

Scaling down motor memories: de-adaptation after motor learning

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Abstract

Although adaptation to novel motor tasks is sometimes a very slow process, de-adaptation is usually extremely rapid. Such rapid de-adaptation is seen in dynamic learning in which subjects can take hundreds of movements to learn a novel force environment but only a few movements to de-adapt back to a normal or “null” force environment. We investigated whether this effect is unique to the null environment or reveals a more general rapid adaptation mechanism by studying how subjects behave when their dynamic environment changes. We observed that after learning a dynamic force field, subjects took longer to de-adapt when the forces were turned off than to adapt to a novel scaled-down version of the experienced field. This demonstrates that rapid adaptation is not unique to the “null” force environment. Moreover, we examined subjects’ ability to adapt from a learned field to either a scaled down field or to a field in which the sign of the forces changed. Even though in both conditions the required change in force output was identical, subjects were significantly faster at adapting to the scaled down field. The result suggests that rapid de-adaptation reflects a capacity to scale down the relative contribution of existing control modules to the motor output.

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While it may take a human subject several hundred movements to learn certain dynamic perturbations, normal behavior is often restored within a few movements after the perturbation is removed [7,13]. This asymmetry between the rate of adaptation to a novel dynamic perturbation and adaptation back to the normal situation (termed de-adaptation) might be explained if the CNS is viewed as having access to a “null” control module for the unperturbed arm in addition to an auxiliary module, located in working memory, for the dynamic perturbation. De-adaptation could then be achieved by switching off the auxiliary module.

Rapid adaptation to a previously experienced dynamic environment is not limited to returning to an unperturbed dynamic environment. Subjects also adapt rapidly when they return to a perturbation experienced several hours earlier. Brashers-Krug et al. [3] had subjects learn an initial dynamic

field and then, after a short break, an equal and opposite field. On returning to the first field their performance was initially poor and they learned slowly. In contrast, when several hours were allowed to pass between learning the fields, adaptation back to the first field became rapid. The passage of time between exposures allows memory of the first field to become more stable or *consolidate* [14,15]. This suggests that the memory of the unperturbed arm can be regarded as a consolidated module that is typically acquired by adulthood [7].

In our first experiment we aimed to determine whether rapid adaptation is unique to thoroughly consolidated dynamics, like those of the unperturbed arm. Our subjects made reaching movements in novel dynamic environments generated by a robotic manipulandum. Subjects learned a field (C) immediately before exposure to either a field of one-third the strength ($C/3$) or to the “null” field (i.e., the robot’s motor were turned off). In the null field the forces acting on the hand due to the passive properties of the manipulandum were small, so that moving in this condition was similar, although not identical, to moving the arm freely. We show that the transition from field C to the novel field $C/3$ is faster than the tran-

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sition from field C to the null field, despite subjects having never previously experienced field $C/3$. This demonstrated that rapid adaptation is not a property unique to consolidated fields. Since adaptation to $C/3$ was faster than re-adaptation to null we hypothesize that subjects were able to scale down their representation of field C to rapidly adapt to both $C/3$ and null. This would explain why both transitions were learned rapidly, and why adaptation to $C/3$ was faster.

In a second experiment we investigated switching between novel fields acting in opposite directions. We know that subjects transition between novel opposing fields slowly relative to de-adaptation to null [13], but this might reflect the greater distance between opposing fields in terms of experienced force (for example the distance from C to $-C$ is twice that of from C to null). We were also interested in whether subjects were able to scale or negate their representation of a field on initial adaptation or subsequent exposures (re-adaptation). Our subjects learned a force field (A), a new force field (B) and then returned to the first field (A). Field B could either act in the same or the opposite direction to field A , but in both conditions the difference between field A and B was identical in terms of the change in force experienced. We found that rapid adaptation is limited to transitions to scaled down fields acting in the same direction and suggest that de-adaptation to null is a manifestation of this behavior.

