

Effects of Two Different Dynamic Environments on Force Adaptation: Exposure to a New Force but Not the Preceding Force Experience Accounts for Transition- and After-Effects

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This study investigated force adaptation in humans during goal-directed flexion forearm motion. The ability of the motor system to adapt to changes in internal or external forces is essential for the successful control of voluntary movement. In a first experiment, we examined how under- or overdamping differentially affected the length of the adaptation and the arm kinematics between force transitions. We found that transitions diverging from a null-force produced larger transition effects than transitions converging to a null force condition, indicating that re-adaptation was less error-prone. Whether the subjects had previously experienced underdamping or the null-force had no significant impact on the spatial trajectory after switching to overdamping. That is, prior force experience had no differential effect on the spatial transition kinematics. However, the transitions underdamping-to-overdamping and underdamping-to-null force did produce differently strong transition effects. These results indicate that exposure to the new force rather than previous force-field experience is responsible for transition- and after-effects. In a second experiment, we investigated whether learning was law-like—that is, whether it generalized to unvisited workspace. Subjects were tested in new, unvisited workspaces in the null-force condition after sufficient training in either force condition. The occurrence of transferred after-effects indicated that adaptation to both positive and negative damping was mediated by rule-based rather than exclusive associative processes.

Key Words: arm movement, motor control, motor learning, inverse dynamics, sensory-motor integration

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Research in systems neuroscience suggests that humans control goal-directed reaching movements by employing an inverse model of the physical properties of the reaching arm (Blakemore, Goodbody, & Wolpert, 1998; Blakemore, Wolpert, & Frith, 2000; Ghahramani & Wolpert, 1997; Kalveram, 1991; Neilson, Neilson, & O'Dwyer, 1992, 1998; Shadmehr & Mussa-Ivaldi, 1994; Thoroughman & Shadmehr, 1999). Such an inverse model generates the feedforward motor command necessary to produce a desired trajectory within a desired timeframe (Kalveram, 1998; Kawato, 1999). Empirical evidence for the existence of the inverse dynamics models (IDM) comes from studies that exposed humans to external velocity-dependent force-fields (damping) during the execution of goal-directed arm movements. Participants adapted to the new situation by compensating the imposed forces (Gandolfo, Mussa-Ivaldi, & Bizzi, 1996; Lackner & Dizio, 1998; Shadmehr & Mussa-Ivaldi, 1994). Typically, a transition from the null-field to the force-field produced a trajectory deviation in the direction of the damping force, termed the *transition effect* (Shadmehr & Mussa-Ivaldi, 1994). After sufficient training, subjects adapted to the force-field, and the initial trajectory kinematics were restored. Switching off the force-field led to *after-effects* with deviations in the opposite direction. Similar effects have been demonstrated for "internal" loads such as joint interaction torques in two-joint movements (Gottlieb, Song, Hong, Almeida, & Corcos, 1996).

Currently, two explanations are promoted to explain such adaptive ability. Internal model theory proposes that adaptation is mediated by the update of a law-like representation of the altered limb dynamics (Gandolfo et al., 1996; Shadmehr & Mussa-Ivaldi, 1994; Wolpert & Ghahramani, 2000). The update could be accomplished by estimating the damping coefficient of the imposed force-field and using it to program compensatory muscle torques. Gandolfo et al. (1996) indeed found evidence that the motor system approximates the viscous force-field during the adaptation process. Alternatively, adaptation could result from a revised local link of state-space coordinates. According to this view, the central controller modifies a neuronal look-up table by correlating the central input with the output of the motor system. These correlations could be regarded as a local mapping between the state of the arm in kinematic parameters and the corresponding forces imposed on the system at every distinct state (Shadmehr & Mussa-Ivaldi, 1994). Although partly contradictory to the internal model hypothesis, this idea is not new. Marr (1969) and Albus (1971) assigned such a state-space associating function to the cerebellum. They assumed that the convergence of climbing and mossy fibers onto the Purkinje cell of the cerebellar cortex would provide the necessary anatomical architecture to perform such an associative function. In addition, Hein and Held (1962) theoretically argued in favor of this associative hypothesis.

The two competing theories make different predictions. The internal model hypothesis predicts that a rule of the physical properties of the limb is the basis of the feedforward controller. Thus, training in one workspace should generalize to other workspaces even when movement had not yet been trained in those workspaces. The central nervous system (CNS) assumes the validity of the currently employed inverse model as long as it is not informed otherwise. That is, if a limb is moved in an untrained portion of its workspace after removal of the force-field, the CNS initially assumes that the force field is still present. Consequently, after-effects would be expected similar to those seen in the trained region. Such after-effects are termed *transferred after-effects*, since they are transferred to the

untrained region. In contrast, if adaptation is implemented as hypothesized by the state-space theory, learning is restricted to trained workspaces. Only those entries in the look-up table can be updated where forces were experienced. Hence, no update should occur in yet unvisited workspaces, since forces, joint angles, and velocity of the limb are unknown and can consequently not be associated. The state-space hypothesis therefore predicts the absence of transferred after-effects when tested in a new workspace after switching off the force field.

An array of recent studies provided psychophysical support for the concept of a law-like representation of limb dynamics (Gandolfo et al., 1996; Shadmehr & Mussa-Ivaldi, 1994; Wolpert & Ghahramani, 2000). However, current evidence is not yet entirely unequivocal in its support of the internal model concept. For example, it is not known whether changes in force direction and magnitude have a differential effect on adaptive motor behavior. How do adaptation rates vary as the physical stimulus is systematically altered? And, equally important, how fast and how complete is the process of re-adaptation to the previous null-force condition? These questions are essential for an understanding of the computational mechanisms underlying the adaptive responses. They also ought to shed additional light on the controversy about what theory best explains this form of force adaptation.

Thus, the aim of the present study was two-fold: First, we investigated the effects of various damping forces on single-joint, forearm flexion movements. The imposed damping forces varied in magnitude and direction. In a second experiment, we examined whether adaptation to different damping forces is mediated by law-like mechanisms. Both experiments should enhance our understanding about the possible nature of IDM in human motor control.

Methods

Experiment 1

Subjects. Thirteen subjects (7 female, 6 male, aged 20 to 40) participated in this study. All subjects were right handed, and none of them had a history of previous neurological disorders. Participants were briefed about the procedure of the experiment and gave informed consent. The local ethics committee approved both experiments.

Apparatus. Subjects performed single-joint elbow flexion movements in the horizontal plane with their right forearm. The forearm was inserted into an orthosis, which was attached to the lever arm of a manipulandum (see Figure 1a). The wrist joint was fixed and not free to move. Shoulder flexion/extension, abduction/adduction, and shoulder rotation was not possible. The shoulder could, in theory, translate, if the trunk were moved backward. However, this was discouraged and monitored by the researcher throughout the experiment.

