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RESEARCH ARTICLE

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Adaptation to visual feedback delays in manual tracking: evidence against the Smith Predictor model of human visually guided action

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Abstract We report adaptation to delayed visual feedback during a manual tracking task, testing the nature of the adapted responses with frequency analysis. Two groups of seven subjects tracked unpredictable targets using a handheld joystick, alternating between pursuit and compensatory display trials. The test group then practised for 1 h per day with a visual feedback delay of 300 ms; the control group practice under normal undelayed conditions. Introduction of the visual feedback delay significantly disrupted tracking performance, with an increase in errors and a reduction in frequency of corrective movements. Subjects showed clear evidence of adaptation during the 5 day experiment, decreasing tracking error and decreasing the mean power of intermittent corrections. However, there was no evidence of a return towards the initial high frequency intermittent tracking. We suggest that the adaptation observed in this study reflects the modification of predictive feedforward actions, but that these data do not support control based on Smith Prediction.

Introduction

Sensory-motor adaptation is essential whenever one's body or the interaction between body and environment changes, and adaptation is crucial in the accurate control and execution of new motor skills. For many years, researchers have investigated the effects of introducing different types of spatial perturbation to motor tasks, in order to demonstrate the adaptability of our sensorimotor system, for example, the spatial distortions brought about by wearing optical prisms, or by angular rotation of visual feedback, or by changes in the gain of feedback. Likewise many studies have tested adaptation to task dynamics, imposing unexpected changes in resistive or assistive forces. The effects of disrupting temporal aspects of sensory feedback (e.g. delaying visual feedback) have been less extensively investigated (Foulkes and Miall 2000; Cunningham et al. 2001). Since sensory delays impose strict limits on the performance of feedback control systems, it is thought necessary to accurately estimate the delay, in order to integrate feedforward control with feedback error detection and correction.

One strategy for control in such circumstances has become known as Smith Prediction (Smith 1959). While originally designed for control of industrial equipment, it has been proposed as a model of the role of the cerebellum in visuo-motor control (Miall et al. 1993b). The controller uses an internal forward model of the dynamics of the controlled object (the arm), and places this within an internal negative feedback loop. Since this loop does not include any of the sensory delays imposed by the visual system, its open loop gain can be very high, resulting in accurate control. In order to account for the later arrival of visual feedback of the movements, the Smith Predictor also internally models the sensory delays, effectively delaying the predicted feedback signal to synchronise it with the true external feedback. Any discrepancies can be fed back into the controller without destabilising the system. In essence, an accurate Smith Predictor externalises the feedback delays from the control loop. It is therefore an important model of how physiological systems might operate, given unavoidable delays in their sensory-motor loops.

Experimentally imposing a delay of more than about 100 ms onto visual feedback in a human manual tracking task immediately causes increased performance errors (Pew et al. 1967; Miall et al. 1985, 1986; Foulkes and Miall 2000). Subjects initially react to this error by reducing the average frequency of their intermittent corrective actions, and by reducing the average speed of each correction. This allows relatively stable performance, but is clearly sub-optimal. By adaptively changing

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the internal estimate of sensory delays within a Smith Predictor to reflect the new imposed delay, performance could return close to normal. Computer simulations (Miall et al. 1993) show that the intermittent movements typically seen in visual tracking tasks, whose rate is determined by internal and external loop delays (Miall 1996; Miall et al. 1993a) are destabilised by the added delay. They become stable but low frequency if the open loop gain is reduced. However, the open loop gain and the rate of intermittent movements return to the original high values when the internal model is adjusted to reflect the new delay. Hence if humans relay on a control strategy analogous to Smith Prediction, we would expect an increase in average frequency of intermittent actions as they adapt to an imposed feedback delay.

Foulkes and Miall (2000) attempted to measure this change in the internal estimate of the time delay by recording responses to an imposed "impulse response" during manual tracking with feedback delays, using a step change in position (a velocity impulse). However, the results were inconclusive: while clear evidence of a reduction in tracking errors was found as subjects trained with the time delay, there was no clear evidence for a change in impulse response functions. A more sensitive way of investigating adaptation may therefore be to observe any after-effect of removing the delay during the tracking task. We predict that, as subjects become better adapted at tracking in the presence of the delay, occasional unpredictable return to zero delay conditions would expose any underlying changes in tracking performance.

