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RESEARCH ARTICLE

Different adaptation rates to abrupt and gradual changes in environmental dynamics

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Abstract
Adaptation to an abrupt change in the dynamics of the interaction between the arm and the physical environment has been reported as occurring more rapidly but with less retention than adaptation to a gradual change in interaction dynamics. Faster adaptation to an abrupt change in interaction dynamics appears inconsistent with kinematic error sensitivity which has been shown to be greater for small errors than large errors. However, the comparison of adaptation rates was based on incomplete adaptation. Furthermore, the metric which was used as a proxy of the changing internal state, namely the linear regression between the force disturbance and the compensatory force (the adaptation index), does not distinguish between internal state inaccuracy resulting from amplitude or temporal errors. To resolve the apparent inconsistency, we compared the evolution of the internal state during complete adaptation to an abrupt and gradual change in interaction dynamics. We found no difference in the rate at which the adaptation index increased during adaptation to a gradual compared to an abrupt change in interaction dynamics. In addition, we separately examined amplitude and temporal errors using different metrics, and found that amplitude error was reduced more rapidly under the gradual than the abrupt condition, whereas temporal error (quantified by smoothness) was reduced more rapidly under the abrupt condition. We did not find any significant change in phase lag during adaptation under either condition. Our results also demonstrate that even after adaptation is complete, online feedback correction still plays a significant role in the control of reaching.

Keywords Motor adaptation · Arm · Error · Force · Rate constant

Introduction

Humans are able to perform skilful actions while physically interacting with objects in the environment, because they can adapt muscle force and impedance to control the dynamics of the interaction. They can even compensate for instability in the environment (Milner 2002). When interaction dynamics change unexpectedly, there can be large errors in task related goals. These errors are gradually corrected as familiarity with the new interaction dynamics is acquired through movement repetition. Performance improves with training, but a remarkable feature of the improvement is a precipitous drop in the error following an abrupt change in the interaction dynamics. The drop in error is accompanied by an initial increase in feedforward antagonistic muscle co-contraction which gradually decreases as adaptation progresses (Thoroughman and Shadmehr 1999; Franklin et al. 2003).

Co-contraction effectively increases limb stiffness which counteracts the perturbing effect of changes in interaction dynamics regardless of the accuracy of the internal representation of the interaction dynamics, also referred to as the internal state. Because internal state error is large immediately following an abrupt change in the interaction dynamics co-contraction represents an effective strategy to quickly reduce the kinematic error which may increase the rate of adapting the internal state to the new interaction dynamics, since the central nervous system is more sensitive to small kinematic errors than large kinematic errors. As Marko et al. (2012) showed, there is proportionately greater adaptation of the internal state following small kinematic errors than large kinematic errors, hereafter referred to as error sensitivity. On the other hand, if the interaction dynamics change

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gradually rather than abruptly, the relatively small kinematic errors should already engender high error sensitivity. Therefore, as long as the internal state is accurately maintained as the dynamics change, there should be little need to reduce kinematic error by co-contraction. However, the observed increase in kinematic error as force-field strength gradually increases (Klassen et al. 2005; Pekny et al. 2011) suggests that the internal state may become less accurate when the interaction dynamics gradually change.

Because of the non-specific compensatory effect of co-contraction, kinematic error is not a reliable indicator of changes to the internal state. Therefore, to better assess the internal state, the error-clamp technique was devised to measure the feedforward force being exerted to counteract the interaction dynamics (Scheidt et al. 2000; Milner and Franklin 2005; Hinder and Milner 2005). This technique was adapted by Smith et al. (2006) to investigate retention after motor adaptation. They quantified adaptation in terms of the slope of the linear regression between the force exerted by the subject on error-clamp trials and the ideal force required to cancel the effect of the interaction dynamics, which they referred to as the adaptation index.

When applied to abrupt versus gradual change in interaction dynamics, the adaptation index appears to increase at a faster rate under the abrupt than the gradual condition (Huang and Shadmehr 2009). However, the greater sensitivity to small errors (Marko et al. 2012) would suggest that the adaptation index should increase more quickly under the gradual than the abrupt condition. We propose that this discrepancy might be resolved in several ways. First, the errors under the gradual condition may initially be too small to evoke a change in the internal state. Second, the marked increase in co-contraction under the abrupt condition may reduce the kinematic error to a level comparable with the gradual condition. Third, Huang and Shadmehr (2009) examined only partial adaptation and it may be that a time constant for adaptation determined from complete adaptation presents a different picture. Their results hint at this, since they found a difference in retention of the internal state between the abrupt and gradual conditions when the adaptation index was matched at 0.5 (incomplete adaptation), but the difference disappeared when the number of training trials was matched rather than the adaptation index.

We have undertaken more detailed analysis of adaptation under these two conditions to determine the reason for the apparent discrepancy between sensitivity to kinematic error and rate of adaptation of the internal state. This includes the introduction of metrics of the internal state that separate amplitude and temporal components of adaptation. One group of subjects trained in a velocity-dependent force field which gradually increased in strength until it reached a maximum value, whereas another group trained in the same force field, which was abruptly activated and maintained at its maximum strength. The training period was sufficiently long for all metrics of the internal state to reach asymptotic values. In the final 50 trials of the training period, both groups were performing movements in the maximum strength force field.

Materials and methods

Subjects

In total, 28 healthy subjects (age 19–46, 8 female) participated in this study. Subjects were divided into two groups of which 15 subjects formed the gradual group and 13 subjects formed the abrupt group. All subjects were right-handed and had normal vision. They reported no prior experience in performing a similar task, and had no history of neuromuscular or neurological disorders. The study was approved by the Research Ethics Board of McGill University and conformed to the Declaration of Helsinki.