Thirty-four healthy right-handed subjects (aged 19–27) participated in the study after providing written informed consent. The experiment was approved by the local ethics committee. None of the subjects reported sensory or motor deficits. While seated, subjects grasped the handle of a robotic manipulandum (Phantom Haptic Interface 3.0; Sensable Technologies, Woburn, MA) which they moved to targets located in a horizontal plane. The targets and the position of the hand were represented as 2 cm diameter virtual spheres using a three-dimensional projection system. For full details of the apparatus see [4]. The force exerted by the manipulandum on the hand was servo-controlled at 1 kHz to create a velocity-dependent rotary force field, F_k , according to the equation:

$$F_k = k \begin{bmatrix} 0 & -1 \\ 1 & 0 \end{bmatrix} \begin{bmatrix} \dot{x} \\ \dot{y} \end{bmatrix}, \quad (1)$$

where F_k is the vector of forces acting in the horizontal plane, \dot{x} and \dot{y} are velocities in the horizontal plane and the parameter k ($\text{N m}^{-1} \text{s}^{-1}$) represents the viscosity of the field. The parameter k was varied to alter the dynamic environment between stages in the experiment. When the motors are turned off subjects adapt to the manipulandum dynamics very quickly. We consider this condition (F_0) a close approximation to the “null” field.

Subjects made out-and-back movements to one of eight targets from a central starting position located 10 cm below and 22 cm in front of the shoulder level in the subject’s mid-sagittal plane. The targets were equally spaced on a circle of radius 15 cm centered on the starting position and in the hori-

zontal plane. Subjects were instructed to move their hand out to the target and back to the starting position in a single, quick, continuous motion and were asked not to make corrective adjustments during the movement. A delay of 1.5 s separated the completion of one trial and the presentation of the next target. A warning message was displayed in the workspace immediately following any movement which took less than 500 ms or more than 700 ms to complete. The targets were presented in sets of eight movements called “cycles”, and the directions were randomized within a cycle. Prior to beginning the experiment all subjects performed a familiarization block of 40 trials in which the manipulandum did not apply any forces.

In the first experiment 18 subjects made 320 movements in a force field with $k = 12 \text{ N m}^{-1} \text{ s}^{-1}$, which we refer to as F_{+12} followed immediately by 160 movements in either F_{+4} ($n = 9$) or the null field F_0 ($n = 9$). Three catch trials, in which the field changed to F_{+4} , were included on trials 263, 282 and 303.

The second experiment consisted of 640 consecutive trials divided into four stages labeled 1, 2, 3 and 4. Each stage consisted of 160 trials (i.e., 20 cycles of eight trials). The viscosity of the dynamic environment imposed by the manipulandum changed between stages. Since there was no pause between stages, subjects were unaware of when the dynamic environment would change. Sixteen subjects were randomly assigned to one of two groups of eight people. During stages 1 and 3 the manipulandum generated F_{+4} . The forces subjects experienced in stages 2 and 4 depended on their group. For the “+8” group the forces experienced in stages 2 and 4 tripled in magnitude from F_{+4} to F_{+12} , while for the “-8” group the forces reversed direction F_{+4} to F_{-4} . Hence, all subjects experienced forces that, for a given velocity, differed from those in F_{+4} by $8 \text{ N m}^{-1} \text{ s}^{-1}$ but acted in either the same (+8 group) or the opposite (-8 group) direction. Stage 2 also included eight catch trials, in which F_{+4} was temporarily reinstated. The catch trials occurred at approximately equal intervals across stage 2. The intervals between catch trials were not exactly equal to prevent subjects anticipating when they would occur. Stages 3 and 4 were repetitions of stages 1 and 2. After every 56 trials subjects were given a rest period of approximately 30 s to prevent excessive fatigue, and there was no way for subjects to anticipate the transition between stages.

Note that the F_{+12} to F_{+4} group in experiment 1 experienced the same change in force as both groups in experiment 2, but with no prior experience of F_{+4} . This allows us to compare the results between experiments.

The three-dimensional position of the hand (center of the manipulandum handle) was recorded at 200 Hz using the encoders of the manipulandum. To quantify learning of the fields, for each trajectory we calculated the mean absolute perpendicular displacement (MPD) from the line between the starting point and the target. This measure was particularly suitable because the forces acted perpendicular to the direction of movement.

Learning was examined by fitting the following falling exponential model to the learning curves of individual subjects trials:

$$E(i) = \alpha + \beta e^{-i/\tau} \quad (2)$$

In the model, E is the MPD on trial i relative to the start of a stage, α is a scalar offset representing a subject's performance learning plateau, β is the gain and τ represents the time constant of adaptation.

We used parametric statistics except where the data deviated from a normal distribution. Accordingly, we employed non-parametric statistics when comparing time constants (τ).

