eNeuro

Research Article: New Research* | *Sensory and Motor Systems

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https://doi.org/10.1523/ENEURO.0266-20.2020

Cite as: eNeuro 2020; 10.1523/ENEURO.0266-20.2020

Received: 17 June 2020
Revised: 19 August 2020
Accepted: 9 September 2020

Rapid changes in movement representations during human reaching could be preserved in memory for at least 850ms

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Running Head: Adaptive feedback control

***Key-words**:* Forcefield adaptation, adaptive feedback control, online corrections, movement representations, electromyogram, via-point, reaching control; motor adaptation; motor learning, internal models; sensorimotor control.

Authors contributions: JM, PL, FC designed the study, collected/analyzed the data and drafted the manuscript.

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Number of pages: 27

Number of figures: **5**

Number of words in the abstract: 246

Number of words in significance statement: 88

Number of words in the introduction: 529

Number of words in discussion: 2136

Acknowledgments:

Conflict of interest: The authors state they have no conflict of interest.

Funding sources: This work was funded by FRS-FNRS PDR grant no T.0048.19

ABSTRACT

Humans adapt to mechanical perturbations such as force fields during reaching within tens of trials. However, recent findings suggested that this adaptation may start within one single trial, i.e., online corrective movements can become tuned to the unanticipated perturbations within a trial. This was highlighted in previous works with a reaching experiment in which participants had to stop at a via-point (VP) located between the start and the goal. A force field was applied during the first and second parts of the movement and then occasionally unexpectedly switched off at the VP during catch trials. The results showed an after-effect during the second part of the movement when participants exited the VP. This behavioural result was interpreted as a standard after-effect, but it remained unclear how it was related to conventional trial-by-trial learning. The current study aimed to investigate how long do such changes in movement representations last in memory. For this, we have studied the same reaching task with VP in two situations: one with very short residing time in the VP and the second with an imposed minimum 500ms dwell time in the VP. In both situations, during the unexpected absence of the force field after VP, after-effects were observed. This suggests that online corrections to the internal representation of reach dynamics can be preserved in memory for around 850ms of resting time on average. Therefore, rapid changes occurring within movements can thus be preserved in memory long enough to influence trial-by-trial motor adaptation.

SIGNIFICANCE STATEMENT

Recent studies suggested that adaptive feedback control happens within a reach movement and the feedback responses are tuned specifically to the single-trial perturbation. Here we show that these feedback mediated changes in movement representations can last for around 850ms and are available to reproduce the characteristics of the newly acquired correction process. Current data replicate previous studies showing that feedback corrections are associated with changes in online representations, and demonstrate that these changes are preserved in memory long enough to be an important component of standard trial-by-trial adaptation.

INTRODUCTION

Humans adapt to force field perturbation during reaching movements within a few minutes of practice (Brashers-Krug et al. 1996; Shadmehr and Brashers-Krug 1997; Shadmehr and Mussa-Ivaldi 1994). But learning is hampered when attempting to adapt to opposing force fields sequentially or intermittently (Caithness et al. 2004; Gandolfo et al. 1996; Karniel and Mussa-Ivaldi 2002). The reasoning for the relative inability to learn opposing perturbations is that, given no explicit contextual information about the forcefield, the motor memory attempts to learn the mean of the force fields applied on the recent trials (Scheidt et al. 2001) using a single internal model of the mean of the random environment (Takahashi et al. 2001), or the internal models for different perturbations share common resources (Tong and Flanagan 2003). In these scenarios, it was demonstrated that the presence of explicit contextual cues associated with each perturbation or different representations could facilitate the adaptation to opposing perturbations, by acquiring multiple internal models simultaneously and predictively switching between them (Addou et al. 2011; Cothros et al. 2008; Hirashima and Nozaki 2012; Imamizu et al. 2007; Osu et al. 2004; Wada et al. 2003).

However, more recent studies highlighted the possibility of concomitant learning of opposing and unexpected force fields that could be explained as the expression of online, continuous adaptive control (Crevecoeur et al. 2020a, 2020b). This supports the possibility that online feedback corrections happening within a trial are not stereotyped but are associated with specific changes in movement representation (Joiner et al. 2017). It remains to be elucidated whether the underlying mechanism associated with feedback adaptation plays a role in the trial-by-trial adaptation that characterizes learning across trials.

A central piece of evidence for rapid adaptation is based on the presence of after-effects expressed after a stop-over at a via-point (VP) (Crevecoeur et al. 2020b). On catch trials, a force field was applied during the first part of the movement and then unexpectedly switched off after the via-point. When participants exited the VP, after-effects were observed, which were specific to the perturbation experienced before VP within the same trial, and were consistent with the after-effects observed in conventional trial-by-trial adaptation scenarios. The movement after VP was interpreted as an after effect, showing that the feedback correction elicited prior to the via-point could change movement representations online.

It remained unclear whether these changes in reach representation observed in trials with via-point were short-lived, or whether they could participate in trial-by-trial adaptation. More precisely, it is unknown whether the motor system forgets the effect of online feedback corrections very fast, as it arises due to transient disturbances; or if these changes are retained in memory for enough time to impact behaviour in the next trial. If the online feedback corrections are retained, then it suggests that much of trial-by-trial adaptation and after-effects may be acquired within perturbed movements. Alternatively, if feedback-related changes in movement representation decay very fast, then trial-by-trial learning must be based on offline adjustments. In the present work, we replicated previous findings and found that these online feedback corrections elicited after-effects that could be retained in memory for at least 850ms. Therefore feedback adaptation constitutes a candidate component of more conventional trial-by-trial learning.

MATERIAL AND METHODS

Experimental design

18 right-handed healthy adults (age = 22.9±1.9, 10 female) were recruited for the study. All of them provided written informed consent. The experimental paradigm was approved by the

Ethics Committee of the host institution and complied with the Declaration of Helsinki. Participants were compensated for their participation.