Damping forces were generated by a torque motor attached to the shaft of the manipulandum. The amplitude of the damping force applied to the manipulandum was proportional to the angular velocity of the subject's arm movement:

$$F = -B\omega \quad (1)$$

where B is the damping coefficient and ω is angular velocity. The torque motor received its input from a computer. Two types of damping were applied: 3 cNm/s° and -2 cNm/s° . A negative damping coefficient translated into a movement-assist-

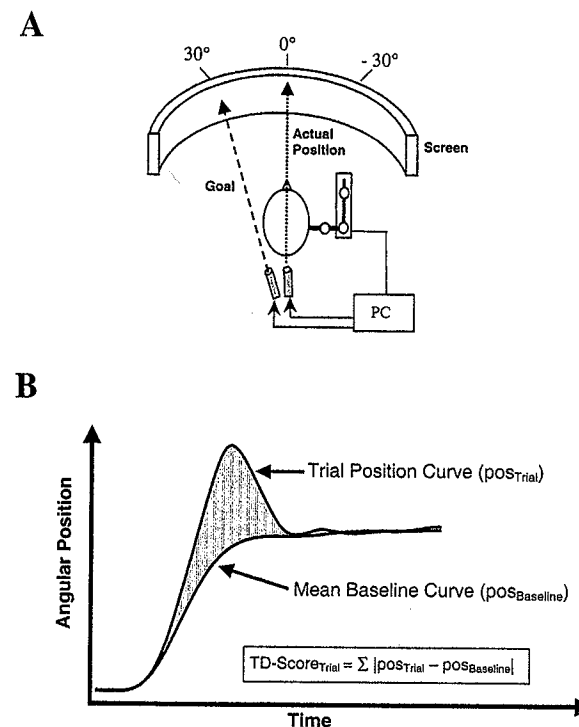


Figure 1 — Arm robot, apparatus, and TD score. (A) Subjects sat in the center of a convex screen in about 1.5-m distance. Subjects viewed two illuminated arrows on the screen, one indicating the goal position (goal arrow), the other indicating the actual position of the arm (position arrow). (B) The TD score between two curves is a measure to quantify the difference between current curve and baseline curve. To compute the TD score for a given trial, for each sample the position value of the baseline curve ($pos_{Baseline}$) is subtracted from the position value of the actual curve (pos_{Trial}). To obtain the TD score value, the absolute results are subsequently summed up. TD score values are degree-seconds.

ing velocity-dependent flexor force; a positive value implied that the torque motor generated an extensor force that opposed forearm flexion. Angular position and velocity were recorded by a potentiometer and tachometer at the motor shaft, sampled at 520 Hz and digitized with a 12-bit analog-to-digital converter (Burr-Brown MPV 904). Digital data were stored on hard disk and then filtered with a 4th-order Butterworth filter at a cutoff frequency of 10 Hz using MATLAB software.

Participants viewed two illuminated arrows on a convex screen about 1.5 m in front of them. One arrow—the goal arrow—corresponded to the start position at 0°, the other to the actual angular position of the forearm. Zero-degree angular position corresponded to 90° angular position of the elbow (angle between elbow and upper arm). The subject's were seated in the center of the screen. At the beginning of each trial, the arm-position arrow corresponded to the start position.

Procedure. Prior to movement onset, subjects were instructed to align goal- and arm-position arrows at 0° . Subsequently, the goal arrow jumped to a 30° position on the screen, and subjects performed a goal-directed forearm flexion movement to the 30° target position.

Each subject performed 141 trials. Trial duration was 2 s. The inter-trial interval was approximately 2 s. During the first 15 and the final 9 trials of the experiment, no external damping was applied. The first 2 trials served as calibration trials and were discarded from analysis. In 14 trials, the goal arrow moved sinusoidally with various amplitudes (20 to 40°) to the left and right from the start position. The sinusoidal motions were interspersed between the step-like trials to brake the monotony of the trials. These sinusoidal movement trials were not subject to further analysis. Altogether, 125 trials were analyzed (141 trials in total minus 14 sinusoidal movements minus 2 calibration trials).

A schema of the experimental design is shown in Table 1. The experiment consisted of 15 consecutive blocks of trials, each block containing a series of 9 trials with the same damping factor (with the exception of the first block, which contained 15 trials). The sequence of blocks was balanced to produce five types of transitions. Each transition appeared at least twice (see Table 1). The tested types of transitions were: 0 to 3 cNms/ $^\circ$, 3 to 0 cNms/ $^\circ$, 0 to -2 cNms/ $^\circ$, -2 to 0 cNms/ $^\circ$, and -2 to 3 cNms/ $^\circ$. During transitions with incrementing damping (increase in

Table 1 Design of Experiment 1 With Every Block Consisting of 9 Trials, Except the First Which Consisted of 15 Trials

Block	Damping factor	Direction of applied force
1	0	
2	3	Extensor
3	0	
4	-2	Flexor
5	0	
6	-2	Flexor
7	3	Extensor
8	0	
9	-2	Flexor
10	0	
11	3	Extensor
12	0	
13	-2	Flexor
14	3	Extensor
15	0	

Note. Subjects were exposed to the same damping condition in each trial within one block. The first column refers to the block number, the second column to the type of damping, and the third column depicts the direction of the applied force: Positive damping corresponds to movement-opposing extensor force, negative damping to movement assisting flexor force. Transition effects occur at the beginning of each block, following the change of damping factor.

damping coefficient), subjects experienced an extensor force, during decrementing damping, a flexor force.

Experiment 2

Subjects. Twenty-four subjects participated in this study (12 female, 12 male). The female participants' age ranged from 20 to 30 years, and the average age was 23.67 years. The male participants' age ranged from 24 to 38 years, and the average age was 27.0 years. All subjects were right handed, and none of them had a history of previous neurological or medical disorders. All subjects were newly recruited and were naive with respect to the goals of the experiment. They were assigned to the respective experimental conditions in a counterbalanced fashion so that each group comprised an equal number of male and female members. Participants were briefed about the procedure of the experiment and gave informed consent. The local ethics committee had approved the experimental procedure.

Apparatus. The apparatus was the same as described in experiment 1.

Procedure. Subjects were instructed to perform a goal-directed forearm flexion movement to the respective target position. Prior to movement onset, the two arrows were aligned at -30° or 10° , depending on the experimental condition. Subsequently, the goal arrow jumped either to a position of 0° (initial position -30°) or 40° (initial position 10°) on the screen. Thus, two workspaces were determined on the screen. A "right" workspace with movements from -30° to 0° , and a "left" workspace with subjects moving from 10° to 40° . Hence, initial and final arm position and elbow joint-angle differed between left and right workspaces. Left and right workspaces are illustrated in Figure 2.