Subjects sat in front of a two degree-of-freedom serial link robot (Interactive Motion Technologies Inc., Cambridge MA) with the trunk supported and held against the chair back by a shoulder harness. The height of the chair was adjusted, so that the subject had full view of an opaque horizontal screen which hid the arm. Subjects held the handle of the robot with their right hand. An LCD projector (60 Hz refresh rate) displayed the handle position and targets on the horizontal screen, although the arm itself could not be seen. The arm was supported in the horizontal plane at shoulder level by an air sled placed either under the upper arm or forearm, depending on the subject's preference. Before beginning the experiment, the center of the workspace was located by having the subject move the arm to a position with the shoulder at 45° horizontal flexion relative to the line joining the shoulders and the elbow at 90°. Force was applied to the hand by the robot and optical encoders located at the robot joints were used to calculate the position of the handle during the movement. The forces applied at the robot handle were recorded using a six-axis force-torque transducer (ATI Gamma, Apex NC). Handle position and force signals were sampled at 400 Hz. The signals were low-pass Butterworth-filtered at 20 Hz and the position was numerically differentiated to obtain velocity.

Experimental task

Each trial began with a start circle appearing on the horizontal screen. Subjects were instructed to move the handle to the start circle and hold it there until a target circle appeared. The handle position was displayed as a 0.5 cm-diameter circle and the start and target circles were 2 cm in diameter. The two targets were spaced 25 cm apart along a straight line directly in front of the subject along the midline of the body. Subjects were instructed to move from the start circle to the target circle along a straight line in one continuous motion without corrective movements and to complete the movement within 600 ± 50 ms. Based on the movement duration, the subjects were given feedback about their movement speed by a change in the color of the second target after completion of the movement. The color of the target changed from blue to green if the movement was too slow, it changed from blue to red if the movement was too fast or it stayed blue if the speed was appropriate. This feedback allowed the subject to maintain similar movement velocity under all the experimental conditions. Subjects were instructed to stay at the second target and allow the robot to move the arm back to the start position. The second target disappeared as the arm was pulled back. After a short delay, the next trial began and the process described above was repeated.

Force field

During training, a force field generated by the robot was applied to the hand. Although subjects were not told that there would be a force field, they had been given instructions about how to move between the start and target positions, as described above. This force field consisted of a clockwise velocity-dependent force described by the following equation:

$$\begin{bmatrix} f_x \\ f_y \end{bmatrix} = \mathbf{B} \begin{bmatrix} v_x \\ v_y \end{bmatrix}, \tag{1}$$

where f_x and f_y indicate the force magnitude applied to the hand in the x (lateral)-direction and y (longitudinal)-direction, respectively, and v_x and v_y are the velocities of the hand in the corresponding directions. $\mathbf{B}$ is the matrix which defines the magnitude of the force field:

$$\mathbf{B} = \beta \begin{bmatrix} 0 & 1 \\ -1 & 0 \end{bmatrix}, \tag{2}$$

where the maximum value of β was 15 Ns/m.

Under the gradual condition, β increased linearly from one trial to the next until reaching 15 Ns/m, while, under the abrupt condition, β was constant at 15 Ns/m for 200 trials (Fig. 1), that is

$$\beta_{\text{gradual}} = \begin{matrix} 0 & 1 \le n \le 50 \\ \left(\frac{15}{150}\right)(n-50) & 51 \le n \le 200 \\ 15 & 201 \le n \le 250 \\ 0 & 251 \le n \le 300 \end{matrix}, \tag{3}$$

$$\beta_{\text{abrupt}} = \begin{matrix} 0 & 1 \le n \le 50 \\ 15 & 51 \le n \le 250 \\ 0 & 251 \le n \le 300 \end{matrix}, \tag{4}$$

where n indicates the trial number.

Experimental procedure

The experiment consisted of 300 trials divided into four blocks for the gradual condition and three blocks for the abrupt condition, as defined by Eqs. (3) and (4) above (Fig. 1). Both groups of subjects began by performing a block of 50 trials in the null field (the robot did not apply any force on the hand). This allowed subjects to become familiar with the task and with the apparatus. The force field was then activated without informing the subject. Under the gradual condition, subjects then performed a block of 150 trials in the force field which gradually increased in magnitude (Eq. 3). The force-field magnitude reached its maximum value at the end of this block. The third block consisted of 50 trials at maximum force-field strength. In

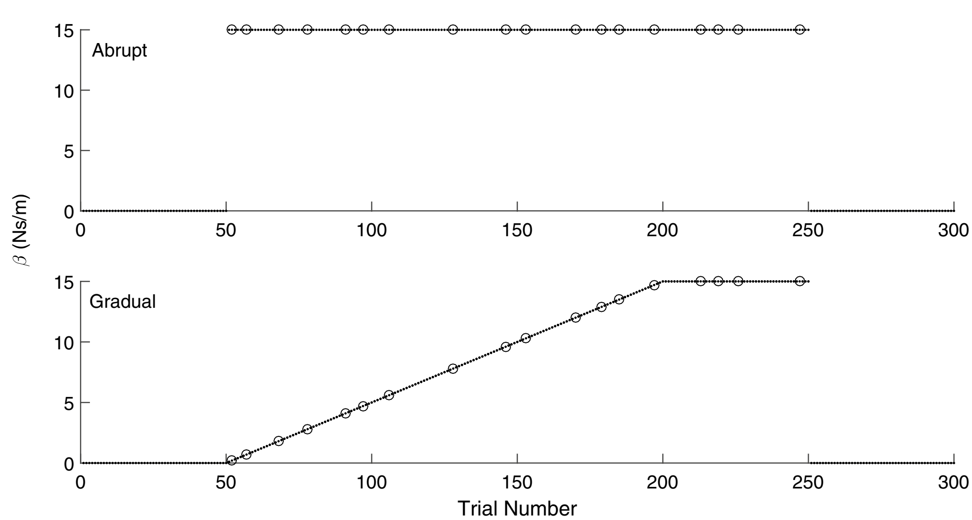


Fig. 1 Force-field strength (β) for each trial under the abrupt (top panel) and gradual (bottom panel) conditions. The protocol begins and ends with 50 null-field trials under both conditions. The open circles indicate error-clamp trials

the fourth block, subjects performed 50 additional washout trials in the null field. The last block allowed aftereffects to be quantified to assess learning. Under the abrupt condition, subjects performed 200 trials at maximum force-field strength in the second block (Eq. 4). The third block under the abrupt condition was the same as the fourth block under the gradual condition with 50 null-field trials.