Because the process of adaptation to the delay is expected to involve changes to feedforward control, we also aimed to test the performance of subjects under two tracking modes: pursuit and compensatory display (Poulton 1974). In a pursuit display, the subject can directly observe the target's trajectory and receives both target motion and error information. In this sort of display, the subject is able to use visual feedforward strategies to predict the target's movement (Weir et al. 1989). In a compensatory display, the subject is presented only with the error between the target and the cursor and receives no direct information about the target's trajectory. Hence, the subject is heavily reliant on visual feedback signals. By alternating between the two display modes, we aimed to test how adaptation to the feedback delay affects feedforward and feedback dominated tracking strategies.

Methods

Participants

Fifteen neurologically normal right handed subjects (five males and ten females, 18–31 years) participated in the study. All were undergraduates or postgraduates from the University of Birmingham with normal or corrected to normal vision, and were naive to the nature of the task. Participants were recruited on a voluntary basis and received research credits or cash on completion of the study. Written informed consent was obtained prior to testing in accordance with the local ethical committee regulations.

Experimental apparatus and tracking task

Participants were seated approximately 60 cm in front of a 45 cm computer monitor (with 1,280×1,024 pixel resolution). A 13×10° display box was generated displaying a black background bisected by a light blue crosshair. A white circular target, 0.2° in diameter, was initially positioned on the crosshair, and a 0.2×0.2° square green cursor was controlled by the position of a hand-held joystick. A modified game console joystick was used, 8 cm in length, of light weight and low friction (Radio Spares 162–984 with the self-centring spring removed). There were no dynamics between the joystick and the monitor cursor display. Joystick tracking movements were measured at 75 Hz via an analog-digital converter connected to the PC. Visual feedback delays between the joystick and cursor were introduced by the computer software.

Each trial lasted 20 s, and trials alternated between pursuit and compensatory tracking. During pursuit the participant saw the target circle smoothly move along an unpredictable 2-d path, and attempted to follow this with the joystick-controlled cursor. In compensatory tracking the target circle remained stationary on the central crosshairs, while the cursor was displaced from its position by the unpredictable 2-d target trajectory. Hence to return the cursor to the central target, the subject needed to compensate for the target trajectory. The pseudo-random target trajectory was generated independently in each axis by the sum of five non-harmonic sinusoids (0.06, 0.11, 0.13, 0.25 and 0.33 Hz) whose relative phases were randomised for each trial. After generation of the waveform, its excursion in each axis was tested, and a new waveform generated if the excursion was greater than 1,000 pixels horizontally or 800 pixels vertically. Finally the initial and final 3 s of the trajectory were attenuated with half cosine functions so that the trajectory smoothly accelerated away from and returned to the centre at start and end of each trial.

Training and testing

Each participant attended five 1 h sessions held across five consecutive days (Monday to Friday). One participant was unexpectedly unable to attend on Friday, and was tested on the following Monday. Individual participants were trained and tested at a similar time of day for all of their experimental sessions. Participants were randomly divided into test and control groups. All participants performed an identical number of trials and the primary experimental manipulation was whether visual feedback of cursor location relative to joystick position was delayed or not during the main training sessions (i.e., 300 ms vs. 0 ms visual feedback delay).

On the first day of testing all participants performed a block of ten 20 s practice trials to ensure task familiarity and for participants to get accustomed to the experimental setting. This was immediately followed by ten baseline trials, without feedback delay.