It was emphasized that the subjects should move as quickly and as accurately as possible. At the end of each trial, the target arrow jumped to the starting position of the subsequent trial, and subjects extended their forearm back to the designated start position. During flexion movements, subjects received continu-

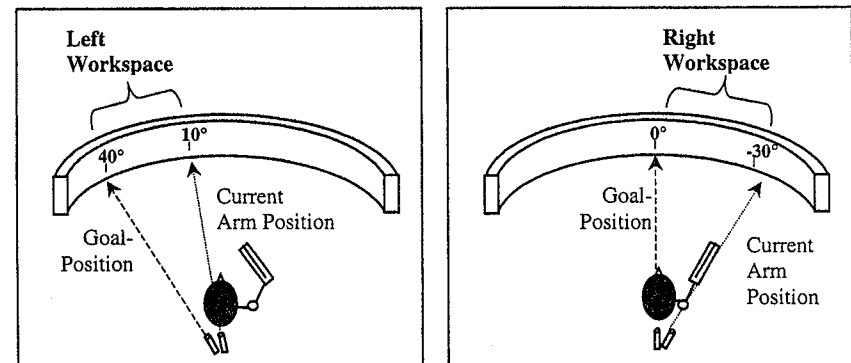


Figure 2 — Left and right workspaces. Left workspace stretches from 10° to 40° on the convex screen; right workspace stretches from -30° to 0° . Depending on the experimental group they were assigned to, subjects either moved in the left or right workspace. Subjects performed flexion movements irrespective of the workspace in which they moved, thus starting movement at 10° and ending at 40° (or 30° and 0° , respectively).

ous visual feedback about the actual arm arrow's position. To avoid additional learning effects due to a visual error feedback signal, the arm position arrow was switched off during the extension movement, and visual position feedback was only available prior the onset of the movement and after movement was terminated. For the purpose of this study, only the flexion movements were analyzed.

During specific trials, the torque motor generated damping forces of either 3 cNms/° or -2 cNms/°. Each experimental block contained 12 trials. Five blocks were administered leading to a total of 60 trials. In each block, subjects were alternately exposed to either no force or damping force. In our design, damping force was switched on in blocks 2 and 4 and switched off in blocks 3 and 5. Consequently, any effects observed in blocks 2 and 4 were *transition-effects*, and any effects observed in blocks 3 and 5 were *transferred after-effects*.

Twenty-four subjects were randomly assigned to one of the four conditions defined by the sequence of workspaces and the type of damping force, with 6 subjects in each group. Each group contained an equal number of male and female participants. Two groups performed movements in the negative damping conditions, and two groups performed in the positive damping condition. In all conditions, subjects alternately moved in a null field and a damping force for as long as one block (12 trials), always starting with a no-force block. For each damping condition, one subgroup was assigned to the condition "Left workspace first", and the other subgroup to the condition "Right workspace first". In our design, order of workspace and sequence were balanced to control for potential side effects or sequence effects. The complete experimental procedure is depicted in Table 2.

Table 2 Design of Experiment 2 With Each Block Containing 12 Trails

Block	Groups 1 or 3 <i>Left-workspace-first</i>	Groups 2 or 4 <i>Right-workspace-first</i>	Damping factor
1 st Block	Left	Right	0
2 nd Block	Right	Left	-2 or 3
3 rd Block	Left	Right	0
4 th Block	Left	Right	-2 or 3
5 th Block	Right	Left	0

Note. Force conditions differed between groups. Flexion movements of Groups 1 and 2 received trials with a flexor force (damping factor -2) during the 2nd and 4th blocks, whereas Groups 3 and 4 received an extensor force (damping factor 3) during the same blocks.

Measurements

Angular position and velocity were recorded for each trial. The length of each trajectory was standardized to 900 samples. Curves were aligned to movement onset. Movement onset was determined as the time when angular position exceeded 2°. All data preceding the movement onset by 100 samples were discarded. Only flexion movements were considered for analysis; the data representing the extension movement while moving the position cursor back to the starting position were ignored.

1. Baseline Trajectory. In experiment 1, the individual *baseline trajectory* was determined for each subject as the mean trajectory of trials 3–15 and the last 8 trials. Trials 1 and 2 were calibration trials and were discarded from further analysis.

In experiment 2, the baseline curve was defined as the mean curve of trials 4 to 12 in the first no-force condition.

2. Trajectory Difference Score (Only Experiment 1). We analyzed the position trajectory as a function of time. To measure and quantify the difference between a given position curve and the baseline curve, we computed the cumulated absolute difference between the curves. This difference was termed the *trajectory difference score* (TD score) and computed using the following equation:

$$TD\ score_{Trial} = \sum |pos_{Trial} - pos_{Baseline}| \quad (2)$$

where *pos* stands for angular position (see also Figure 1b). A high TD score value indicates a large difference between the two curves concerning time course and amplitude. A low TD score value indicates a great similarity between the curves. TD score is a measure for the surface of an area in the degree-seconds plane; thus, TD score units are in degree-seconds.

3. Peak Angular Velocity (Only Experiment 2). TD score measures the difference between trial and baseline but is insensitive for the distinction between hyper- and hypometric movements. Since transferred after-effects are defined as mirror images of transition effects, hypermetric transition effects would be associated with hypometric transferred after-effects and vice versa. In experiment 2, it is therefore necessary to contrast hypermetric to hypometric movement. For that reason, a second measure was introduced to draw the distinction: peak angular velocity (*V_{max}*). *V_{max}* is defined as the maximum value of the first derivative of the position curve. Increased peak angular velocity is considered characteristic for hypermetric movements, whereas decreased peak angular velocity is considered characteristic for hypometric movements. Although the proper definitions of hypermetric and hypometric movements refer to displacement and not to velocity, these terms may also be characterized by increased and decreased movement velocity.

Data Analysis

Transition Effects (Both Experiments). A transition effect was defined as the disturbance in movement performance caused by the change in damping force (transition) imposed on the arm. It was expected that a change in damping force results in the deviation of time course and amplitude of the position curve. The transition effect was quantified by comparing the TD or *V_{max}* scores succeeding a transition (post-transitional trial) with the scores prior to the transition (pre-transitional trial).

Transition types 0 to 3, -2 to 0, and -2 to 3 appeared twice, and transition types 3 to 0 and 0 to -2 appeared four times in our design. It is generally possible that, due to training or habituation, transitions at the end of a session produced weaker effects than earlier transitions. We therefore investigated if any order effects were observed after repeated exposure to the same type of transition. Order effects were defined as a difference in the magnitude after repeated exposure. To account for possible order effects, statistical comparisons were carried out using a two-factorial General Linear Model (GLM) procedure for repeated measurements with the two within-subject factors *Transition* (pre-transitional trial vs. post-transitional trial) and *Sequence* (first transition vs. second transition vs. third vs. fourth). Significance levels were Bonferroni- α -adjusted. After adjustment, significance was assumed when the significance level did not exceed $p < .01$.