In our first experiment all subjects learned F_{+12} for 320 movements and were then required to learn either F_{+4} or return to the null field F_0 . The mean absolute perpendicular displacement (MPD) of the three catch trials, in which F_{+4} was experienced, and the first trial after switching to F_{+4} were 0.80 ± 0.07 cm and 0.84 ± 0.07 cm.

We calculated the mean strength of the peak force applied to the hand during each trial of experiment 1. As expected, the magnitude of the peak forces experienced by subjects in field F_{+12} (9.48 ± 0.38 N) were approximately three times greater than those experienced in F_{+4} (2.63 ± 0.05 N).

The data from this experiment, for trials immediately following the transition to F_{+4} or the null field F_0 , are summarized in Fig. 1 which shows that the null group (F_0) adapts slower than the F_{+4} group. Fitting the exponential model (see Eq. (2)) to the first 40 individual trials of the MPD data from the F_{+4} group gave a median time constant of $\tau = 2.8$ (lower quartile, upper quartile: 1.5, 3.4) trials (nonlinear least squares fit, median $R^2 = 0.34$, minimum $R^2 = 0.15$). Fitting the first 40 individual trials of the MPD data from the null field group gave a median time constant of $\tau = 4.5$ (lower quartile, upper quartile: 4.3, 5.0) trials (nonlinear least squares fit, median $R^2 = 0.52$, minimum $R^2 = 0.30$). This was higher than for the F_{+4} group (Wilcoxon rank sum test on τ ; $P < 0.005$). Our subjects, therefore, adapted more rapidly to a novel field

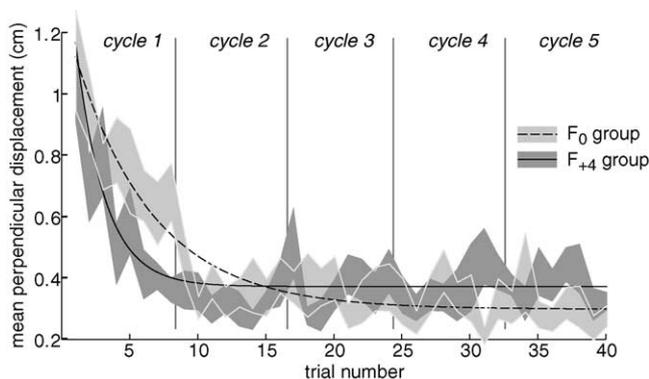


Fig. 1. The first 40 trials after learning F_{+12} where the field changes to either F_{+4} or the null field F_0 . Subjects take longer to adapt to the null field than to F_{+4} . The lines indicate mean exponential fit while the shaded areas indicate MPD \pm S.E. across subjects.

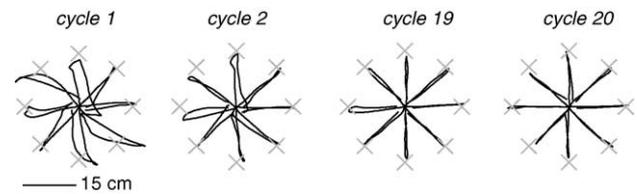


Fig. 2. Typical hand paths in F_{+4} early and late in stage 1 of experiment 2.

which was closer to F_{+12} than the null field. This demonstrates that the rapid de-adaptation effect is not entirely due to the dynamics of the unperturbed arm being well consolidated in memory and is consistent with a rapid scaling of the learned representation of F_{+12} .

All subjects showed strong learning in stage 1. The first few movements in F_{+4} were strongly perturbed perpendicular to the direction of motion, resulting in looped movements, but by the 20th cycle subjects' hand paths were approximately straight and directed toward the target (Fig. 2).

After adapting to the initial force field in stage 1, subjects were exposed to a second field in stage 2 which either acted with the same strength but in the opposite direction (F_{-4} for subjects assigned to the -8 group) or maintained the same direction and tripled in magnitude (F_{+12} for subjects assigned to the $+8$ group). We calculated the mean strength of the peak force experienced during each trial of experiment 2. The peak forces experienced by subjects in fields F_{+4} and F_{-4} were of approximately equal magnitude, though they acted in opposite directions (2.88 ± 0.07 N and 2.75 ± 0.10 N, respectively). The peak force experienced in field F_{+12} was approximately three times stronger (9.39 ± 0.43 N). Both groups adapted to the new field and produced relatively straight hand paths by the end of the stage (see Fig. 3). At the end of stage 2 the hand paths of the -8 group were approximately as straight as they had been at the end of stage 1 (paired t test, MPD over the last three cycles; $P > 0.05$). The hand paths of the $+8$ group were not as straight at the end of stage 2 as they were at the end of stage 1 (paired t test; MPD over the last three cycles; $P < 0.0001$). In addition, the -8 group was straighter than the $+8$ group at the end of stage 2 (t test, MPD over the last three cycles; $P < 0.01$). Since the variability of force output increases with muscular