Among the trials performed in the force-field (trials 51–250), 18 trials were selected to be error-clamp trials (Scheidt et al. 2000; Smith et al. 2006). During error-clamp trials, a virtual channel was formed by creating stiff elastic walls on either side of the line from start point to target point which prevented the trajectories from deviating from the straight line. The channel was implemented with a stiffness of 5000 N/m and viscosity of 50 Ns/m. The force profile which the subject applied to the channel provided a measure of how well the force field had been learned. The trials in which the error clamp was applied were the same for all subjects in both conditions, namely trials 52, 57, 68, 78, 91, 97, 106, 128, 146, 153, 170, 179, 185, 197, 213, 219, 226, and 247 (Fig. 1).

Data processing

For each trial, movement onset was defined as the time when the movement velocity exceeded 5% of its peak and the movement ended when the velocity fell below 5% of the peak. To characterize the adaptation process, the following metrics were computed over the interval between movement onset and movement end based on the lateral force (f_x) exerted by subjects on error-clamp trials and the lateral force (f_r) which the robot would have applied had the trial been a force field trial which we refer to as the *ideal force*.

1. the adaptation index as defined by Smith et al. (2006), namely the coefficient (slope) of the linear regression between $f_x(t)$ and $f_r(t)$;
2. the normalized force gain defined as $f_x(t)$ at peak velocity divided by the peak velocity and normalized by the peak $f_r(t)$;
3. the lag at the peak cross correlation between $f_r(t)$ and $f_x(t)$;
4. the spectral arc length as defined by Balasubramanian et al. (2012) applied to $f_x(t)$.

Each metric is sensitive to a different feature of the internal state. The adaptation index is sensitive to the gain, phase lag and smoothness of f_x relative to f_r but does not separate their effects, i.e., it is possible to arrive at the same adaptation index by altering only the gain, only the phase lag, or only the smoothness of f_x. The normalized force gain isolates the gain error, i.e., the error in scaling force according to v_y. The phase lag at the peak cross correlation between f_x and f_r isolates the phase error in f_x relative to f_r. The spectral arc length is a measure developed to quantify smoothness of the velocity profile (Balasubramanian et al. 2012). We have adapted it as a measure of the smoothness of the f_x force profile, since the ideal force should be proportional to the velocity.

To set a baseline for learning under the condition where the force-field strength increased gradually, we first subtracted an estimate of f_x under the null-field condition. We assumed that, prior to the first error-clamp trial (52), the force field would have been too weak to evoke a detectable response, so that f_x measured on this trial would be representative of f_x under the null-field condition. Therefore, we created a template for the baseline f_x profile over the interval between movement onset and end (defined above) for each subject based on the f_x profile of trial 52. For each error-clamp trial, the template was time-scaled to match the duration of the movement interval and then subtracted from the f_x profile for that trial. The baseline corrected f_x profiles were used to calculate the metrics listed above. However, it was not possible to construct a baseline f_x profile for the condition where the force-field strength increased abruptly. Although the kinematic error was very similar for the abrupt and gradual groups on the null-field trials which preceded the onset of the force-field trials suggesting the same underlying internal state, it is apparent that the mean f_x profile on trial 52 is markedly different for the two groups (Fig. 2). This indicates that considerable adaptation occurs after a single force-field trial when the force field is introduced abruptly in agreement with our earlier work (Milner and Franklin 2005). Since the f_x profile on the first error-clamp trial under the abrupt condition was not representative of the baseline, we were not able to take into account the baseline in calculating the metrics under the abrupt condition.

The kinematic error was quantified by calculating the maximum deviation of the subject's hand path from a straight line joining the center of the start and end targets. We assume that the maximum deviation is representative of the magnitude of the sensory error received by the central nervous system. To reach the target circle, subjects frequently corrected for errors in lateral position. Corrections can be represented by inflections in the velocity profile (Milner and Ijaz 1990) or equivalently by acceleration zero crossings. We used the number of zero crossings in the lateral (x) acceleration between peak velocity and the end of the movement as a metric of performance. The fewer zero crossings, the better the performance.

Statistical analysis

When an adaptation metric changed in an exponential manner, the following equation:

$$a_1 + a_2 e^{-a_3 T} \tag{5}$$

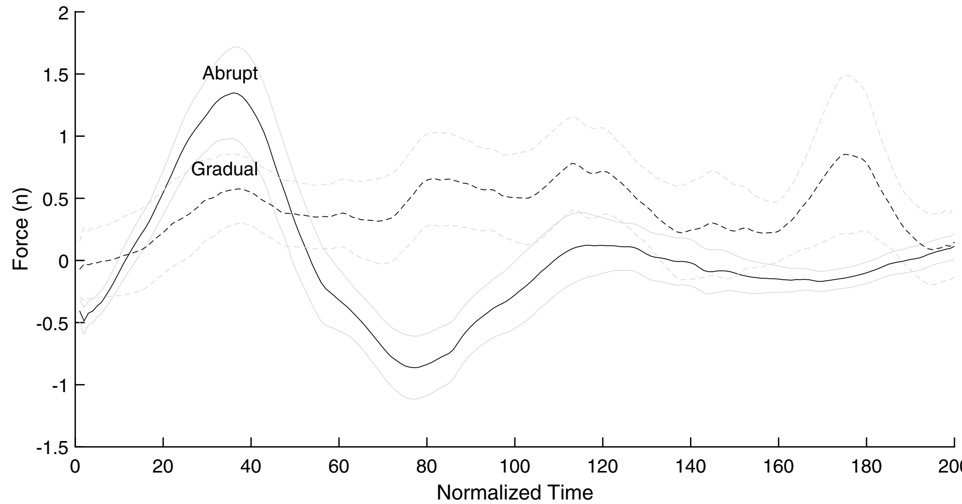


Fig. 2 Mean force profile on the first error-clamp trial (52) for the gradual (dark solid line) and abrupt (dark dashed line) groups shown superimposed. The light lines indicate standard errors