Differential Transition Effects (Only Experiment 1). For each force transition, we calculated the TD score difference between the post- and pre-transitional trial to obtain a measure of the amplitude of the transition effect. For each type of transition, these difference values were then averaged for each subject. A GLM procedure with simple contrasts was carried out to test for amplitude differences between the five types of transition.

Time-to-Adaptation (Only Experiment 1). Adaptation was defined as the restoration of baseline performance. To quantify adaptation speed after each type of transition, we determined *trials-to-baseline*. For each individual, we calculated the number of trials needed until the individual baseline TD score was reached or crossed. Data were then averaged within each subject for each type of transition. To determine the impact of the type of transition on adaptation speed, a GLM with simple contrasts was used to test for differences in the adaptation duration.

Transferred After-Effects (Only Experiment 2). When tested in the untrained workspace, we expected that removal of the extensor force (positive damping) would result in hypermetric trajectories and that hypometric trajectories would be seen after turning off the flexor force (negative damping). To determine the amplitude of possible transferred after-effects, the peak angular velocity (V_{max}) of each post-transitional trial was then compared with its pre-transitional trial peak velocity. A GLM procedure with simple contrasts was carried out to test for amplitude differences between pre- and post-transitional trials.

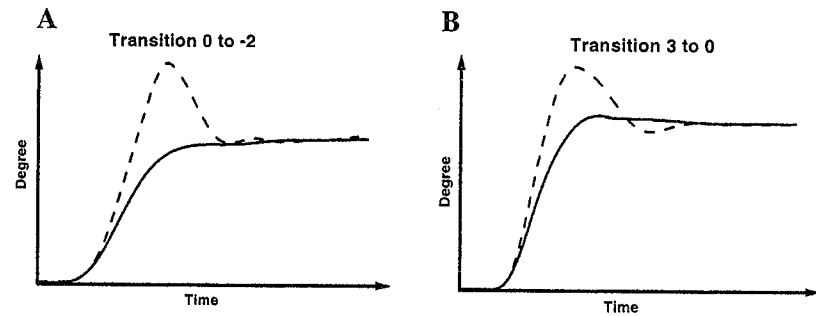
Results

Experiment 1

The transition types can be classified into two categories: decreting damping (pre-transitional damping factor greater than post-transitional damping factor) and incrementing damping. Decrementing damping provoked a characteristic hypermetry in the position trajectory resulting in a typical target overshoot and subsequent correction movement (see Figures 3A, 3B). Velocity peaks were systematically higher compared to baseline performance. Incrementing damping produced a characteristic hypometry in the position trajectory. Contrasted to baseline performance, the movement duration (movement onset to goal reaching) was systematically prolonged, and the slope of the position trajectory was less steep. The velocity peaks were lower compared to baseline performance (see Figures 3C-E).

Note that the shapes of the position curves were similar for all decreting transitions and for all incrementing transitions. The type of transition had an influence on the amplitude of the transition effect rather than the sign of the damping factor (i.e., negative or positive damping).

Underdamping: Decrementing Damping Coefficient



Overdamping: Incrementing Damping Coefficient

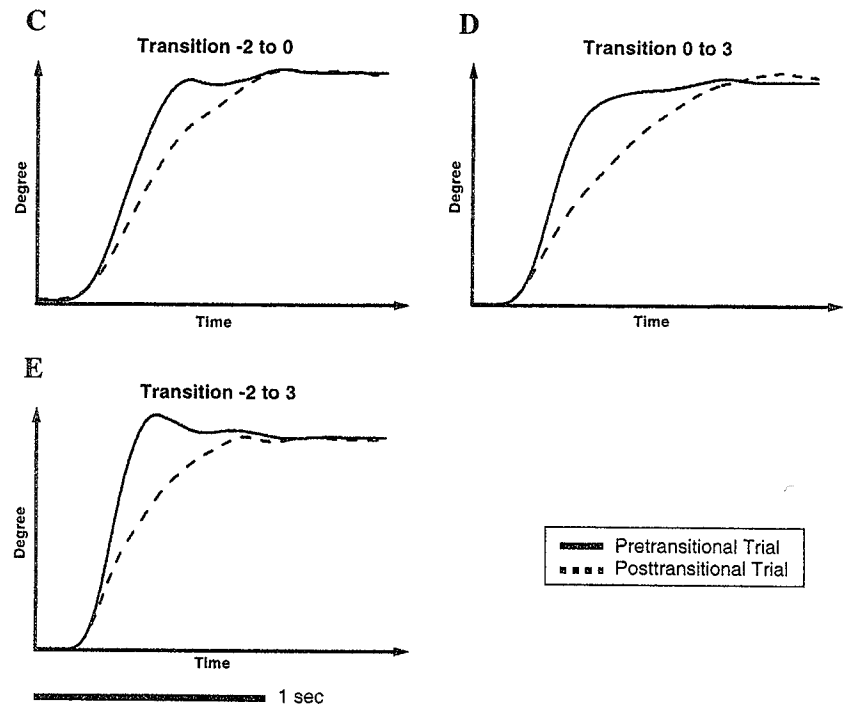


Figure 3A-E — Exemplar curves before and after a transition. Figures 3A and 3B depict examples of underdamping (decrementing damping coefficients), and Figures 3C to 3E depict examples of overdamping (incrementing damping coefficients).

Transition Effects. Modifying the external dynamics produced notable changes in the angular position trajectory. Figure 4A illustrates that the post-transitional TD score differed significantly from the pre-transitional TD score in four out of five transitions (Transition_{0 3}: $F_{1,12} = 76.9, p < .001$; Transition_{0 -2}: $F_{1,12} = 70.8, p < .001$; Transition_{-2 0}: $F_{1,12} = 10.8, p < .01$; Transition_{-2 3}: $F_{1,12} = 30.9, p < .001$). After Bonferroni- α -adjustment, transition type 3 to 0 did not produce a significant transition effect for TD score (Transition_{3 0}: $F_{1,12} = 7.767, p = .016$). However, the group means show the same trend that was seen in the other comparisons.