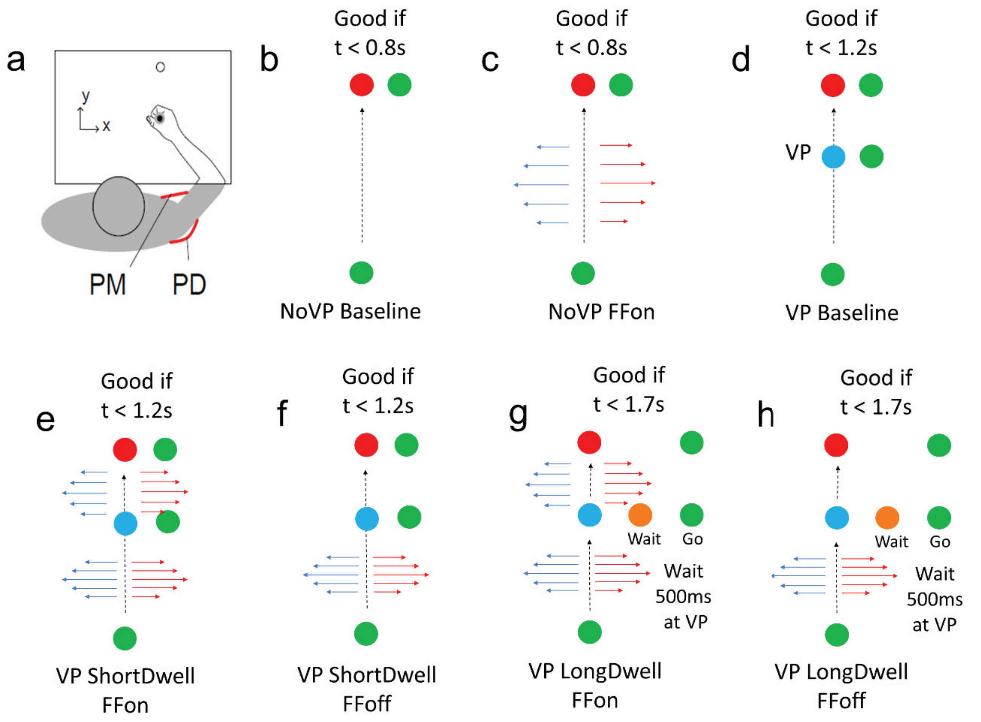

Figure1. a) Experimental setup. Electromyogram was recorded from Pectoralis Major (PM) and Posterior Deltoid (PD). b) Typical simple reaching trial without via-point (VP) and forcefield (FF) c) NoVP trial with forcefield, either clockwise (red arrows) or counterclockwise (blue arrows). d) VP trial without forcefield. Participants were requested to make a short pause at VP and proceed to the final target. e) VP ShortDwell trial with force field before and after VP. f) VP ShortDwell catch trial with forcefield unexpectedly turned off after VP. g) VP LongDwell trial with forcefield before and after VP. h) VP LongDwell catch trial with forcefield unexpectedly turned off after VP. The target would change color when the participants made movements within the instructed time window. For d-h, VP would change color when the participants made a pause at VP and the hand velocity dropped to <3cm/s. For g-h, VP would change color again when the participant stayed at VP for 500ms.

Participants grasped the handle of a robotic arm (KINARM, Kingston, ON, Canada), and were instructed to perform visually guided forward reaching movements towards a virtual target and their forehead resting on a stable resting pad, to minimize head movements.

There were mainly seven types of movement conditions:

1) No via-point trials (NoVP Baseline/B): Participants had to wait at the starting position (a filled circle with radius 0.6cm) for a random delay uniformly distributed between 2s and 4s. The goal position was fixed at 15cm from the starting point and was initially presented as an open red circle. A cue was delivered to initiate the movement by filling the circle in the goal position and for a successful trial, the participants had to reach the goal position within 600ms to 800ms (including reaction time) and stabilize there for at least 1s. Visual feedback was provided to inform them about the reaching time. If they moved too fast, the goal circle changed back to an open circle. If the movement was too slow, it remained red. The goal target became green when they hit it within the specified time window. When they managed to keep the cursor in the goal target for the instructed stabilization period, the trial was successful and a score displayed on the screen was incremented (1 point). The scores and feedback about timing were provided to encourage consistent movement times but all trials were included in the dataset. In all cases, the direct vision of the arm and hand was blocked but the cursor aligned to the handle was always visible.

2) NoVP with force fields (NoVPFF). In these types of trials, participants experienced mechanical perturbation by orthogonal force fields during the forward movement, ie, lateral force proportional to the forward hand velocity ($F_x = \pm L v_y$, L = 13 Nsm^{-1}). Force fields were either clockwise (CW) or counter-clockwise (CCW).

3) Via-point (VP) Baseline trials with slowdown at VP. In these trials, a via-point (filled blue circle of radius 1cm) was located at 10cm on the straight line joining the start and goal position. Participants were instructed to reach the goal position through the VP (Fig 1c). Bonus points (3 points) were given when they paused at the VP and the hand velocity inside the VP dropped below 3cm/s. Feedback about a successful slowdown at the VP was given during the trial by changing the color of the VP filled circle from blue to green.

4 and 5) Via-point trials with short dwell time at VP, force field ON before VP and ON/OFF after VP (VPsFFon/ VPsFFoff). For catch trials, the hand velocity was monitored online so as to turn off the force field if the hand cursor was at the VP and the hand velocity dropped below 3cm/s while at the VP (as shown in Fig 1d).

6 and 7) Same as 4&5, but with long dwell time at VP (VPlFFon/ VPlFFoff). In these trials, participants were forced to stay at the VP for at least 500ms before they proceed to the goal position.