On day 1 the baseline trials were followed by three test blocks (each of 53 trials) where the test group performed the 300 ms delay condition while the control group continued in 0 ms delay condition. Participants were given a 5–10 min rest break between the second and third block. Rest periods of 20 s were also provided every sixth trial to avoid fatigue. A small number of catch trials were also presented at random occasions within the test conditions (four catch trials per block, two pursuit and two compensatory). For the test group (300 ms delay), the delay was suddenly removed half way through a 20 s catch trial. For the control (0 ms delay) group, catch trials consisted of the sudden introduction a visual feedback delay of a 150 ms, chosen to ensure approximate comparability across the test and control conditions and to maintain a similar level of task difficulty. During days 2, 3 and 4 all participants completed 3 training blocks (53 trials per block with 300 or 0 ms delay as appropriate, including 4 catch trials per block). On the fifth day, all participants performed the final three training blocks followed by an additional two trials where their visual feedback was delayed by 400 ms. We will refer to these trials as the 'post-adaptation trials'.

Data analysis

RMS error between the target and cursor positions was calculated over each 20 s trial; for catch trials this was measured only over the final 10 s of the trial. We then performed a frequency analysis on the tracking records. Mean frequency and power values were generated for the baseline trials and separately for unperturbed trials and catch trials for each block. For each trial, the power spectral density functions were calculated (Matlab version 7) for the horizontal and vertical components of the joystick and the target velocity records, after Hanning filtering. The positive difference between target and response was then calculated (the noise spectrum), reflecting mainly the 1–2 Hz intermittent joystick responses that are not present in the target. The horizontal and vertical noise spectra were then averaged, and a block average spectrum calculated across all corresponding trials within a block. Session averages were finally calculated across the three blocks per day (except baseline, one block only). To estimate the peak in the resulting session-averaged noise spectrum, a Gaussian smoothing kernel was applied (FWHM 0.75 Hz), and the maximum power and frequency of the smoothed spectrum measured.

Data were compared across days and conditions using mixed model, repeated measures ANOVA using a threshold for significance of $P \le 0.05$. Where necessary, the degrees of freedom were adjusted using the Greenhouse–Geisser correction for non-sphericity.

Results

General observations

The tracking responses were typical of those reported previously when subjects track with pursuit and compensatory displays, showing greater levels of errors and more intermittent movements under a compensatory display. The responses of the test groups when first exposed to the feedback delays were also typical, with greater intermittency and lower peak velocities (Fig. 1). Figure 1 also displays a typical response during a pursuit mode catch trial from the test group (where a 0 ms delay is introduced at 10 s).

Figure 2 displays the group mean error data for the two experimental conditions and for the two display phases of the task (pursuit vs. compensatory) plotted over the five training days. Visual inspection suggests that there is a general improvement across time in both conditions in the pursuit and compensatory display modes, with greater error made in the compensatory display compared to the pursuit display. There is an increase in tracking error, in both conditions, during the post adaptation trials. However, this increase appears much greater in the 0 ms control group compared to the 300 ms experimental group.

Error analysis for the unperturbed trials

To ensure comparability across the two experimental groups, independent sample *t*-tests on the mean baseline tracking errors in pursuit and compensatory tracking modes revealed no significant difference between the two subject groups [$t(12) \le 1.78$, $P > 0.05$]. However despite this, initial analyses revealed that one subject in the experimental group was found to exhibit a very high and highly variable error rate even in the baseline condition. We excluded this particular subject's data from all subsequent analyses. Thus, seven control subjects and seven test subjects are included in the analyses reported below.

We first performed a mixed three way (group × tracking mode × day) ANOVA on the mean error scores across the five training days. This showed significant main effects of group and tracking mode [$F(1,12) \ge 22.8$, $P < 0.0001$], training day [$F(4,48) = 11.41$, $P < 0.0001$], as well as significant interactions between group and mode [$F(1,12) = 35.8$, $P < 0.0001$].