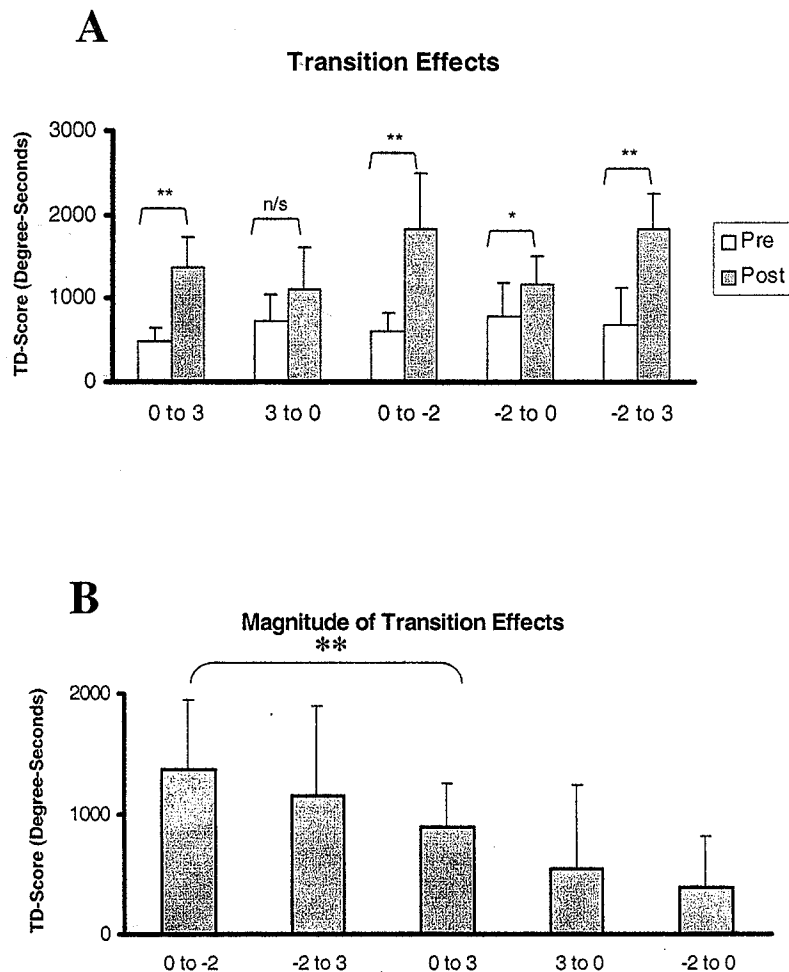


Figure 4— Transition effects and differential magnitude of transition effects. (A) For each type of transition, mean TD scores and standard deviations of the pre-transitional trials are displayed with respect to the mean TD score of the post-transitional trials (* $p < .01$, ** $p < .001$, n/s: not significant, bars: standard deviations). (B) Differential magnitude of transition effects—average difference between post-transitional and pre-transitional TD score (** $p < .001$). For further p and F values, please refer to text.

Each type of transition appeared at least twice. No order or training effects were observed in transition trials. There was no significant difference in the transition effects between the repetitions of the same type of transitions (Transition_{0 3}: $F_{1,12} = 6.213, p < .028$; Transition_{3 0}: $F_{1,12} = 1.041, p < .328$; Transition_{0 -2}: $F_{1,12} = 2.607, p < .132$; Transition_{-2 0}: $F_{1,12} = .305, p < .591$; Transition_{-2 3}: $F_{1,12} = 6.625, p < .024$).

Transitions to null-force systematically produced smaller transition effects than transitions diverging from null-force (see Figure 4B). Strongest effects were caused by transition 0 to -2 (mean TD score: 1361, SD : 583), which significantly differed from all other transition effects except -2 to 3 (Transition_{0 -2} vs. Transition_{-2 3}: $F_{1,12} = .531, p < .48$; Transition_{0 -2} vs. Transition_{0 3}: $F_{1,12} = 9.958, p < .008$; all subsequent differences were also assumed significant). The weakest effect was caused by transition -2 to 0 (mean TD score: 388, SD : 426). In addition to the significant difference to type 0 to -2, transition type -2 to 0 significantly differed from transition type -2 to 3 ($F_{1,12} = 18.612, p < .001$). No further significant differences were observed.

Time-to-Adaptation. After a force transition, baseline performance was generally restored within two to five trials, depending on the preceding type of transition. Typical adaptation curves of 2 participants are displayed in Figures 5A and 5B.

Figure 5C depicts the averaged inter-individual adaptation curves for every type of transition with respect to the mean baseline level. These exemplar data suggest that adaptation was fastest after transition 3 to 0 and slowest after transition -2 to 3. Statistical analyses confirmed these observations. Adaptation times for transitions converging to null-force (3 to 0 and -2 to 0) were significantly shorter than their respective “mirror condition” (0 to 3 and 0 to -2; see Figure 5D; Trials-to-Baseline_{3 0} vs. Trials-to-Baseline_{0 3}: $F_{1,12} = 10.884, p < .01$ and Trials-to-Baseline_{-2 0} vs. Trials-to-Baseline_{0 -2}: $F_{1,12} = 10.117, p < .01$). There was no significant difference in adaptation time between transition 3 to 0 and transition -2 to 0 (Trials-to-Baseline_{3 0} vs. Trials-to-Baseline_{-2 0}: $F_{1,12} = 5.66, p = .035$). For the transition from -2 to 3, which participants considered most “unnatural”, trials-to-baseline ranged between 4 and 6 trials.

Experiment 2

Transition Effects. As in experiment 1, subjects exhibited transition effects in all cases and all damping conditions. Peak velocity in post-transitional trials consistently differed from pre-transitional trials (damping factor -2: Trial₁₂ vs. Trial₁₃: $F_{1,8} = 76.8, p < .001$; Trial₃₆ vs. Trial₃₇: $F_{1,8} = 106.0, p < .001$; damping factor 3: Trial₁₂ vs. Trial₁₃: $F_{1,8} = 69.2, p < .001$; Trial₃₆ vs. Trial₃₇: $F_{1,8} = 77.8, p < .001$).

Transferred After-Effects. Transferred after-effects were detected after removing either the flexor force (negative damping) or extensor force (positive damping), which happened at the transitions between blocks 2 and 3 or between blocks 4 and 5. Figures 6A and 6B show examples of such transferred after-effects (first trial after force removal) with respect to the last trial prior to force removal. To contrast transferred after-effects to transition effects, the first post-transitional trial after force onset (before adaptation took place) was added to the graph. Note that the transferred after-effects were mirror images of the transition effects: Whereas the onset of negative damping produced a hypermetric trajectory, turning off the