Once they reached the VP, the filled blue circle became orange and after 500ms it turned to green, which was a go cue to proceed to the final position (Fig 1e). The notation VPs/lFFon and VPs/lFFoff corresponds to VP trials with forcefield on and off in either ShortDwell or LongDwell situations. To summarize, we had a factorial design of trials: No via-point trials with force field on or off (CW/CCW); via-point trials with force field on or off, catch trials where the force field was turned off after the via-point, and similar via-point trials with the instruction to remain in the via-point for at least 500ms (CW/CCW, ShortDwell/LongDwell, forcefield ON/OFF after VP).

Participants performed two different kind of blocks: *ShortDwell and LongDwell*. Each consisted of 240 trials composed of 100 NoVP baseline trials, 40 NoVPFF trials, 20 VP baseline trials, 40 VPs/lFFon and 40 VPs/lFFoff trials. All trials and force field directions were interleaved randomly within each block, such that the occurrence and direction of the perturbations were unpredictable. Half of the participants did ShortDwell block set before LongDwell block set.

Data analysis and statistics

The 2-dimensional coordinate of the cursor aligned to the robotic handle, and the forces at the interface between the participants' hand and the handle were sampled at 1kHz. Signals were digitally low-pass filtered with a fourth-order, dual-pass Butterworth filter with a cut-off frequency of 50Hz. Velocity signals were obtained from numerical differentiation of position signals (4th order, finite difference algorithm). Electromyogram (EMG) was recorded from the shoulder flexor - Pectoralis Major (PM) and shoulder extensor - Posterior Deltoid (PD), the main muscles recruited when performing lateral corrections against the perturbations used in this experiment (Bagnoli Desktop System, Delsys, Boston, MA, US). EMG electrodes were positioned over the muscle belly after light abrasion of the skin. A dermatrode self-adhering electrode was positioned on the right foot ankle for ground. EMG signals were collected at 1000Hz sampling frequency and digitally band-pass filtered (4th order dual-pass: [10, 400] Hz).

Three events were used as timing references. First, reach onset was defined as the moment when the cursor exited the home target. Second, the moment the cursor reached VP. Third, the moment the cursor exited VP and proceeded towards the final target location. Hand paths were averaged first; within and then across the subjects. For each subject, lateral (v_x) and forward (v_y) component of the peak velocity was computed before and after VP for each trial and averaged per condition. EMG traces were averaged offline, first within and then across subjects and were aligned to the VP exit to compute the characteristics of muscle response after VP, in both ShortDwell and LongDwell, *VPs/lFFoff* and *VPs/lFFon*. For statistical comparison across conditions, EMG was averaged in 100ms bins before VP exit. Paired t-tests and repeated measures ANOVAs were used to find a significant difference with a p-value of less than 0.05. We measured the onset of changes in EMG after the VP exit. EMG traces averaged across trials for each subject were collapsed into a 30ms wide (centered) sliding window, and sliding comparisons through time were performed with paired t-tests. We searched in the time series of p-values the moment the difference across populations of EMG data crossed a threshold ($p < 0.05$), which was immediately followed by a strongly significant difference ($p < 0.001$).

RESULTS

Behavioral traces for simple movements

Simple reaching trials with and without perturbation and adaptation across trials were discussed in detail in some previous works (Crevecoeur et al. 2020b, 2020a). As in these previous reports, for no via-point trials, the current dataset also observed a significant reduction in end-point target overshoot (t-test: $t_{35} = 3.77$; $p < 0.001$) and hand path length (t-test: $t_{35} = 4.33$; $p < 0.001$) between the first and last trials (Fig 2), suggesting that feedback correction for the unanticipated force field trials improved.

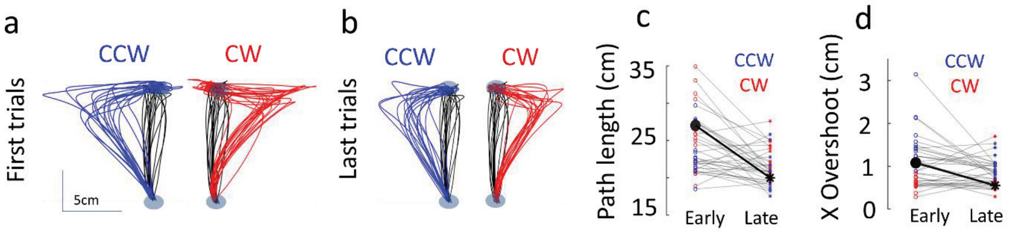

Fig 2: a) First trials of no via-point movements with CCW(blue) and CW(red) forcefields (NoVPFF) plotted with baseline (NoVP) trials (black) for all 18 subjects. b) Last trials of the same, note how the target overshoot is reduced in comparison with first trials. c) Distance travelled (path length) by hand during first and last trials d) End-point target overshoot in the X direction in early and late trials. The thick black dot and star in c and d indicate the mean. There is a significant reduction in target overshoot and path length between early and late trials, which show hints of adaptation.

Via-point dwell time

Turning to via-point trials, we measured the actual dwell time for short and long dwell conditions to verify whether participants complied with task instructions (Fig 3). For analysis, we defined dwell time as the time interval between the VPentry and VPexit for the hand motion. In ShortDwell trials, the mean dwell duration at VP was 345±22ms (for all participants, min = 22ms; max = 499ms). Around 15% of the total ShortDwell trials (variation per subject: 0-37.5%) consisted of dwell duration not in the range 0-500ms were eliminated from further analysis (Fig3a, the red fraction of the histogram). In LongDwell, mean dwell duration was

856±37ms (min = 550ms, max = 1491ms). In this condition, 3% of the total LongDwell trials from all the subjects (variation per subject: 1.25-6.25%) were eliminated, so that LongDwell trials consisted of dwell time within the range 500-1500ms (Fig3b).