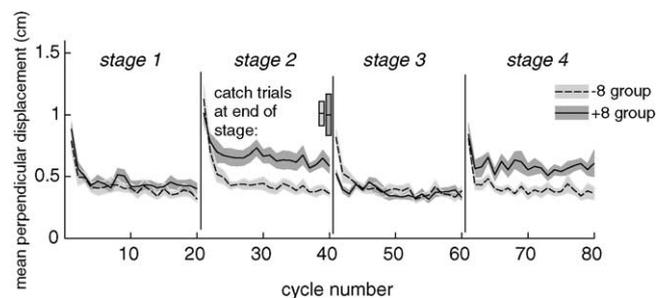


Fig. 3. Mean perpendicular displacement for all subjects averaged across cycles. Shaded regions indicate S.E. across subjects. The catch trials include the last catch trial in stage 2 and the first trial in stage 3.

activation [5,8], we expected to see larger kinematic errors in the +8 group, which was exposed to much stronger forces.

The magnitude of the errors elicited by the catch trials (to F_{+4}) increased for both groups during stage 2, though the errors were in opposite directions. Catch trial performance at the end of the stage was assessed by averaging the MPD across the final catch trial in stage 2 and first trial in stage 3 (which is also effectively a catch trial). For the –8 group the MPD over these trials was 1.06 ± 0.10 cm (mean \pm S.E.) and for the +8 group was 1.0 ± 0.17 cm. Error magnitude in the catch trials was larger than at the end of stage 1 in which subjects were also exposed to F_{+4} (paired t test for each group, $P < 0.005$), confirming that the learning observed in stage 2 was not entirely due to stiffening of the arm. Catch trial MPD at the end of stage 2 did not differ between groups (t test, $P > 0.05$), indicating that the two groups had learned a similar amount about their respective fields by the end of stage 2. Moreover, the exponential model fit to the trial-by-trial data from individual subjects indicated that the learning rate in stage 2 did not differ between groups (Wilcoxon rank sum test on τ ; $P > 0.05$). The catch trial MPD did not differ from the catch trials in experiment 1 (t test; $P > 0.05$), in which the experienced field switched from F_{+12} to F_{+4} .

Re-adaptation to the original field, which occurred in stage 3, was much faster for subjects in the +8 group, for whom the field in stage 2 (F_{+12}) acted in the same direction as the field in stage 1 (F_{+4}). For this group the MPD from the second cycle in stage 3 did not differ from the MPD from the last cycle in stage 1 (paired t test; $P > 0.05$). In contrast, the –8 group performed worse than they had at the end of stage 1 (paired t test; $P < 0.01$). In fact, the –8 group did not achieve an MPD as low as in the last cycle of stage 1 until cycle 7 of stage 3 (repeated t tests on cycles 1–6; $P > 0.05$). In summary, when the field reversed direction in stage 2 it took approximately six cycles (40 trials) to readapt to the first field, but when the field tripled in strength readaptation was complete after a single cycle.

Fitting an exponential model to the trial-by-trial MPD data of each subject for stage 3 showed that the median parameter values for our model were $\alpha = 0.4$, $\beta = 0.8$ and $\tau = 6.4$ (lower quartile, upper quartile: 3.5, 18.2) for the –8 group and $\alpha = 0.4$, $\beta = 0.8$ and $\tau = 0.4$ (lower quartile, upper quartile: 0.2, 2.0) for the +8 group (nonlinear least squares fit; median $R^2 = 0.42$, minimum $R^2 = 0.12$). Data from one subject was excluded from this analysis because the nonlinear fitting algorithm not converge (nonlinear least squares fit; $R^2 < 0.05$). The time constant τ was much lower in the +8 group than the –8 group (Wilcoxon rank sum test; $P < 0.05$) and the plateau α and gain β did not differ between groups (Wilcoxon rank sum test; $P > 0.05$). Fig. 4 clearly shows the difference in readaptation rates between the two groups. τ was also lower in stage 3 than in stage 2 for the +8 group (Wilcoxon signed rank test; $P < 0.05$) but not for the –8 group (Wilcoxon signed rank test; $P > 0.05$).