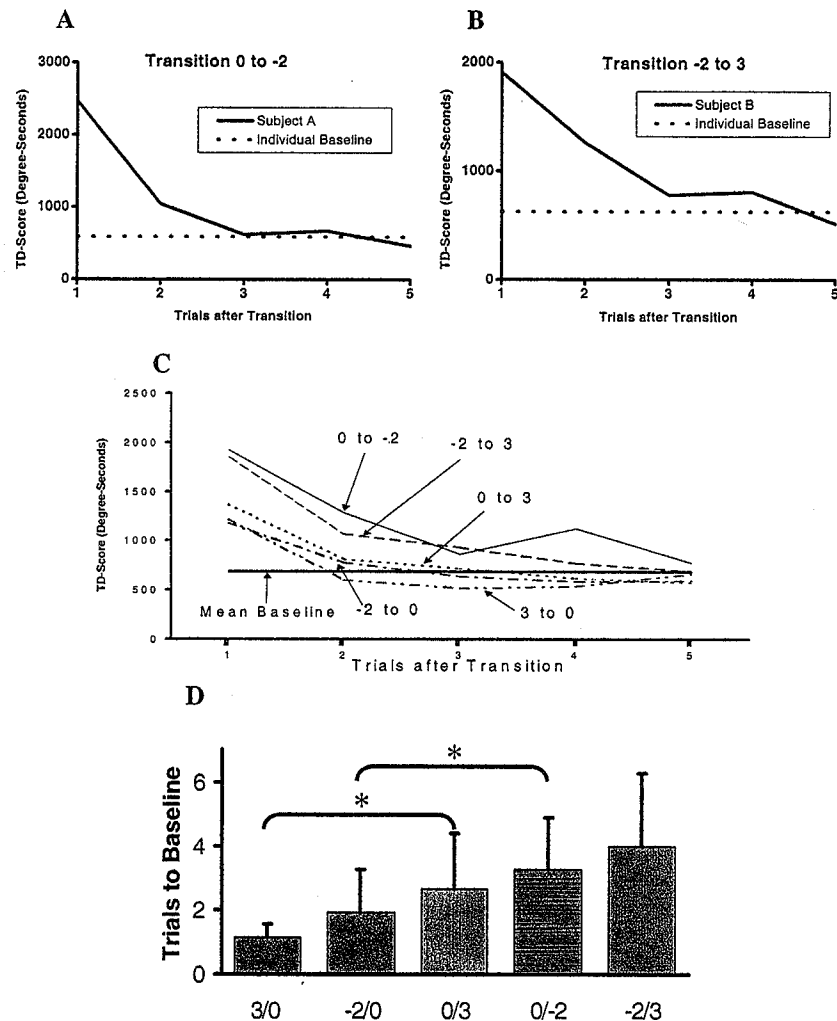


Figure 5 — Adaptation. (A) and (B) Adaptation curves: Exemplar data. Each curve is plotted against the first five trials following the transition. The dotted line represents the subject's individual baseline. Figure 5A displays the adaptation process following transition 0 to -2; Figure 5B displays the adaptation process following transition -2 to 3. (C) Adaptation to baseline performance: Mean adaptation curve for each transition and the inter-individual baseline level. For each transition, TD scores from the five trials following each transition were averaged within each subject and then averaged over all subjects. The graph shows that all mean curves converge to approximately baseline level in a smooth and non-linear fashion. In all cases, adaptation is fairly quick, and baseline level is restored after about one to five trials following the transition. (D) Figure 5D illustrates the adaptation rate dependent on the transition. The graph points up the average number of trials needed after each type of transition to reach or cross baseline level performance (mean rate and standard deviation). The brackets indicate significant difference in adaptation speed ($*p < .01$).

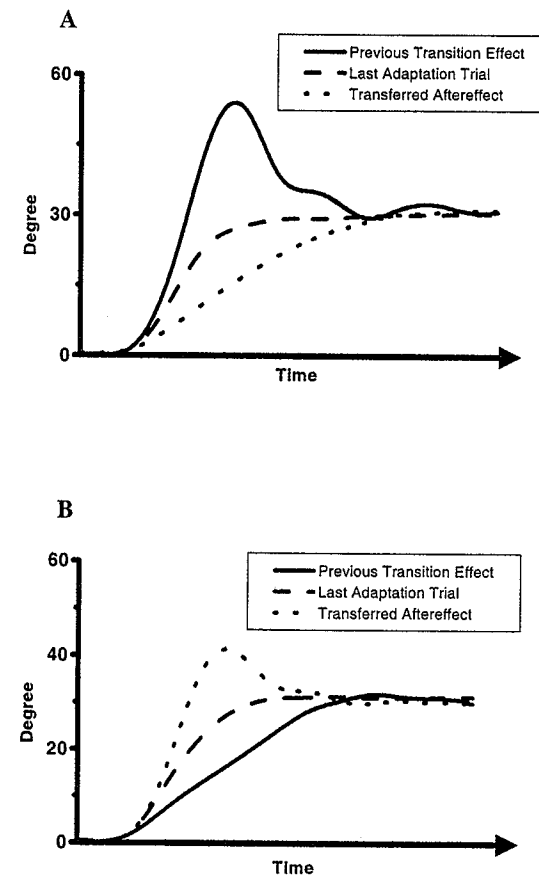


Figure 6 — Exemplar position curves of the previous transition effect (first trial after force onset) of the last adaptation trial (trial preceding force removal) and of transferred after-effect (first trial after force removal and test in an untrained workspace) in experiment 2. Note that removal of the force (\rightarrow transferred after-effect) is always accompanied by a change in workspace (either left to right or right to left), whereas addition of the force (\rightarrow transition effect) is never associated with a change in workspace (either right-right or left-left).

negative force resulted in hypometric path. Conversely, the onset of positive force caused hypometric motion, and turning off the positive force resulted in hypermetric movements. Hence, switching off negative damping appears to have similar effects as switching on positive damping and vice versa, even if tested in an untrained workspace.

Figure 6A displays transferred after-effects after switching off negative force, and Figure 6B displays transferred after-effects after switching off positive force. The curves demonstrate that switching off the negative force clearly leads to hypometric movement, whereas switching off the positive force results in hypermetric movement, even though subjects were tested in an untrained workspace. Transferred after-effects were mirror images of the transition effects.

Accordingly, the analysis of V_{max} revealed significant transferred after-effects for both damping conditions and at both transition points—that is, after the return to a null-force in an untrained workspace in blocks 3 and 5 (damping factor -2 : Trial₂₄ vs. Trial₂₅: $F_{1,8} = 40.9$, $p < .001$; Trial₄₈ vs. Trial₄₉: $F_{1,8} = 52.8$, $p < .001$; damping factor 3 : Trial₂₄ vs. Trial₂₅: $F_{1,8} = 30.9$, $p < .001$; Trial₄₈ vs. Trial₄₉: $F_{1,8} = 154.1$, $p < .001$). Figure 7 illustrates the statistical comparison of transferred after-effects. Maximum angular velocity was significantly decreased after switching off negative damping and was significantly increased after switching off positive damping.