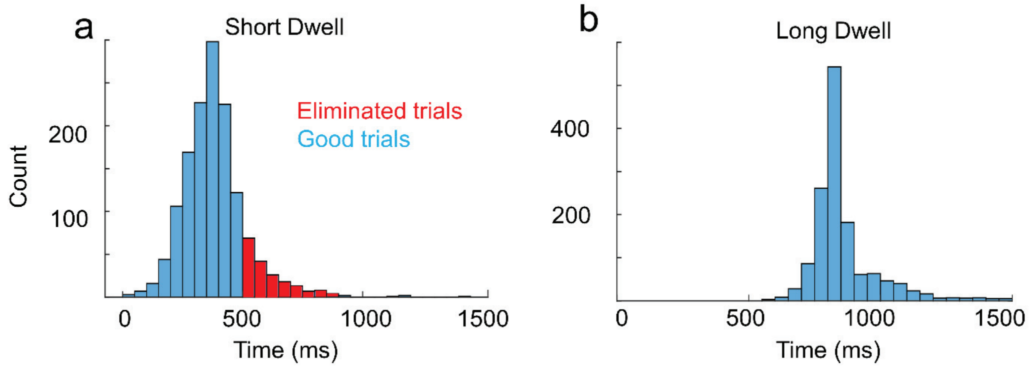

Fig 3. Distribution of actual dwell times for all subjects and all trials in a) ShortDwell and b) LongDwell blocks. Each bin corresponds to 50ms. For ShortDwell, the trials with dwell times longer than 500ms and for LongDwell, the trials with dwell times shorter than 500ms or longer than 1500ms were removed from the analyses.

Behavioral traces for movement through via-point

To trace out the nature of online changes in movement representation happening within the trial, we compared the movement after VP in situations with force field on or off after the via-point (VPs/lFFon and VPs/lFFoff).

Forcefield off (catch trials):

VPs/lFFoff trials were interleaved as catch trials to capture the dynamics of online correction within the trial. When the force field was off after VP, an after-effect was observed in the subsequent chunk of movement, such that the hand path deviated on the other side compared to that of the previously experienced perturbation before VP (Fig 4d,e). The lateral component of the 2nd peak velocity showed inverse modulation in comparison to the hand path deviation experienced prior to the VP (Fig 4f). There was a significant difference from baseline trials for CCW and CW in ShortDwell (CCW: $t_{17} = -8.85$; $p < 0.001$ and CW: $t_{17} = 3.03$; $p < 0.01$) and LongDwell (CCW: $t_{17} = -8.89$; $p < 0.001$ and CW: $t_{17} = 5.80$; $p < 0.001$). But there was no significant difference between ShortDwell and LongDwell trials for CCW ($t_{17} = -0.25$; $p = 0.80$) and CW ($t_{17} = -1.43$; $p = 0.17$). This showed that the dynamics of the online correction adopted before VP were continued after VP and it was comparable for ShortDwell and LongDwell conditions. That means this correction strategy was preserved and exploited even after a pause of around 850ms at the VP.

One possibility was that participants performed faster movements after the VP in the LongDwell condition, resulting in larger forces produced by the force field but it was not the case: we also checked the Y component of the 2nd peak velocity in VPs/lFFoff trials and found no significant difference from baseline trials for CCW and CW in ShortDwell (CCW: $t_{17} = -1.72$; $p = 0.10$ and CW: $t_{17} = -1.74$; $p = 0.1$), but there was a significant difference in LongDwell (CCW: $t_{17} = 4.02$; $p < 0.001$ and CW: $t_{17} = 5.89$; $p < 0.001$). Also, there was no significant difference in the Y component between ShortDwell and LongDwell trials for CCW ($t_{17} = 1.13$; $p = 0.27$), but there was for CW($t_{17} = 2.87$; $p = 0.01$).

In addition, we have done a separate analysis by further splitting the LongDwell trials according to the individual median dwell time (range: 732-867ms; mean = 821ms), so that Early-LongDwell was within the range 500-821ms (mean = 773ms) and Late-LongDwell was within the range 821-1500ms (mean = 934ms). In this case also, when force field was off after VP, there was no significant difference between ShortDwell and Early-LongDwell (CCW: t17 = -0.89;p = 0.38 and CW: t17 = -1.63; p = 0.12), as well as ShortDwell and Late-LongDwell (CCW: t17 = 0.67;p = 0.51 and CW: t17 = -0.46; p = 0.65). Thus, the consistent after-effects were observed regardless of the average duration between the two consecutive chunks of movement in the range 0-1500ms (see Fig 3).

Forcefield on:

When the forcefield was on after VP, participants made lateral deviation (which was evident in Fig 4a,b) as expected and the modulation of lateral (x) component of the 2nd peak velocity shows a similar trend as that of the perturbation they have experienced before VP (Fig 4c). Simple t-tests on the x component of 2nd peak velocity showed a significant difference from baseline trials for CCW and CW in both ShortDwell (CCW: $t_{17} = 23.34$; $p < 0.001$ and CW: $t_{17} = -17.42$; $p < 0.001$) and LongDwell (CCW: $t_{17} = 20.22$; $p < 0.001$ and CW: $t_{17} = -16.65$; $p < 0.001$) situations. This was somehow expected as the duration of pause at VP may not directly influence the peak velocity modulation trend for subsequent perturbation, in comparison with baseline trials. Also, there was a significant difference in the x component between ShortDwell and LongDwell trials for CCW ($t_{17} = 2.41$; $p = 0.03$) and CW($t_{17} = -4.86$; $p < 0.001$).