The time constant for the +8 group in stage 3 did not differ from the F_{+4} group in experiment 1, despite the latter group

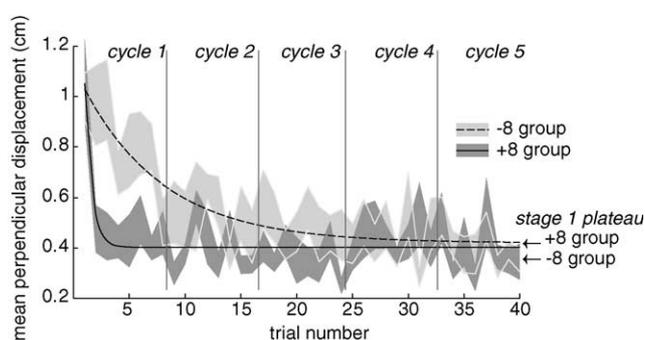


Fig. 4. The first 40 trials of stage 3 illustrates readaptation to the initial field immediately after exposure to the novel field in stage 2. Rapid readaptation is evident in the case where the field acts in the same direction as the original field (+8 group). The +8 group improves beyond the plateau reached at the end of stage 1 (marked with an arrow) after approximately three trials. In contrast, the –8 group has not reached the plateau reached at the end of stage 1 after 40 trials. For the –8 group this level of performance is reached after approximately 48 trials. The lines indicate the mean exponential fit while the shaded areas indicate MPD \pm S.E. across subjects.

having more practice F_{+12} and no prior exposure to F_{+4} . The time constant for the –8 group in stage 3 was larger than the F_{+4} group in the first experiment (Wilcoxon rank sum test; $P < 0.001$).

In stage 4, all subjects were re-exposed to the same field they experienced in stage 2. The MPD in the second cycle of stage 4 did not differ from the last cycle in stage 2 for either group (paired t test, $P > 0.05$). Applying the exponential model to the data from stage 4 gave a median time constant of $\tau = 2.57$ trials for the –8 group and $\tau = 5.93$ trials for the +8 group. There was no evidence of a difference in learning rate in stage 4 between the groups (Wilcoxon rank sum test; $P > 0.05$) or between stages 2 and 4 for either group (Wilcoxon signed rank test; $P > 0.05$). The data from stage 4 showed more inter-subject variability than those from stage 2, probably because some subjects were beginning to fatigue. This may have prevented us showing a learning rate differences in stage 4. Nevertheless, the clear adaptation rate differences between groups that we observed in stage 3 was not apparent in stage 4. The MPD in the first cycle of stage 4 was smaller than that from the first cycle of stage 2 for both groups (paired t test; $P < 0.05$), indicating some retention of learning from stage 2.

De-adaptation after learning a dynamic force field is a widely known example of rapid switching between motor behaviors. It has been suggested that the phenomenon reveals modularity in the neural circuitry responsible for controlling dynamics [7,18]. We observed that after learning a dynamic force field, subjects took longer to de-adapt when the forces were turned off than to adapt to a scaled-down version of the field that they had not experienced before. Subjects were also much faster at adapting to a scaled down field than to an equal and opposite field, even though the required change in force output was the same. Our results suggest that de-adaptation is a manifestation of a more general behavior in which transitions to force fields of reduced magnitude, but acting in the same direction, are learned rapidly.

Recent robotic control and human motor control models have suggested modular control schemes in which an existing set of controllers is gated either discretely, using a multiplexing switch [9,10], or continuously by scaling the outputs of the controllers [6,18]. In the latter scheme, known as a *mixture model*, switching is seen as rapid adjustment of weighting factors. In the discrete model, the rate of switching only depends on the structure of the multiplexing switch and not on the controllers from which it derives its input. The rate of switching in the mixture model depends on how much the weighting parameters must change between conditions. In a discrete model, re-adaptation to null is seen as rapidly switching to an existing controller for the free arm, whereas adaptation to a novel field would require gradually tuning an existing controller (which may initially be selected by switching). Note that we assume the dynamics of the free arm are modified minimally by the passive robot. Our results showed that it took longer to re-adapt to the null field after learning F_{+12} than to adapt to the novel field F_{+4} , which is consistent with a mixture model and is not consistent with a discrete switching model.