Two way (group × day) ANOVAs were then performed separately on the mean error scores for the pursuit task and the compensatory task, across the training sessions. For pursuit, this revealed a significant

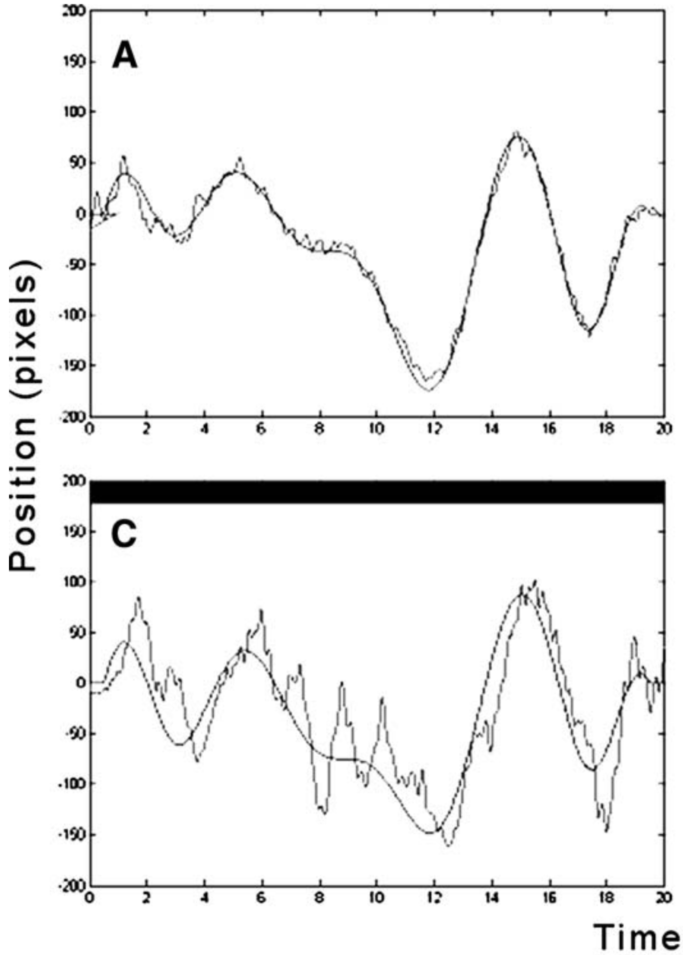

Fig. 1 Tracking records showing horizontal position of the target (*smooth line*) and cursor over 4 typical 20 s trials. **a** 0 ms delay baseline trial in pursuit mode, **b** 300 ms delay feedback trial, in pursuit mode, **c** 300 ms delay trial in compensatory tracking mode, **d** 300 ms catch trial where the delay is returned to 0 ms delay after 10 s. All examples are from the same subject, on the third testing day. The *heavy black bars* indicate the presence of the visual feedback delay

main effect for day [$F(4,48) = 8.335$, $P < 0.0001$] and for group [$F(1,12) = 14.31$, $P < 0.003$]. The interaction between day and group was also found to be significant [$F(4,48) = 2.71$, $P = 0.041$], suggesting differential learning between the two groups. For the compensatory display, significant main effects were found for day [$F(4,48) = 10.102$, $P < 0.0001$] and for group [$F(1,12) = 32.48$, $P < 0.0001$]. However, no significant interaction was found in this case [$F(1,12) = 0.49$, $P > 0.7$], and Fig. 2b shows a reduction in error across time, even in the control group.

Independent sample *t*-tests on the post adaptation trials revealed significant differences between the two groups for pursuit tracking [$t(12) = 3.83$, $P < 0.05$], but not for compensatory tracking [$t(12) = 1.55$, $P > 0.05$]. This suggests that subjects in the experimental condition perform better when a delay of 400 ms is introduced compared to subjects in the control (0 ms) condition, but only in the pursuit mode. For the test group only, average performance with the 400 ms delay was better than their performance on day 1, when first exposed to the 300 ms delay.

Error analysis of catch trials

To examine the progressive effect of learning on performance in the catch trials, we repeated the three way (group × tracking mode × day) ANOVA first used for the unperturbed trails. This again showed significant main effects of group [$F(1,12) = 5.06$, $P = 0.044$], tracking mode [$F(1,12) = 75.6$, $P < 0.0001$], day [$F(4,48) = 2.56$, $P = 0.050$], while the interaction between group and mode was outside significance [$F(1,12) = 4.33$, $P = 0.059$]. Hence the changes in performance with time were similar in the catch trials to those seen in the normal trials, although the reduced amount of catch trial data led to weaker statistical results. Separate two-way group × day analyses for the pursuit and compensatory catch trials revealed only group effects, significant for compensatory tracking [$F(1,12) = 5.50$, $P = 0.037$], but not significant for pursuit [$F(1,12) = 3.66$, $P = 0.080$].