was fit to the mean values of the metric for each condition, where T is the trial number. The Matlab non-linear regression routine 'fitnlm' was used to fit Eq. 5 to the data. To compare the rate constants between conditions, we used a bootstrap technique to compute a 95% confidence interval for a_3. The bootstrap consisted of computing the residuals of the function obtained by fitting Eq. 5 to the mean data, adding the residuals (randomly sampled) to the function and refitting the resulting data points to obtain a distribution of values for a_3. The refitting was done 1000 times to obtain a distribution of 1000 values for a_3 which were sorted in ascending order to find the 2.5 and 97.5 percentiles which formed the confidence interval. We also compared the values of each metric under the two conditions for trial 197 when the strength of the force field under the gradual condition was nearly equal to that under the abrupt condition and for trial 247 near the end of training using a t test if the distributions were normal or a non-parametric Wilcoxon ranked sum test if the distributions were not normal.

Results

Figure 3 compares the trial-by-trial evolution of the group means for the maximum hand-path deviation under the abrupt and gradual conditions. As expected, the maximum hand-path deviation increased dramatically on the first trial in the force field (trial 51) under the abrupt condition. In

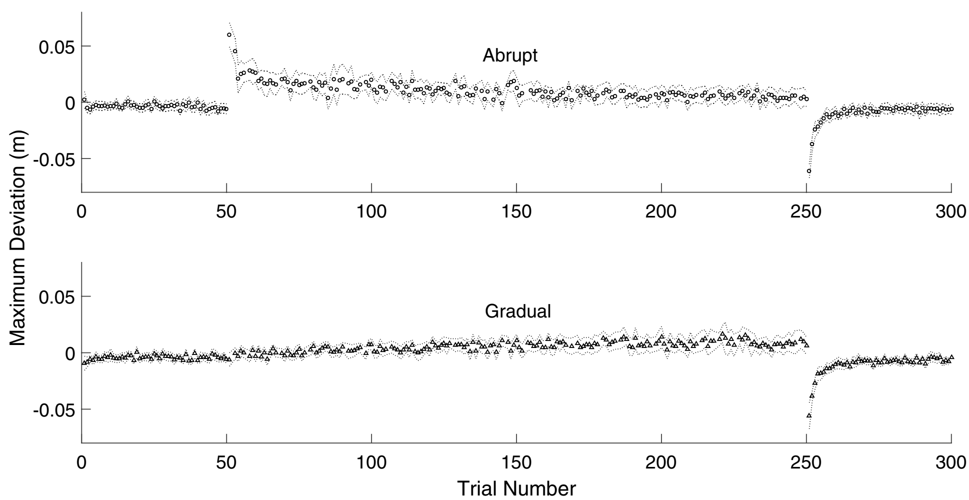


Fig. 3 Group mean maximum hand-path deviation is plotted with the 95% confidence interval shown by dotted lines for the abrupt transition in interaction dynamics (circles top panel) and the gradual transition in interaction dynamics (triangles bottom panel) for trials without error clamp. The first 50 trials were performed in the null field. The force field was abruptly increased to full strength for the abrupt group on trial 51, whereas the force-field strength increased linearly from trial 51–200 for the gradual group. The force field was at the same strength for both groups from trial 201–250. The null field was reinstated from trial 251–300

comparison, there was no noticeable change in the maximum hand-path deviation under the gradual condition. However, the hand-path deviation was rapidly reduced under the abrupt condition, whereas it gradually increased under the gradual condition. The time constant for reduction of the maximum hand-path deviation under the abrupt condition was 21 trials based on fitting Eq. 5 to the data from trial 51 to 200 ($R^2=0.60$). Linear regression analysis showed that there was a significant positive slope in the maximum hand-path deviation from trial 51–200 under the gradual condition ($R^2=0.57$, $p<0.00001$). There was no significant difference between the two conditions on trial 200 where the force-field strength under the two conditions first reached equality (abrupt mean 0.0078 ± 0.013 m, gradual mean 0.014 ± 0. 018 m, $p=0.34$) or on trial 250 at the end of training (abrupt mean 0.0031 ± 0.0123 m, gradual mean 0.0060 ± 0.015 m, $p=0.58$). When the null field was abruptly re-introduced on trial 251, the maximum hand-path deviation under both conditions increased dramatically to almost the same extent (abrupt mean 0.061 ± 0.011 m, gradual mean 0.056 ± 0.023 m, $p=0.42$). During the washout, the maximum hand-path deviation was reduced at very similar rates under the two conditions. Almost all of the variance was accounted for by Eq. (5) ($R^2=0.95$ for both conditions) which yielded a time constant of 2.3 trials under the abrupt condition compared to 2.5 trials under the gradual condition.

The performance metric highlights the similarities and differences in error correction under the two conditions (Fig. 4). There was a relatively linear decrease in acceleration zero crossings during the initial 50 null-field trials for both groups of subjects. The number of acceleration zero crossings then increased at the beginning of training in the force field under the abrupt condition, such that it was significantly greater than under the gradual condition ($p<0.00001$ over the first 10 trials), but there was no significant difference in the number of zero crossings between trial 51 and trial 200 ($p=0.17$). However, there was a weak but significant linear trend for zero-crossing reduction (slope = − 0.0017, $R^2=0.10$). In contrast, the number of zero crossings grew linearly between trials 51 and 200 under the gradual condition (slope = 0.0053, $R^2=0.70$), and the difference between trial 51 and trial 200 was significant ($p=0.033$). Comparing consecutive groups of 10 trials, the number of zero crossings remained significantly greater under the abrupt than the gradual condition until trial 145 after which it remained similar for the two conditions. When the null field was re-introduced on trial 251, there was a very similar decline in acceleration zero crossings for both groups of subjects.

