 (1.80)	<i>t</i> = 2.410, <i>p</i> = .030
Trial 41	Right	-.39 (.51)	Left	.72 (.53)	<i>t</i> = -1.503, <i>p</i> = .155
Trial 51—damping	Left	-1.77 (.88)	Right	-4.37 (.92)	<i>t</i> = 2.038, <i>p</i> = .061
Trial 61	Right	-.35 (.69)	Left	.46 (.62)	<i>t</i> = -.875, <i>p</i> = .396
Trial 71—damping	Left	1.14 (.59)	Right	-2.48 (1.04)	<i>t</i> = 3.020, <i>p</i> = .009

Fig. 3 Baseline trajectories and the first three trajectories of the fourth damping block of one representative subject of each experimental group



onset by more than 100 samples (ca. 190 ms) were discarded and the length of each trajectory was standardized to 900 samples (ca. 1.7 s).

In the first damping block, when neither group could have formed an expectation as to when a damping force was applied, the two experimental groups did not differ in their target accuracy as expressed by DS-p of the first trial (trial 11; 1st damping block: $F_{(1/30)} = 1.06$, $p = .313$). However, the target error in the second (trial 31) and fourth (trial 71) damping blocks was significantly smaller in the associative than in the non-associative group (GROUP effect for second damping block: $F_{(1/30)} = 12.21$, $p = .002$; fourth damping block: $F_{(1/30)} = 11.01$, $p = .002$). In the third damping block (trial 51), the group difference did not reach statistical significance ($F_{(1/30)} = 3.28$, $p = .08$), although the trend was the same as in damping blocks 2 and 4. The effects are illustrated in Fig. 4.

When we averaged the first trials of the second to fourth damping block for statistical analysis, we found a highly significant effect of GROUP ($F_{(1/30)} = 19.21$, $p = .001$). Thus, considering as a whole all those damping blocks in which the associative group could build an expectation about force application, the associative group showed a considerably smaller positional difference score than the non-associative group.

Analysis of DS-v

The means and standard errors of DS-v ($^{\circ}/s$) in the first trials of the four damping blocks are illustrated in Fig. 5; a positive DS-v represents slower movements with respect to the baseline, a negative DS-v indicates faster movements during force application. As evident from Fig. 5, we found that the non-associative group moved—on average—faster than the associative group, whose movement velocity was closer to baseline velocity (significant GROUP effect of DS-v: $F_{(1/30)} = 6.78$, $p = .014$). Although both groups were equally affected by the damping force during the first block, only the associative

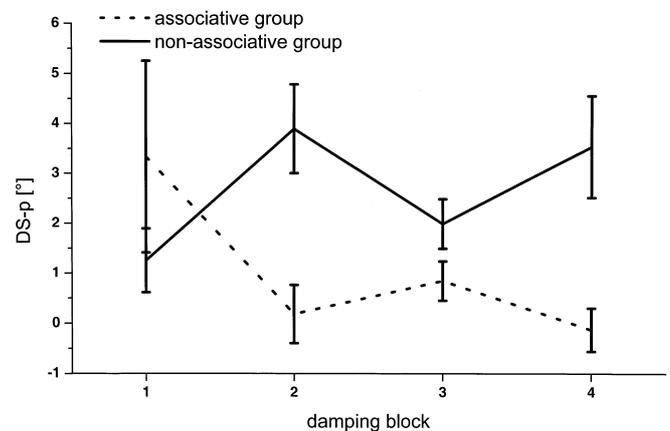


Fig. 4 Mean group positional difference score ($DS-p$) and standard error ($^{\circ}$) in the four damping blocks

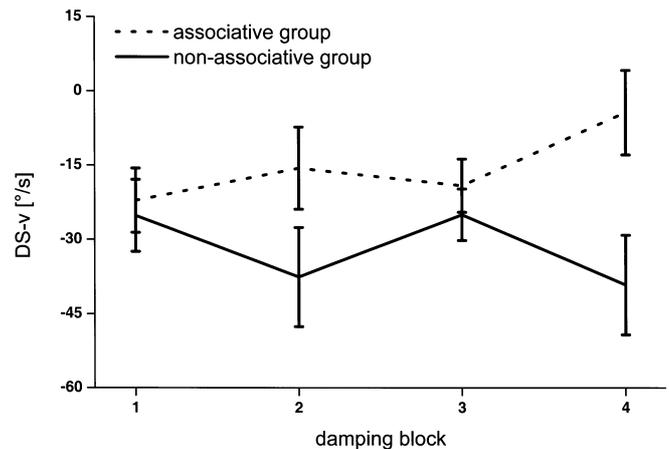


Fig. 5 Mean group velocity difference score ($DS-v$) and standard error ($^{\circ}/s$) in the four damping blocks

group managed to return close to baseline velocity in the following damping blocks, while the non-associative group showed no signs of improved performance. Accordingly, in the last damping block, DS-v did not

Table 2 Mean peak velocity and standard error ($^{\circ}/s$) in the associative and non-associative groups in the first trial of each damping and non-damping block