If a switching model was used to switch to a new controller when transitioning from F_{+12} to F_{+4} or F_0 then we would expect the forces experienced and the states visited on the first trial after the transition to be an important contextual cue to such a transition. The size of these cues would be smaller for a transition between F_{+12} and F_{+4} than between F_{+12} and F_0 so that a switching model would predict a faster identification when going to F_0 . Nevertheless, we observed a slower transition to F_0 compared to F_{+4} suggesting that the size of the contextual cue is less important than the amount by which the force generated needs to decrease.

Our second experiment examined switching between novel fields. Subjects learned field F_{+4} , followed by one of two other fields (called F_{+12} and F_{-4}) which differed from field F_{+4} by $\pm 8 \text{ N m}^{-1} \text{ s}^{-1}$. The two groups each learned their second field at approximately the same rate and exhibited similar aftereffects, indicating that the fields were of comparable difficulty. When the second field acted in the opposite direction to the initial field F_{-4} , adaptation back to F_{+4} occurred slowly; at approximately the same rate as initial adaptation. When the second field was F_{+12} which acted in the same direction as, but was stronger than, F_{+4} adaptation occurred much faster. Finally, when subjects were exposed to the same field they experienced in stage 2 for a second time (in stage 4), adaptation occurred at approximately the same rate as initial adaptation in both groups. The +8 group was no faster to adapt to F_{+4} in stage 3 of experiment 2 than subjects in experiment 1. This was despite having prior experience with F_{+4} and less practice at F_{+12} than those in the first experiment. The rapid adaptation we observed in switching from F_{+12} to F_{+4} is therefore probably not due to subjects maintaining, and switching back to, the representation of F_{+4} that they learned on their initial exposure. These results suggest that the rate of adaptation to a novel field depends on the relative magnitude and direction of the previous field and not

on earlier experience with the field. Specifically, adaptation is more rapid if the previous field was stronger than, and acts in the same direction as, the original field.

Recent studies have shown that adaptation and de-adaptation to both discretely varying [12,16] and stochastically varying [11] dynamic fields can be modeled as an autoregressive process. In these models the kinematic error on the current trial is linearly dependent on the error on the previous trial and the strength of the field on the current and previous trials. Such a model can not easily account for our data. As these models are linear, transitioning between two constant-strength fields (as in our experiment) will lead to learning curves that are self-similar (except for a global scaling) and therefore predict the same learning rates for all transitions. However, we find that transitions towards weaker fields of the same sign are faster than transitions to stronger fields, or those with opposite signs, suggesting that a linear model is not sufficient to account for our data.

We might explain the differences we observed in the rates of adaptation to each field if it takes longer to learn to activate than to deactivate a motor unit. The rate of adaptation back to the F_{+4} in stage 3 of the second experiment depended on the direction of the second field relative to F_{+4} . Since F_{-4} acts in the opposite direction to F_{+4} , this transition required the activation of a different set of motor units, and therefore learning should be relatively slow. Moving in F_{+4} after F_{+12} requires the set of same muscles to produce less force and therefore largely requires the deactivation of motor units. Accordingly, we observed faster adaptation on this transition. In contrast, the shift from F_{+4} to F_{+12} by the +8 group in stage 4 required leaning to reactivate motor units. Our results clearly showed rapid adaptation in the transition from F_{+12} to F_{+4} , but not from F_{+4} to F_{+12} . Additionally, in experiment 1 the shift from F_{+12} to null required the deactivation of more motor units than F_{+4} , which explains why both transitions were relatively rapid, though the transition to null was the slower of the two. Hence, all the major differences in adaptation rates we observed in our two experiments might be explained with this simple hypothesis.

Because variability in force output increases with muscular activation [5,8], we expected to see larger kinematic errors in F_{+12} than in F_{-4} , even when both fields had been learned to a similar extent. To confirm that equal amounts of learning had taken place we examined the kinematic aftereffects at the end of learning. F_{+12} and F_{-4} differed from F_{+4} by $\pm 8 \text{ N m}^{-1} \text{ s}^{-1}$, so we expected to observe approximately mirror symmetric kinematic errors when each group returned to F_{+4} . The results showed that the catch trials were of equal magnitude (Fig. 3, bars in stage 2), though opposite in direction, demonstrating that learning in stage 2 was similar for both groups.