Figure 5 provides a snapshot of the evolution of the force recorded on error-clamp trials as adaptation progressed. During the early trials under the gradual condition, there was a noticeable peak in force that was approximately coincident with peak acceleration. Note that this peak is also evident under the abrupt condition on the first error-clamp trial (Fig. 2). As training progressed, a more prominent peak developed near the midpoint of the movement, the location of peak velocity. This occurred sooner under the abrupt condition than under the gradual condition. The development of this central peak reduced the prominence of the early peak in a manner that suggests smooth integration. By the time that the strength of the force field under the gradual condition reached that of the abrupt condition, the force profiles under the two conditions were similar in shape and magnitude (trial 197 in Fig. 5).

Figure 6 compares the trial-by-trial evolution of the group means of the adaptation index during force-field trials. This index provides a measure of how well the lateral force exerted by a subject parallels the ideal force. A value of 1 could generally be achieved only if a subject's lateral force perfectly matched the ideal force. Most of the variance in the time course of the adaptation index under the abrupt condition was accounted for by Eq. 5 ($R^2=0.92$) which yielded

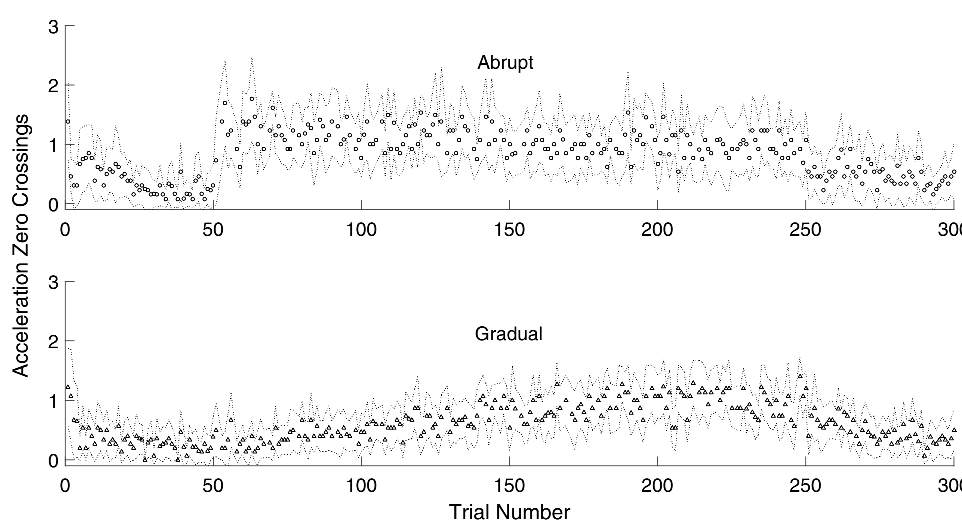


Fig. 4 Group mean acceleration zero crossings is plotted with 95% confidence interval shown by dotted lines for the abrupt group (circles top panel) and the gradual group (triangles bottom panel) for trials without error clamp

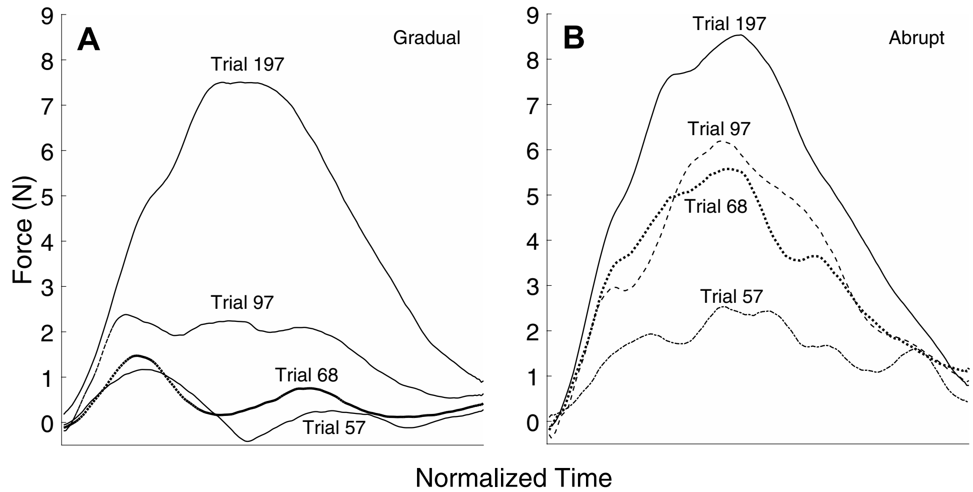


Fig. 5 Mean lateral force (f_x) profiles under the gradual condition (**a**) for selected error-clamp trials and for the corresponding trials under the abrupt condition (**b**), showing the development of the force applied to counteract the force field as training progressed