We checked the Y component of the 2nd peak velocity in VPs/lFFon trials, and there was no significant difference from baseline trials for CCW and CW in ShortDwell (CCW: $t_{17} = 1.59$; $p = 0.13$ and CW: $t_{17} = -0.99$; $p = 0.34$), but significant difference in LongDwell (CCW: $t_{17}=5.56$; $p<0.001$ and CW: $t_{17} = 5.20$; $p < 0.001$). In addition, there was no significant difference in the Y component between ShortDwell and LongDwell trials for CCW ($t_{17} = 1.62.$; $p = 0.12$) and CW($t_{17} = 1.68$; $p = 0.11$). Thus participants control was more sensitive to the force field after the via-point in the long-dwell condition. The analysis of EMG below supports this explanation.

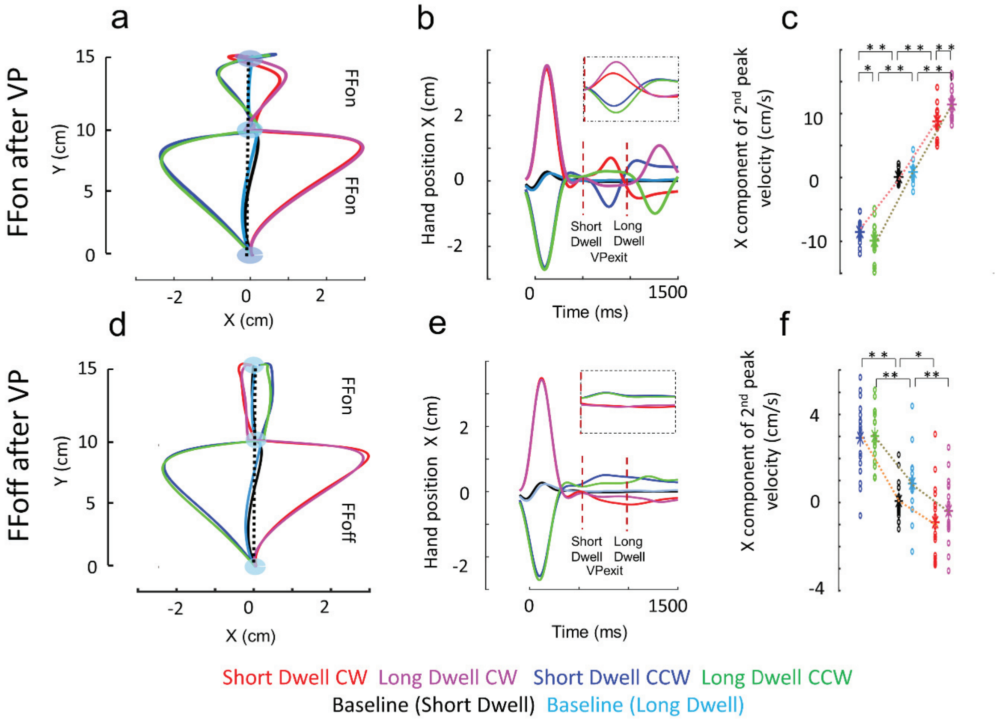

Fig 4. a, b & c correspond to the condition where force field was on before and after VP for both CW and CCW perturbations, while d, e & f correspond to the condition where force field was on before VP, but turned off after VP. VP baseline trials were included for comparison. a, d) Mean hand position in space. The dotted vertical line represents zero deviation. b, e) Mean X hand position across time from the onset of reach. The dotted lines in brown represent the mean VP exit time points. The plots in the dotted inset box (yaxis = [-2 2], xaxis =[0 600]) represent the mean X hand position immediately after VP exit for the next 600ms. c, f) Lateral component of the maximum hand velocity after the VP. ** represents $p<0.001$ and * is $p<0.01$.

EMG activity

Previous studies showed that unexpected perturbation elicits an increase in co-activation (Crevecoeur et al. 2019; Franklin et al. 2008; Milner and Franklin 2005) to counter following disturbances. It remains debated whether co-contraction increases the intrinsic stiffness of muscles, making the joints mechanically rigid (Burdet et al. 2001; Gribble et al. 2003) or whether the advantage of co-contraction is to increase feedback gains and make neural control more robust (Crevecoeur et al. 2019; Crevecoeur and Scott 2014; Pruszynski et al. 2009).

Importantly we found in the current dataset that an increase in co-activation was also elicited within movements including a stopover at the via-point, and the comparison of trials with force field on after the via-point allowed us quantifying the effect of co-contraction on behaviour. We investigated EMG levels of an antagonist pair of shoulder muscles as well as correlates of after-effects across the two conditions. We plotted EMG traces after VP in VPs/lFFon and VPs/lFFoff situations for both pectoralis major and posterior deltoid (Fig 5).

To evaluate whether there was any difference in muscle activity at VP exit across ShortDwell and LongDwell, we computed the difference of mean EMG activity in a window 0-100ms before VP exit, between the two dwell conditions and performed 2way repeated measures ANOVA over factors: muscle (MUS: PEC vs DELT) and forcefield (FF: on vs off) and found there was no effect of MUS ($F_{(1,143)} = 2.77$; $p = 0.11$), FF ($F_{(1,143)} = 1.12$; $p = 0.30$) and their interaction ($F_{(1,143)} = 3.50$; $p = 0.08$). There was no significant difference between forcefield on/off situations in agonist and antagonist muscles. In other words, in both FFon and FFoff conditions (Short VS LongDwell) we measured similar correlates of agonist-antagonist activity just prior to the exiting the via-point, that accounted for the after-effects when the force field was unexpectedly turned off.

We also calculated the mean EMG activity 100ms before the VP exit (dotted square boxes in Fig 5) and the difference between baseline and ShortDwell (CW/CCW/FFon/FFoff pooled together, PEC: $t_{71} = -8.24$;$p < 0.001$ and DELT: $t_{71} = -6.19$; $p < 0.001$) as well as baseline and LongDwell (PEC: $t_{71} = -2.6$;$p = 0.01$ and DELT: $t_{71} = -5.9$; $p < 0.001$). The higher muscle activity in both muscles compared to baseline trials could raise the possibility of co-contraction just before the VP exit.