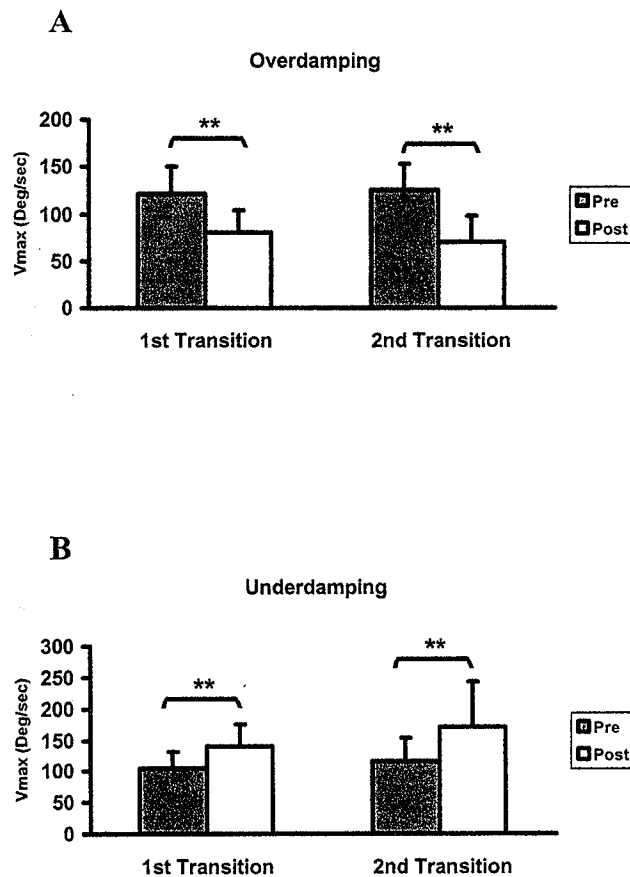


Figure 7 — Transferred after-effects: Statistical comparison of maximal movement velocity after training subjects in a force condition and subsequently removing the force. The bars reflect the averaged V_{max} corresponding to the pre- versus post-transitional trials—that is, before and after force removal (means and standard deviations). In all cases and in all damping conditions, post-transitional trials (trial 25 and trial 49) significantly differed from pre-transitional trials (trial 24 and trial 48). The figures show that removing negative force resulted in a deceleration of arm movement (hypometry, Figure 7A), whereas removing the positive force produced accelerated movement (hypermetry, Figure 7B), $**p < .001$.

Discussion

General Findings

In the present study, switching between different types of external, velocity-dependent damping forces induced transition effects of differential magnitude. Adding a movement assisting flexor force (negative- or underdamping) caused larger trajectory deviations than adding a movement opposing extensor force (positive- or overdamping; see Figure 4). We did not find any linear scaling effects. That is, the magnitude of the transition effects was not proportional to the difference between pre- and post-transitional damping factor. Adaptation of performance took place after all types of transitions. Baseline level was generally restored within two to five trials, and adaptation exhibited in most cases a smooth convergence pattern (see Figure 5). Adaptation rate was correlated with the transition effect: The greater the transition effect, the longer it took to recuperate baseline performance.

In experiment 2, transferred after-effects were observed after switching from an under- or overdamping force. Transferred after-effects were mirror images of the preceding transition effects: Removing the negative force resulted in hypometric movement, and removing the positive force produced hypermetric movement. These results suggest that training movement dynamics in one workspace generalize to the other, untrained workspace.

Transition Effects

Most authors commonly define transition effects as the behavioral consequence of perturbing movement execution by adding a force to the preceding null-force condition (Gandolfo et al., 1996; Kawato, 1999; Lackner & Dizio, 1998; Shadmehr & Mussa-Ivaldi, 1994). After-effects are defined as the consequence of force removal and are generally explained as the neural controller's attempt to compensate a no-longer-existing damping force (Kawato, 1999; Shadmehr & Mussa-Ivaldi, 1994). This definition implies that any added force to the arm's inherent dynamics constitutes an "unnatural" condition that is to be neutralized in order to warrant precise motor control. That is, transition effects are believed to result from changing the "normal" limb dynamics, while after-effects are considered to be the consequence of the previous exposure to additional external forces. Our results are, at least to some extent, inconsistent with this strict definition of after-effects: We found that transitions diverging from a null-force (damping factors 0 to -2 and 0 to 3 cNm/s/°) produced larger transition effects than transitions converging to a null force condition (damping factors -2 to 0 and 3 to 0 cNm/s/°), indicating that re-adaptation was less error-prone. This finding is in line with reports of numerous psychophysical adaptation studies showing that after-effects are generally smaller than transition-effects. However, in our experimental design, transition -2 to 3 constituted a new case, where the classical distinction between transition- and after-effect could not be made: The effects resulted from applying a new damping force rather than returning to the null-force condition. We found that the trajectory deviation after transition types -2 to 3 and 0 to 3 did not significantly differ regarding their magnitude, although both transition types produced significant transition effects (see Figure 4B). These results suggest that the two different types of perturbations did equally affect movement execution. It thus made no difference whether

the subjects had previously experienced the negative damping condition or the no-damping condition. Hence, switching from different forces to one particular force (-2 to 3 and 0 to 3) did not produce differently strong transition effects, whereas switching from the same force to different forces (-2 to 0 and -2 to 3) did produce differently strong transition effects (see Figure 4B). These results indicate that, contrary to common definitions, the exposure to the previous force field does not appear responsible for transition- and after-effects. It is rather the newly added force that produces such effects. Such behavior is indicative of a neural controller that switches between parallel inverse dynamic models—in this case between a highly overtrained model and two models that were just recently acquired.

Transferred After-Effects Indicate a Generalization of Force Adaptation

Subjects adapted quickly to the altered dynamic conditions. In the second experiment, we addressed the question, whether such adaptation can be explained by a law-like representation of movement dynamics. In this experiment, the initial and final elbow joint-angle differed between the two workspaces. Adding a damping force that was strictly associated with only one of the two workspaces resulted in distinct, workspace-dependent joint dynamics. To account for the workspace-specific torque-angle differences during movement, the CNS needed to generate different neural motor commands to rotate the elbow joint. The occurrence of transferred after-effects can only be explained by assuming that subjects anticipated similar force conditions and attempted to compensate damping in the workspace where no damping had been previously experienced. These results argue against a learning process where experienced force and visited space is associated and subsequently stored in some form of look-up table. In contrast, our observations demonstrate that the adaptive representation of dynamics generalized to yet unvisited hemi-fields (see Figures 6 & 7). These findings replicate previous results (e.g., Shadmehr & Mussa-Ivaldi, 1994), but also extend earlier studies by showing that the same adaptation mechanism seems to be applied under different dynamic environments.

Our data are compatible with the theoretical concept of inverse modeling. Since an inverse dynamics model represents the inverse input-output characteristics of the motor system, it should be valid for the entire motion range of the joint. This seems to be true for the generalization of newly acquired inverse kinematics (Latash, 1999). However, numerous studies have shown that models of the inverse dynamics merely exhibit limited extrapolation to unvisited workspaces (Sainburg, Ghez, & Kalakanis, 1999) and that performance smoothly and continuously decays with increasing distance of the actual target to the target of the training session (Gandolfo et al., 1996).