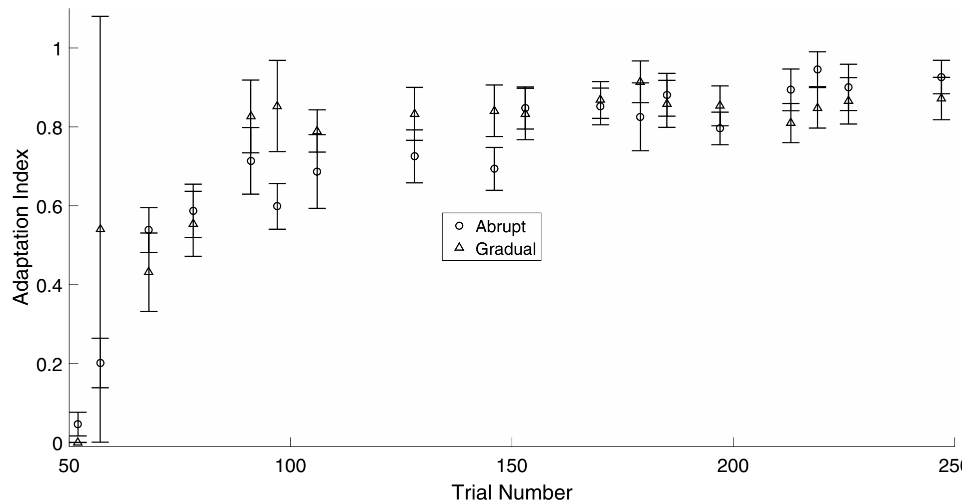
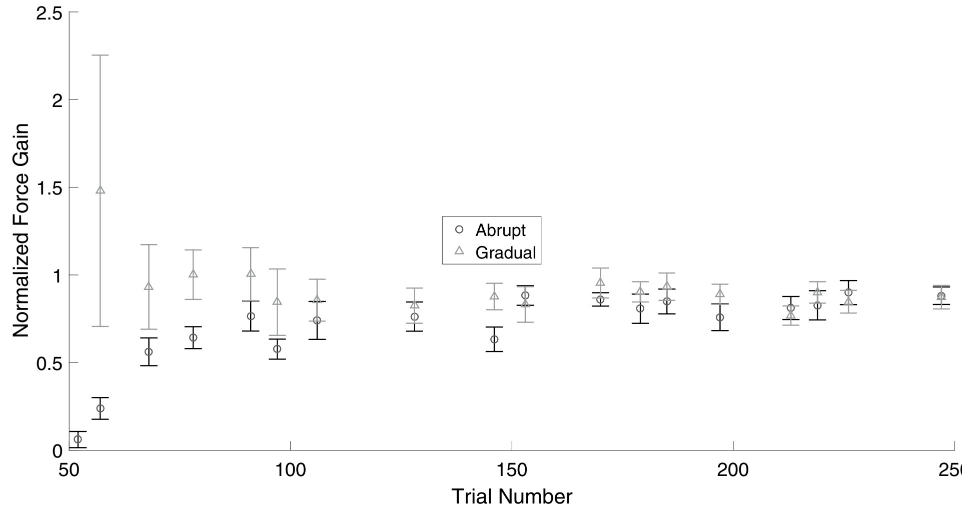


Fig. 6 Group mean adaptation index is plotted with standard error bars for the abrupt group (circles) and the gradual group (triangles) for error-clamp trials

a time constant of 30 trials with a 95% confidence interval of [22, 42]. Similarly, Eq. (5) accounted for much of the variance under the gradual condition ($R^2=0.87$), yielding a time constant of 19 trials with a 95% confidence interval of [12, 31]. Since the confidence intervals overlapped, we could not detect any difference in the rate at which the adaptation index increased under the two conditions. If we had subtracted the baseline force under the abrupt condition, the result would be substantially the same, since the principal effect of baseline subtraction is to add an offset to the data. We simulated the effect of subtracting the baseline using the mean baseline force for the gradual group (Fig. 2) as a proxy for the baseline force of the abrupt group. The simulation resulted in a negligible (1.3%) change in the time constant for the abrupt group. Although the adaptation index initially differed between the two conditions, by trial 197, there was no significant difference ($p=0.41$) between the abrupt (mean 0.80 ± 0.15) and gradual (mean 0.85 ± 0.20) conditions. The mean value of the final adaptation index determined from trial 247 was not significantly different ($p=0.64$) between abrupt (0.93 ± 0.15) and gradual (0.87 ± 0.21) conditions.

Figure 7 compares the trial-by-trial evolution of the group means of the normalized force gain which is a measure of how closely the subjects' peak lateral force matched the ideal peak force, the ideal being equal to 1. Under the abrupt condition, most of the variance in the normalized force gain was accounted for by Eq. (5) ($R^2=0.89$) yielding a time constant of 20 trials with a 95% confidence interval of [14, 29]. Under the gradual condition, a similar amount of the variance was accounted for by Eq. 5 ($R^2=0.88$) which yielded a time constant of 4.6 trials with a 95% confidence interval of [1.0, 6.6]. Given that there was no overlap in the confidence intervals, we would infer that the normalized force gain increased more rapidly under the gradual than the abrupt condition. To determine whether subtraction of the baseline force could affect the time constant under the abrupt condition, we simulated the subtraction of the baseline force by subtracting the peak of the mean baseline force recorded

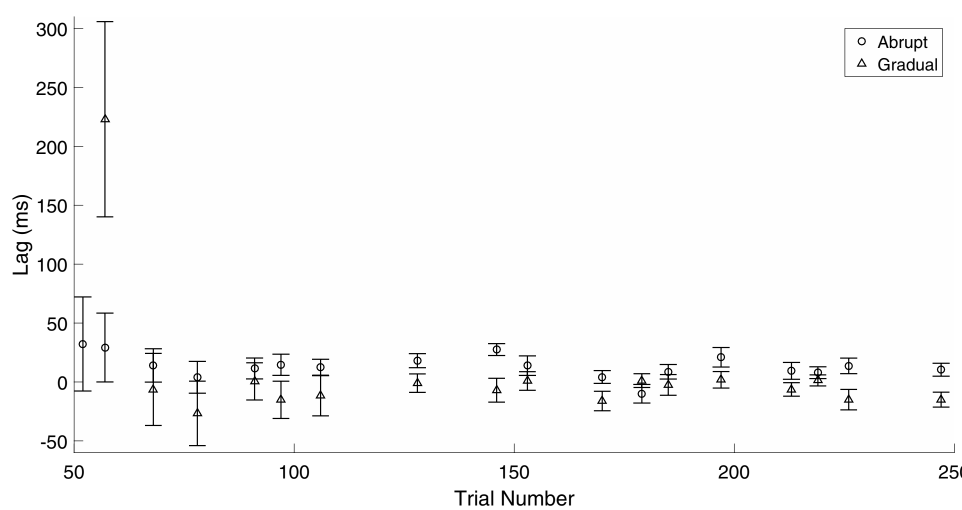
Fig. 7 Group mean normalized force gain is plotted with standard error bars for the abrupt group (circles) and the gradual group (triangles) for error-clamp trials



under the gradual condition (Fig. 2) from the mean peak force recorded on each error-clamp trial under the abrupt condition. We assumed that since the kinematic error was similar under the abrupt and gradual conditions prior to switching on the force field that the mean baseline force under the gradual condition could serve as a proxy for the mean baseline force under the abrupt condition. The effect was to reduce the time constant under the abrupt condition from 20 to 19 trials which was still far outside of the 95% confidence interval for the gradual condition. Although the normalized force gain initially differed, by trial 197, there was no significant difference ($p = 0.18$) between the abrupt (mean 0.76 ± 0.27) and gradual (mean 0.89 ± 0.22) conditions. The mean value of the final normalized force gain as determined from trial 247 was nearly identical under the abrupt (0.88 ± 0.18) and gradual conditions (0.87 ± 0.26).