Then we calculated the pairwise difference between ShortDwell and LongDwell trials for each subject for VPs/lFFon and VPs/lFFoff situations for each muscle. For FF on condition, the overall muscle activity in a window 0-100ms before VP exit was less in amplitude for

LongDwell compared to ShortDwell (Forcefield on, CW/CCW pooled together; PEC: t_{35} = -5.35; $p < 0.001$ and DELT: t_{35} = -4.78; $p < 0.001$). That means, there was a tendency to co-contract at the via-point which decreased over the course of residing time in the VP. Importantly, for FF off condition also, the overall muscle activity 0-100ms before VP exit was less in amplitude for LongDwell compared to ShortDwell (Forcefield off, CW/CCW pooled together; PEC: t_{35} = -5.35; $p < 0.001$ and DELT: t_{35} = -5.25; $p < 0.001$), which allows us to confirm that it had no influence on the after effect. In principle, co-contraction would result in a trajectory that is less sensitive to perturbation or errors, thus these results were expected. The foregoing analysis provides a confirmation: we observed different levels of co-contraction while similar after-effect, suggesting that the level of co-activation was not statistically related to the after-effect. Interestingly we observed that the trajectories after the VP were more impacted in the LongDwell condition when the force field remained on, which likely resulted from a combination of changes in representation (highlighted by the after-effects) and from a change in control gains associated with co-contraction.

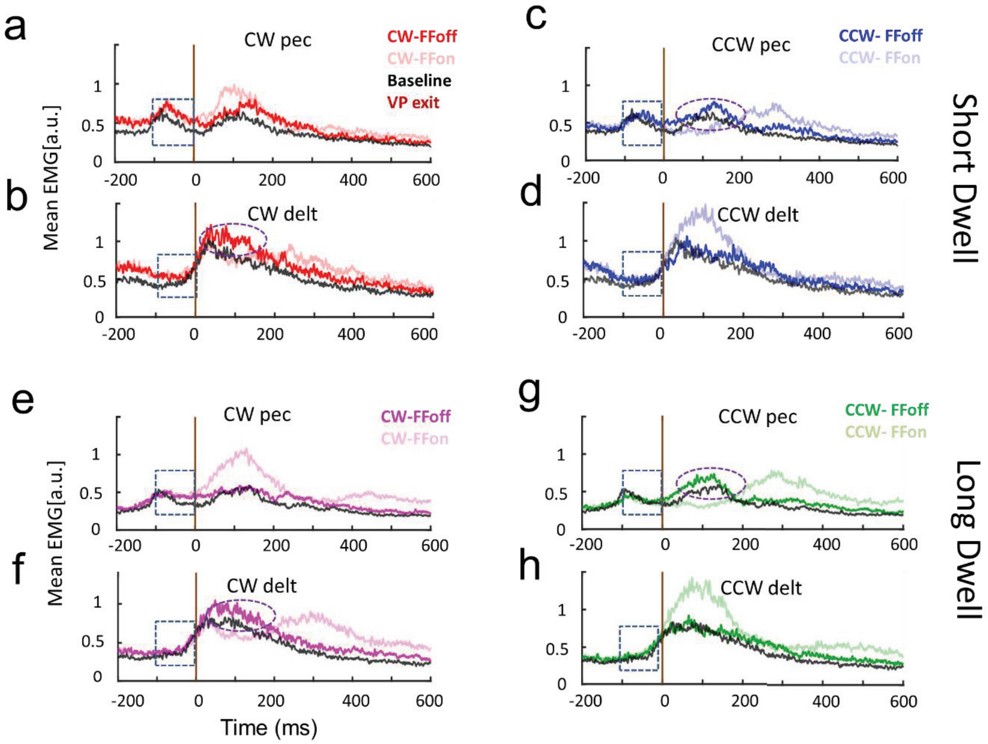

Fig 5. EMG correlates after VP in ShortDwell (a,b,c,d) and LongDwell (e,f,g,h) trials. Each trace represents mean across subjects. a,b,e,f for CW perturbation, c,d,g,h for CCW perturbation. All EMG traces were aligned at the time of the VP exit (Dark Brown line), the "0ms" in the horizontal axis indicates the timing of the VP exit. Force field on (VPs/lFFon - light shade) and off conditions (VPs/lFFoff- dark shade) were compared with VP baseline trials. The dotted oval shape represented higher activation in antagonist muscle. 100ms time window before VP exit was highlighted in dotted square boxes.

We further sought to characterize EMG correlates of force field anticipation after the via-point by performing comparisons based on a sliding window. EMG agonist (CW pec, CCW delt) followed a similar profile with and without force field until after VP, and this activity was higher than baseline. The antagonist (CCW pec, CW delt) muscle modulation also reflected correction for the unexpected deviation induced by switching off the force field (dotted oval in Fig 5). A similar observation was made in LongDwell trials. We have conducted paired t-tests for the mean of 30ms sliding window for the FFon and FFoff conditions and found the time points at which the on/off traces started to show a significant difference from VP exit, for

ShortDwell:- agonist pair = -22±15ms, antagonist pair = -14±15ms and for LongDwell:- agonist pair: = -26±15ms, antagonist pair: = -37±15ms. (The average hand tangential velocity at the exact moment of VPexit was 0.23 ± 0.03cm/s for ShortDwell and 0.24 ± 0.02cm/s for LongDwell)

To summarize the analyses of EMG results, we highlighted a spontaneous tendency to co-contract at the via-point, which decayed over the course of the dwell time interval. This tendency had an impact on the perturbation-related motion when the force field remained on likely due to intrinsic changes in limb impedance and to an increase in robustness. In contrast, there was no systematic directional bias in muscle state that could account for the rapid after-effect in either condition (short and long dwell times), and these after-effects were statistically similar despite the difference in co-contraction. In addition, we reported correlates of agonist activity when exiting the via-point, and antagonist response when the force field was turned off. These detailed EMG analyses allowed us to emphasize the impact of co-contraction, and to dissociate it from the near-instantaneous after-effects that, we found, could be preserved in the motor system for at least 850ms.