Evidence for Multiple Inverse Models

In the above mentioned studies, transfer took place in a limited fashion and smoothly deteriorated in proportion to the distance to the originally trained area. This implies the existence of multiple internal modules, each corresponding to a specific context. The contribution of these modules to the overall motor output can be differentially weighted, depending on their estimated relevance for the given context (Ghahramani & Wolpert, 1997; Mussa-Ivaldi, 1999; Wolpert & Kawato, 1998).

Previous support for the multiple-module hypothesis comes from studies showing that humans can move in two different force fields without interference when the learning of the two fields is separated in time by at least 5 hours. That is, a stable and precise representation of two different internal models can be retained in parallel (Shadmehr & Brashers-Krug, 1997), with a context-dependent selection of the appropriate module (Kravitz, 1972; Merz, Kalveram, & Huber, 1978). The assumption of multiple parallel modules requires a context-identification process that recognizes the current kinematic and dynamic context and adjusts the gain of the contribution of each module to the overall motor signal. Ghahramani and Wolpert (1997) have shown that two incompatible, competing kinematic modules can exist in parallel and are selected depending on their estimated relevance for the given context. In their experiment, the importance attached to the contribution of one particular module decays in a sigmoidal fashion, with increasing distance to the original training site. Their finding suggests that spatial contiguity is a critical factor in detecting context and selecting the relevant module.

Our results are consistent with the notion that different representations of the dynamics were acquired for each damping condition rather than the continuous update of a single adaptive representation. This view can explain several of our findings: It is safe to assume that for the participants moving in null-force, the condition was overlearned through everyday experience. Therefore, switching off the added force (transition to zero) produced smaller transition effects than exposure to a new damping force. In this respect, after-effects are not believed to result from the exposure to a previous damping force but are simply the consequence of changing to a more automated, overlearned inverse dynamics model. However, if subjects did not return to a null-force, but were exposed to a second, not overlearned force condition (transition -2 to 3), the previous damping force did not significantly influence the trajectory kinematics.

As an alternative to the multiple-module hypothesis, it is conceivable that only one IDM exists in the brain that is continuously updated once the limb dynamics change. Although one cannot fully discard this notion on the basis of our data, previous research as well as our results favor the multiple-module hypothesis. The advantage of the multiple-module assumption is its capacity to combine independent modules to cope with complex task requirements. For example, separate training of a visuo-motor and a dynamic transformation notably facilitated movement, when both transformations were simultaneously presented (Flanagan et al., 1999). Further, the single model hypothesis draws a distinction between a single model of the inverse dynamics and a single model of inverse kinematics. Such networks are capable of performing a dynamic-kinematic transformation but do not allow for the composition of discrete dynamic-to-dynamic or separate kinematic-to-kinematic transformations. However, theoretical work has been done that reconciles the conflicting ideas of single versus multiple internal models (Kalveram, 1992).

Analysis on the Muscle Level

How does the motor controller address and coordinate adaptation and generalization on the muscle level?

Studies of single-joint movements indicate that a single control scheme can be applied at different joints and that differences in kinematic and myoelectric patterns may be explained by the biomechanical constraints of each joint (Pfann et

al., 1998). Under no-force conditions, goal-directed, single-joint movements commonly exhibit a symmetrical, bell-shaped velocity profile (Jaric, Gottlieb, Latash, & Corcos, 1998) that is produced by alternating bursts of agonist and antagonist electromyographic (EMG) activity (Pfann, Hoffmann, Gottlieb, Strick, & Corcos, 1998). In contrast to the alternating innervation pattern under normal conditions, Milner (2002) has shown that, with negative damping, muscle co-contraction is elevated in a wrist movement, possibly to stabilize rapid movements and presumably enhanced by reflex action. Co-contraction declined only gradually after the target was reached (Milner, 2002). This study shows that subjects appear to use different muscle innervation schemes depending on the actual viscosity condition: Alternating biphasic innervation during zero and positive damping versus co-contraction during negative damping.

Under negative damping conditions, antagonist activation appears to be necessary during the early movement phase to brake movement and avoid excessive acceleration (Milner, 2002). Since the common biphasic innervation pattern is characterized by a lack of early antagonist activation, a transition to negative damping initially leads to insufficient retardation and excessive acceleration during the early movement phase.

These considerations might be relevant for the interpretation of the transition effects observed in experiment 1 of the present study. Our results demonstrate that different force transitions had differential effects on movement kinematics. It is possible that a transition from zero damping to negative damping would have required a change of innervation scheme (alternating innervation to co-contraction). Since the transition could not be anticipated, it was impossible to appropriately initiate a change of innervation scheme. This lack of scheme change might account for the observed destabilization of movement execution and the large transition effects.

A transition from zero to positive damping and vice versa, however, did not require a change in muscle scheme but only a shift in the scaling of muscle innervation amplitude (Jaric et al., 1998), eventually leading to smaller transition effects. Finally, a transition from negative damping to zero or positive damping did destabilize movement to a lesser extent than transition to negative damping, since agonist/antagonist compound was already co-contracted and consequently stable against unexpected changes in movement dynamics.

Internal Model Theory Versus Equilibrium Point Control

Although our findings are interpretable within the context of internal model theory, we need to consider that the motor system accomplishes force adaptation through a different mechanism. An alternative view is provided by the equilibrium point hypothesis that abstains from referring to complex inverse dynamics calculations (for review, see Latash, 1993). In contrast to inverse model theory, the λ version of the equilibrium point theory does not assume the direct specification of a force required for movement. It is positional in nature and assumes that movements are produced as the consequence of the shift of a centrally defined equilibrium limb position. According to this view, muscle force is directly dependent on the difference between the muscle's actual length and a threshold length λ for reflex-like motoneuron activation. The crucial parameter controlled by the nervous system is the threshold length λ . Muscle force further depends on length- and velocity-dependent afferent feedback and reflex delays (Latash, 1993).

Gribble and Ostry (2000) have developed a motor-adaptation model that is based on the λ version of the equilibrium point hypothesis. It accounts for motor adaptation to external loads and does not require the complex inverse dynamics computation of compensatory muscle forces as hypothesized by inverse model theory. However, consistent with inverse model theory, their model also assumes a priori knowledge of the relation between position and forces. A priori knowledge of the expected force conditions is essential to guarantee errorless performance in generalization tasks. Thus, uniform with inverse model theory, Gribble and Ostry's model also requires an incorporation of limb dynamics and external loads into the control signal. Therefore, the authors refrain from claiming that their model is entirely incompatible with inverse model theory (Gribble & Ostry, 2000). It rather appears to be an extension of a more general notion of inverse modeling. Gribble and Ostry's model represents a tempting and simple alternative to the complex force computation proposed by inverse modeling. However, it remains unclear whether it proves to be useful in explaining phenomena that inverse model theory can explain, such as adaptation to systems with a wide range of different dynamics or other mechanical environments. Future research investigating the differences (and similarities) between inverse modeling and equilibrium point theory will be necessary to either reject or reconcile the different approaches.

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