Figure 8 compares the trial-by-trial evolution of the group means of the lag at peak cross correlation which is effectively a measure of the delay between the ideal force peak and the peak lateral force exerted by the subject, i.e., the actual force. The mean initial lag was positive, although not significantly different from zero under the abrupt condition ($p = 0.44$). With the exception of three trials (128, 146, and 197), the lag was never significantly different from zero. Under the gradual condition, the lag was not defined for trial 52, since subtraction of the baseline resulted in the actual force being set to zero. The mean lag on the next error-clamp trial (57) was positive. However, thereafter, it was not significantly different from zero with the exception of the final error-clamp trial. This suggests that, on average, subjects were able to modulate their lateral force in phase with the y-velocity with little training, i.e., there was an innate phase relationship between the force disturbance and the applied force. The lag value at trial 197 was 21 ± 30 ms under the abrupt condition compared to 2 ± 27 ms under the gradual condition, and was not significantly different ($p = 0.11$). The difference was significant on trial 247 ($p = 0.0065$),

Fig. 8 Group mean lag is plotted with the standard error bars for the abrupt group (circles) and the gradual group (triangles) for error-clamp trials



i.e., not significantly different from zero under the abrupt condition (10 ± 20 ms), but negative under the gradual condition (− 15 ± 24 ms).

Figure 9 compares the trial-by-trial evolution of the spectral arc length. Note that the spectral arc length is defined as being negative, so that as it increases towards zero, it represents a smoother profile. Since the force on the first error-clamp trial (52) was zero under the gradual condition following subtraction of the baseline, the spectral arc length was not defined until the second error-clamp trial (57). Equation (5) accounted for almost all of the variance in the spectral arc length under both the abrupt ($R^2 = 0.92$) and the gradual ($R^2 = 0.97$) conditions, yielding time constants of 7.4 trials under the abrupt condition with a 95% confidence interval of [4.7, 11] and 18 trials under the gradual condition with a 95% confidence interval of [15, 21]. To obtain a qualitative estimate of the effect of not subtracting the baseline force under the abrupt condition, we compared the time constants obtained under the gradual condition with and without baseline subtraction. The effect of not subtracting the baseline was to reduce the time constant. We would expect the effect to be similar but less pronounced under the abrupt condition because of the relatively larger force magnitude during the early training trials compared to the gradual baseline force (Figs. 2, 5). Thus, the spectral arc length was reduced, i.e., the force became smoother, more quickly under the abrupt than the gradual condition. By trial 197, there was no significant difference ($p = 0.75$) in the spectral arc length between the two conditions (abrupt mean − 1.79 ± 0.12, gradual mean − 1.76 ± 0.04). The mean value of the spectral arc length at the end of training (trial 247) was also not significantly different (abrupt mean − 1.79 ± 0.11, gradual mean − 1.77 ± 0.04, $p = 0.89$).

Discussion

We investigated performance and adaptation following an abrupt or gradual change in interaction dynamics between the arm and the physical environment. Kinematic error and performance progressed with opposite trends under the two conditions, i.e., kinematic error and number of acceleration zero crossings increased as force-field strength increased under the gradual condition, whereas the opposite tendency was observed under the abrupt condition. Learning metrics related to gain and smoothness of the adaptive response, i.e., the lateral force, evolved at different rates under the abrupt and gradual conditions, whereas phase lag was relatively constant under both conditions. By the time that the strength of the force field under the gradual condition attained that of the abrupt condition, there were no statistically significant differences in any of the adaptation metrics, even though subjects training under the abrupt condition had performed 150 trials with the same interaction dynamics, whereas subjects training under the gradual condition had experienced continuously changing interaction dynamics.

Our expectation was that higher sensitivity for small kinematic errors should produce a more rapid increase in the adaptation index under the gradual than the abrupt condition and our results, based on fitting time constants to adaptation metrics, suggest that this is the case, although the effect did not reach statistical significance. We can clearly say, however, that the adaptation index did not increase more rapidly under the abrupt condition than under the gradual condition. We found that the force gain increased with a shorter time constant under the gradual than the abrupt condition, although the spectral arc length (smoothness) increased with a longer time constant. We can refute the three points which we proposed as explanations for a possible discrepancy between error sensitivity and adaptation. First, our results