DISCUSSION

We investigated the temporal nature of rapid changes in movement representation due to unexpected force field perturbations. For this, we have studied the reaching task through a via-point on the pathway in two situations: one with very short residing time at the via-point (ShortDwell) and the second with an imposed minimum 500ms dwell time at the via-point (LongDwell). First, in support of previous works (Crevecoeur et al. 2020b, 2020a), we observed feedback adaptation across no via-point trials evidenced by a reduction in target overshoot and path length, when opposing force fields were applied randomly. That means online feedback corrections were tuned to specific perturbation within each individual trial although the force fields could not be anticipated. Additionally, the current dataset replicated the previous findings

(Crevecoeur et al. 2020a) that EMG imprints of changes in feedback corrections occurred within 250ms of reach onset, with this cohort of participants (data not shown). Second, in via-point trials, we observed the presence of an after-effect to the movement correction after the via-point that was opposed to the perturbation experienced before, when participants exited the via-point in less than 500ms (ShortDwell). Similar to standard after-effects evoked by a single force field trial, the presence of after-effects after the via-point was understood as the expression of changes in movement representation occurring online. Third, comparable after-effects in terms of hand path deviation and peak lateral velocity were observed in behavior and EMG recordings with an average 850ms dwell time at VP (LongDwell), and even beyond as observed when the trials were split according to their actual dwell time. In all, our results showed that somatosensory feedback about movement error could have long-lasting effects and be preserved during intervals comparable to different conditions of movement planning as in the context of trial-by-trial adaptation.

Our main motivation was to relate rapid after-effects evoked within a sequence of movements with residing times of the order of less than 500ms to those expressed in a time scale closer to a second. In standard reaching experiments, consecutive trials are typically separated by a few seconds. A direct comparison between after-effects after the VP and those following standard force field trials could not be conclusive because the limb configuration is not the same, however since these rapid feedback-related adjustments were preserved up to a time interval closer to one second, we suggest that they play a central role in well-known standard trial-by-trial learning. In other words, trial-by-trial adaptation and after-effects would result at least partially from within-movement neural processing associated with feedback control.

Adaptation of online feedback correction across trials

In force field adaptation experiments, one common assumption is that the prediction by forward models cannot change within a movement due to sensory delays, hence this mechanisms would only be available after the trial and therefore the reaching movements that employ only a feedforward controller could not account for the within-trial adjustments (Wada et al. 2003; Yousif and Diedrichsen 2012). In such cases, since the motion-dependent adaptive responses cannot be based on real-time sensory feedback, the feedforward adaptive responses must be programmed in advance based on predictions (Sing et al. 2013) and the delayed feedback responses were used to learn a predictive feedforward response (Thoroughman and Shadmehr 1999). Alternatively, real-time online corrections could be achieved through a feedback controller that must contain a forward model capable of accurate real-time prediction of the state of the limb, and combine the state predictions (Wagner and Smith 2008). In the case of random inconsistent perturbations scenarios, it was shown that the gain of sensory feedback responses appears to increase (Liu and Todorov 2007), and feedforward adaptive responses to decrease (Gonzalez Castro et al. 2014). Such cases highlighted “the adaptation of online feedback correction” (Joiner et al. 2017; Yousif and Diedrichsen 2012), more specifically “feedback adaptation” i.e., trial-by-trial fine-tuning of feedback responses to the specific perturbation happening within each trial (Crevecoeur et al. 2020b). In our case, across trials, there is an accumulation of learning, but this is not due to the predictive factor, instead, we argue that this is due to the feedback mediated online corrective process (feedback adaptation) since it is expressed very quickly in the ShortDwell condition.

In line with these concepts, it was demonstrated that the prediction of the current state of the limb could happen within long-latency feedback pathways (latency ~60-100ms)(Crevecoeur and Kurtzer 2018; Crevecoeur and Scott 2013; Scott 2016), which is faster than trial time. Long-latency feedback correction is also sensitive to force field adaptation and can facilitate trial-by-trial learning (Ahmadi-Pajouh et al. 2012; Cluff and Scott 2013; Maeda et al. 2020). Thus this pathway may support sensory-prediction and adaptation functionally, and its latency relative to reach time leaves time for potential changes within a movement. Without restricting to long-latency feedback, changes in feedback response were measured within ~250ms of reach onset (Crevecoeur et al. 2020a). In all, we believe that the assumption that movement representations are fixed within a reaching movement requires revision.

Traces of online feedback correction as after-effects in VP trials

In case of any perturbation during reaching movement, within a short period of movement initiation, sensory feedback starts to influence motor command updating throughout the movement (Brashers-Krug et al. 1996; Kawato 1999; Lackner and Dizio 1994; Shadmehr et al. 2010; Wolpert et al. 2011). Our developments suggest that a change in movement representation occurs in parallel during movement. Then the question is how long does this movement representation persist in the memory? Conventional trial-by-trial studies reported the variation in hand dynamics and movement trajectory from one trial to another.In these situations, there was an inter-trial interval of one or two seconds to return the hand to the starting position either passively or actively (Caithness et al. 2004; Donchin et al. 2003; Gandolfo et al. 1996; Izawa et al. 2008; Kording et al. 2007; Smith et al. 2006; Tong and Flanagan 2003). The idea of providing via-points in between the start and final position facilitated tracking the online feedback mediated corrective processes and associated adaptation within chunks of movement.