Analogous rapid adaptation effects have not been observed when making reaching movements under visuomotor transformations. Wigmore et al. [17] performed an experiment where the subjects alternated between visuomotor rotations of various magnitudes. In contrast with our results, they did

not find rapid adaptation between any two rotations, including transitions back to the null rotation. Abeele and Bock have also found evidence for gradual, non-modular, transitions between visuomotor rotations [1,2]. These findings highlight the considerable differences in how we learn dynamic and kinematic (visuomotor) tasks.

The results we have presented show that subjects sometimes adapt to novel force fields faster than they de-adapt when the forces are turned off. This occurs when subjects learn a novel force field followed by a scaled down version of the same field. Subjects also adapt to a scaled down field faster than to an equal and opposite field. This suggests a general behavior whereby subjects adapt to reduced forces very quickly but take longer to adapt to stronger forces and forces acting in a different direction. While the causes for this behavior require further investigation, we suggest that it might be explained if it takes longer to learn to activate than to deactivate a motor unit.

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References

- [1] S. Abeele, O. Bock, Mechanisms for sensorimotor adaptation to rotated visual input, *Exp. Brain Res.* 139 (2001) 248–253.
- [2] S. Abeele, O. Bock, Sensorimotor adaptation to rotated visual input: different mechanisms for small versus large rotations, *Exp. Brain Res.* 140 (2001) 407–410.
- [3] T. Brashers-Krug, R. Shadmehr, E. Bizzi, Consolidation in human motor memory, *Nature* 382 (1996) 252–255.
- [4] S.J. Goodbody, D.M. Wolpert, Temporal and amplitude generalization in motor learning, *J. Neurophysiol.* 79 (1998) 1825–1838.
- [5] C.M. Harris, D.M. Wolpert, Signal-dependent noise determines motor planning, *Nature* 394 (1998) 780–784 (News and Views, pp. 725–726).
- [6] M. Haruno, D.M. Wolpert, M. Kawato, Mosaic model for sensorimotor learning and control, *Neural Comput.* 13 (2001) 2201–2220.
- [7] P. Jansen-Osmann, S. Richter, J. Konczak, K.T. Kalveram, Force adaptation transfers to untrained workspace regions in children: evidence for developing inverse dynamic motor models, *Exp. Brain Res.* 143 (2002) 212–220.
- [8] K.E. Jones, A.F. De, C. Hamilton, D.M. Wolpert, Sources of signal-dependent noise during isometric force production, *J. Neurophysiol.* 88 (2002) 1533–1544.
- [9] K.S. Narendra, J. Balakrishnan, Adaptive control using multiple models, *IEEE Trans. Automatic Control* 42 (1997) 171–187.
- [10] K.S. Narendra, J. Balakrishnan, M. Ciliz, Adaptation and learning using multiple models, switching and tuning, *IEEE Control Syst. Mag.* 37–51 (1995).
- [11] R.A. Scheidt, J.B. Dingwell, F.A. Mussa-Ivaldi, Learning to move amid uncertainty, *J. Neurophysiol.* 86 (2001) 971–985.
- [12] R.A. Scheidt, D.J. Reinkensmeyer, M.A. Conditt, W.Z. Rymer, F.A. Mussa-Ivaldi, Persistence of motor adaptation during constrained, multi-joint, arm movements, *J. Neurophysiol.* 84 (2000) 853–862.
- [13] R. Shadmehr, J. Brandt, S. Corkin, Time-dependent motor memory processes in amnesic subjects, *J. Neurophysiol.* 80 (1998) 1590–1597.
- [14] R. Shadmehr, T. Brashers-Krug, Functional stages in the formation of human long-term motor memory, *J. Neurosci.* 17 (1997) 409–419.
- [15] R. Shadmehr, H.H. Holcomb, Neural correlates of motor memory consolidation, *Science* 277 (1997) 821–825.
- [16] K.A. Thoroughman, R. Shadmehr, Learning through adaptive combination of motor primitives, *Nature* 407 (2000) 742–747.
- [17] V. Wigmore, C. Tong, J.R. Flanagan, Visuomotor rotations of varying size and direction compete for a single internal model in motor working memory, *J. Exp. Psychol. Hum. Percept. Perform.* 28 (2002) 447–457.
- [18] D.M. Wolpert, M. Kawato, Multiple paired forward and inverse models for motor control, *Neural Netw.* 11 (1998) 1317–1329.