	Mean peak velocity ($^{\circ}/s$)	
	Associative	Non-associative
Baseline	-76.95 (6.62)	-66.14 (5.15)
Trial 11—damping	-99.06 (8.74)	-94.23 (8.47)
Trial 21	-59.31 (8.99)	-45.52 (4.20)
Trial 31—damping	-92.51 (6.88)	-103.70 (12.43)
Trial 41	-52.71 (6.95)	-42.19 (4.63)
Trial 51—damping	-95.97 (6.93)	-91.05 (5.65)
Trial 61	-58.98 (9.63)	-48.51 (4.86)
Trial 71—damping	-81.17 (5.58)	-105.24 (11.73)

significantly differ from zero in the associative group, while this was the case in the non-associative group (associative group: $t = -.63$, $p = .535$; non-associative group: $t = -3.89$, $p = .001$). There was no effect of damping block ($F_{(3/90)} = .23$, $p = .876$).

Analysis of peak velocity

In addition to DS-v, which was normalized to baseline velocity, we analyzed peak velocity ($^{\circ}/s$) in the first trial of each block. Table 2 shows mean peak velocity and standard error ($^{\circ}/s$) in the associative and non-associative groups in the baseline block and following damping and nondamping blocks. Peak velocity was slower in the nondamping than in the damping blocks, and it was somewhat slower in the non-associative than in the associative group, except from the second and fourth damping blocks. Differences in baseline velocity are controlled by computing the change in velocity relative to the baseline velocity (DS-v) for statistical analysis.

Discussion

Effects of linking location to external force application

After experiencing the first damping block, subjects of the associative group returned to pre-exposure kinematic performance levels within the subsequent three damping blocks. In contrast, the non-associative group showed little or no signs of kinematic improvement that were indicative of successful force compensation. Because the only treatment difference between both groups was the opportunity of the associative group to form an association between force and initial position, the results show that a contextual cue could trigger the selection of an appropriate motor response that would compensate for the changes in limb dynamics.

In the damping blocks we found an influence of the side of force application on the positional difference score in both non-associative and associative subgroups, which underlied the statistical group effects. It was shown that the positional difference score was larger in move-

ments starting on the right than in those starting on the left when a force was applied and that this effect was larger in the non-associative groups than in the associative groups for the second to fourth damping blocks. The side effect might be due to the fact that movements on the left ended almost at maximum elbow flexion range of the manipulandum and were thus easier to stop on the target than movements starting on the right, which had to be stopped approximately in the medium flexion range.

The interpretation that the initial position was a helpful cue that could be used in selecting an appropriate motor response is supported by the velocity difference score. The finding that unpredicted applications of an assisting damping force lead to higher movement velocities compared with the baseline velocity in the non-associative group and that velocities were not reduced with practice implies a lag of compensation and thus learning in this group. In contrast, movement velocity in the associative group during the damping block was almost equal to baseline velocity. The velocity analysis shows that subjects who could associate initial position with force were more successful in modulating the control variable velocity than subjects where force was not associated to initial position.

Topology of multiple parallel IDMs

Karniel and Mussa-Ivaldi (2002) did not find an adaptation to alternating force fields. Error analysis and a modeling approach proposed that one IDM, which was continuously updated according to the prevailing dynamics, accounted for the motor behavior found in their study. The experimental paradigm used in our study was a block design though. We could show that subjects adapted to the changed dynamics and that this adaptation was facilitated by indicative context cues.

In the study by Karniel and Mussa-Ivaldi (2002), force adaptation was cued by temporal order. In our study, it was cued by initial position. Furthermore, in the Karniel and Mussa-Ivaldi study, a multi-target-design was realized, while in our work, only two targets were presented. In a multi-target-design, a generalized visual-to-motor transformation rule (an IDM) is possibly learned. In a double-target design like ours, it might be a single specific motor program that is learned.

If an IDM was actually learned, generalization would be expected to occur, which would be evident in transferred aftereffects. That is, after removal of the damping force and when moving to new targets, subjects should exhibit a target error in the opposite direction of that found when first introducing the damping force. These aftereffects should be present because subjects apply the same model to the new movements, although the force is no longer present. In the course of the experiment, the transferred aftereffects should reduce, and an additional model (or the same model with different parameters) would be applied.

Table 1 reveals that the positional difference score was small in the nondamping blocks from the beginning, indicating that we did not find transferred aftereffects in our experiment. This suggests that the movements starting on the left and right might be perceived as being so different, that subjects did not try to apply the same model to both sides. This interpretation is in line with the observation of side effects: When a damping force was applied, movements starting on the right side were obviously more difficult than those starting on the left side. Because of this, we cannot make a final statement concerning the question whether an internal dynamic model was actually learned, if it was learned but not applied, or if we found local learning of the specific movement.

An additional experiment with a similar design, but with movements less diverse could help to solve the question of local learning vs. model learning. Nevertheless, even if subjects did not generalize, but used a separate motor program for each side from the beginning, the result that positional difference score was smaller in the associative group in the damping blocks shows that a contextual cue could trigger the selection of an appropriate motor response that would compensate for the changes in limb dynamics.

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