In our case, first, during ShortDwell condition, we have observed clear after-effects during the follow-through movement after VP (Fig 4 d,e,f). Why did the hand path deviate after VP? After-effects are known to reveal the change in motor command and the nature of the adaptive process by highlighting the discrepancy between expected and actual dynamics (Bhushan and Shadmehr 1999; Shadmehr and Mussa-Ivaldi 1994). During the first phase of the movement, the hand experienced perturbation and it has been shown that the hand force to counteract this disturbance became tuned to the hand velocity, which was consistent with online adaptation (Crevecoeur et al. 2020b). This corrective process and thus evolved movement representation continued after VP as the CNS expected a continuation of perturbation. In the absence of this, the discrepancy in the expected and actual hand dynamics resulted in an after-effect.

Long-lasting effects of somatosensory feedback about movement error: a basis of trial-by-trial adaptation?

Rapid feedback adaptation may still differ from the mechanism engaged in memory retrieval associated with different planning conditions. Indeed, follow-through movements with a short movement pause at VP reported that sensorimotor states that differ in their recent temporal history (~600ms) could engage distinct representations, but importantly they decayed over time (Howard et al. 2012). That means, the more you rest at VP (or stay at inter-trial interval period), the associated plan started to fade and the memory of the force field could not be recalled; Wainscott and colleagues reported a reduction in the interference of random perturbation learning, when a perturbed movement followed the distinct previous movement, within a time interval of 500ms (Wainscott et al. 2005). Also, even contextual pre-movement (Sarwary et al. 2015), planning (Howard et al. 2015; Sheahan et al. 2016) or motor imagery (Sheahan et al. 2018) of the second phase of follow-through movement could facilitate simultaneous learning of opposing perturbations, provided with a short dwell time at a via-point.

Our results contrast with differences in planning associated with a via-point, since in our case we still observed significant after-effects during the second phase of the movement (Fig 4 d,e,f), after residing time that exceded the time associated with a decay in the motor memory of 600ms. In light of these previous observations, the fact that the after-effects evoked within a sequence with a via-point are stable across residing time intervals, is not a trivial result. Indeed, one could have expected that the lifetime of the rapid adjustment paralleled its time scale, as proposed in previous models that consider multiple time scales of adaptation (Kording et al. 2007). In this scenario, it was reasonable to expect that a feedback related change in movement representation within ~400ms (from starting point to VP), would disappear within the next time window of similar length. It was clearly not the case. Thus it seems that feedback-related changes in representation and differences evoked by distinct planning conditions do not have the same dynamics and their respective roles in trial-by-trial adaptation remain to be elucidated.

In our case, the feedback correction before the VP could play the same role as the lead-in movement but surprisingly we did not observe that it decayed so quickly, and our data suggested that it could even carry over across trials. The presence of feedback correction even after a short pause of around 0-1500ms time duration at VP suggested that somatosensory feedback about movement error could have long-lasting effects in comparison with different conditions of planning, and these effects might constitute the basis of standard trial-by-trial learning.

Our results support the view that standard aftereffects may directly follow from feedback adjustments instead of requiring a subsequent re-planning. In ShortDwell scenario, we found that the aftereffects are the result of online feedback control, rather than feedforward control in the classical sense as this task did not involve a re-planning separated in time from the first segment, instead, the aftereffect must have been related to immediate feedback adjustments prior to the via-point. Similar aftereffects are observed in LongDwell condition, which means that feedback-related change in movement representation is preserved and utilized during the second chunk of movement. We exploited LongDwell condition as a bridge between ShortDwell and ordinary trial-by-trial adaptation, so as to highlight the role of within movement neural processing associated with feedback control.

The results in the current study are in a way congruent with others who tested different inter-trial intervals, such that the feedback error memory trace (which sustains up to 4s) continuously promotes adaptation until the next movement (Huang and Shadmehr 2007). Here we attempted to dissociate feedback-related aftereffect that is preserved, from possible build-up or consolidation, which requires longer inter-trial interval (Bock et al. 2005; Francis 2005; Huang and Shadmehr 2007). Reduced inter-trial interval evokes error sensitive (feedback) component to play a prominent role in adaptation than predictive–error-insensitive component.

Feedforward and feedback processes interaction

We clearly concentrate on feedback adaptation and highlight its potential contribution but we do not reject the possibility that changes in movement representation occur offline, similar to feedforward adaptation. In fact, previous studies have suggested that the feedback response and feedforward adaptation could work independently at least to some extent (Kasuga et al. 2015; Yousif and Diedrichsen 2012). However, our study raises the question of how much feedback and feedforward adaptation truly differ, or under which circumstances does one process prevail or influence the other. When we consider the no via-point trials with force fields, intermixed with baseline and via-point trials, the influence of the anticipation component was absent. In order to reveal the characteristics of online feedback corrections and feedback adaptation, we exploited via-point trials. Since the movements observed as after-effects account for both feedforward force patterns and feedback control gains (Bhushan and Shadmehr 1999), the after-effects observed in our task during the second phase of movement carry the imprint of changes in feedback responses, that might eventually update the feedforward process. In such case, it could be that gradual changes in feedforward representation result from repeated feedback corrections, which contrasts with previous models according to which changes in feedback control follow feedforward adaptation (Ahmadi-Pajouh et al. 2012; Maeda et al. 2018; Wagner and Smith 2008). Ultimately we do not discard feedforward control and we recognize that there can be a sequential (feedback – feedforward – feedback) update at a time scale faster than a trial but we believe it is more accurate to describe our findings in terms of an internal representation, which changes very rapidly and within a trial.

CONCLUSION

In conclusion, our data further support that the fast time scales of motor adaptation are sufficiently fast to influence an on-going movement, and the associated changes in movement representation are preserved during intervals of time comparable to different conditions of planning. Hence the imprints of online feedback adaptation could be a major component of trial-by-trial adaptation in the motor system.

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