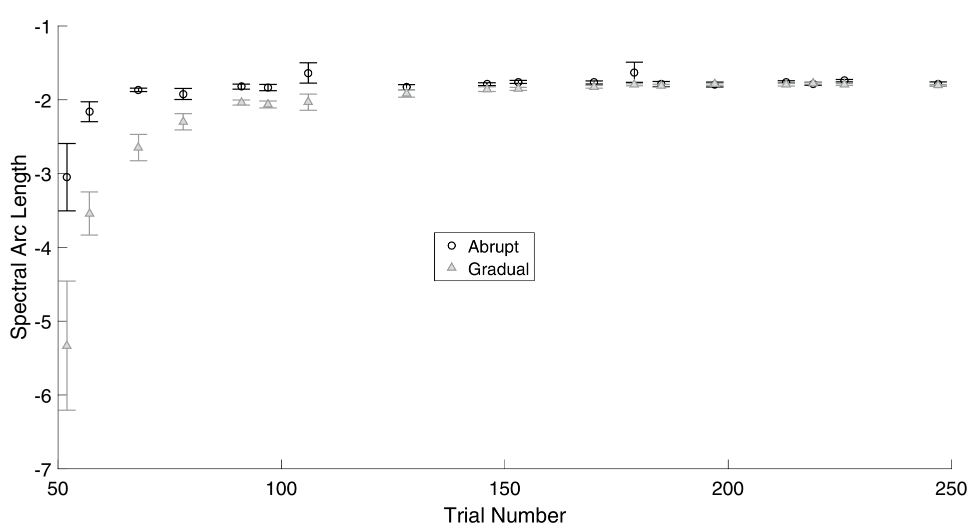


Fig. 9 Group mean spectral arc length is plotted with the standard error bars for the abrupt group (circles) and the gradual group (triangles) for error-clamp trials

suggest that, under the gradual condition, the internal state had changed by the second error-clamp trial, so it is unlikely that, initially, the errors were too small to evoke a change in the internal state. Second, it is clear from Fig. 3 that the kinematic error under the abrupt condition was not reduced to a level comparable with the gradual condition, but that under the gradual condition it grew until it was comparable to that under the abrupt condition. Third, our results are not consistent with those of Huang and Shadmehr (2009), who examined only partial adaptation, as we detail in the following paragraph.

Huang and Shadmehr (2009) found that subjects took longer to reach an adaptation index of 0.5 under the gradual than the abrupt condition. However, based on the fit derived from Eq. (5), our results suggest that an adaptation index of 0.5 would have been achieved after 14 trials under the gradual condition compared to 22 trials under the abrupt condition. This discrepancy would likely be even greater if baseline force had been subtracted from the error-clamp trials under the abrupt condition. Since not subtracting the baseline overestimates the applied force, it would actually require more than 22 trials to reach an adaptation index of 0.5 under the abrupt condition had the baseline been subtracted. The discrepancy between our results those of Huang and Shadmehr (2009) may be explained, at least in part, by a difference in the tasks. In their study, subjects did not stop at the target. Rather, they were required to move quickly and pass through the target after which the hand was slowed by a damping field. Although, in their study and ours, the adaptation index was calculated over the interval between the start of the movement and arrival at the target, in their study, the interval ended near the time of peak velocity, whereas, in our study, the interval ended near the time of movement termination. The greater number of error corrections required to reach the target under the abrupt condition than the gradual condition during the early part of training in the force field (Fig. 4) could account for the difference in the number of trials to achieve an adaptation index of 0.5. In addition, their subjects were given financial incentives for accuracy which was not the case in our study. Under the gradual condition, where errors were relatively small initially, financial incentives would probably make little difference in the rate of adaptation. However, under the abrupt condition, financial incentives would be expected to provide motivation to reduce error quickly which could partly account for the faster adaptation under the abrupt than the gradual condition reported by Huang and Shadmehr (2009).

Although it seems somewhat paradoxical that as the internal state became more accurate under the gradual condition, the maximum hand-path deviation continuously grew, the most likely explanation is that the update of the internal state was insufficient to compensate for the combined effect of increasing force-field strength and imperfect retention of the past internal state. A related finding was that the performance, as determined from the number of zero crossings during deceleration, changed very little under the abrupt condition and decreased significantly under the gradual condition (more zero crossings). This indicates that there was always some reliance on sensory feedback to correct for errors during movements in the force field. Since the amount of error correction increased as the force-field strength increased, it follows that there is a fundamental limitation in the ability of the central nervous system to counteract this type of disturbance. This limitation is not related to the ability to detect the force disturbance, since the lateral force increased as the force-field strength increased. Rather, it is likely a limitation in the ability to accurately judge the force gain, since the normalized force gain remained below 0.9 even after extensive training. The ability to accurately judge how the disturbing force is modulated with velocity or to accurately control muscle force may be limited, as well. The continuous improvement in performance during the initial null-field training and the rapid recovery of performance during the null-field washout suggests that subjects could accurately compensate for the passive dynamics of the robot, i.e., its inertia. This is likely because the central nervous system has had a lifetime of experience moving under conditions where the interaction dynamics are inertial. The velocity force-field dynamics are not natural, since there are no real-world circumstances under which disturbing forces would be encountered which are proportional to velocity but push in a direction perpendicular to the direction of motion.

Our results suggest that adaptation of amplitude and temporal aspects of the internal state, such as gain and smoothness, evolve differently and likely depend on the characteristics of the interaction dynamics. A model such as that proposed by Franklin et al. (2008) and recently elaborated by Albert and Shadmehr (2016) could provide additional insight into the mechanism of adaptation to a change in interaction dynamics. Small changes in the output of somatosensory receptors arising from even slight changes in interaction dynamics feed back through reflex pathways to modify motor output. A mechanism which shifts a proportion of the slight change in motor output forward in time and incorporates it into the motor command for the subsequent trial could account for the rapid adaptation of internal state phase lag and the more gradual adaptation of internal state gain and smoothness. The model does not explicitly incorporate a forgetting factor, but this is something that can be added without altering the fundamental learning rule upon which the model is based.

In summary, we have examined adaptation of different features of the internal state to a change in interaction dynamics, namely change in force gain, phase lag, and smoothness, and have shown that the time constants of metrics associated with these features can depend on whether the interaction dynamics change gradually or abruptly. The greatest differences were observed in the rate at which the force amplitude is adjusted to match the disturbing force of the interaction dynamics and the rate at which the force becomes smoother. Our results suggest that adaptation of force amplitude to a gradual change in interaction dynamics is rapidly established, because the central nervous system is able to predict the increments in force and adopts a strategy of compensating for a fixed proportion of the increase. On the other hand, smoothing of the force occurs more slowly, possibly because small fluctuations in force are relatively more pronounced when the peak force is small than when it is large.

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