Repeated measures *t*-tests were carried out to compare the catch trial mean error scores in the test condition (300 ms delay group) to baseline. We predicted that there should be no catch effect in the initial catch trials,

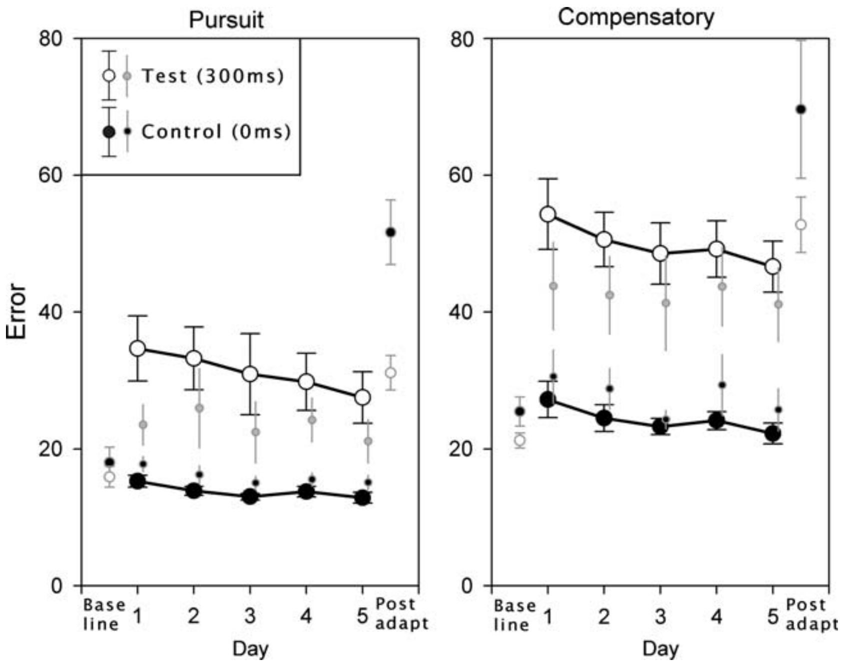

Fig. 2 Mean RMS error scores ±1 SE for the two subject groups (0 and 300 ms delay) against training days. **a** Data from the pursuit display task. Here the baseline RMS errors are shown on the left (*small symbols*), and the post-adaptation errors on the right. For days 1–5, the RMS errors for the unperturbed trials are shown (*large dots*, *solid lines*); errors during the catch trials (*small grey/black dots*) are shown shifted to the right for clarity. **b** Data from the compensatory display task, in the same format as (**a**)

and that a significant catch effect should develop as learning progresses. However the results revealed a significant difference in both display modes on day one [baseline pursuit vs. catch $t(6)\geq 3.90$, $P<0.02$]. In other words, significantly greater errors were made in the catch trials on day 1 compared to baseline trials for both display modes.

We then used regression analyses on the catch trial mean error scores, testing for significant slopes across the 5 days. Inspection of Fig. 2a suggests that the mean errors during the catch trials reduce over the five days for both conditions. However, the slopes of these regression lines were not significantly different from zero. Figure 2b shows corresponding data for compensatory mode tracking, and again, there was no significant slope in either the experimental or control condition, despite a downward trend.

Spectral analysis of the unperturbed trials

Mean values for frequency and power of the principal component of the noise spectra were generated for the baseline trials and then for each day for the unperturbed and the catch trials. To ensure the experimental groups were comparable at baseline, independent samples t-tests were performed on the mean frequency and mean power values for the baseline trials in pursuit and compensatory modes. This revealed no significant difference between the two groups for the mean peak frequency in either tracking mode [$t(12)\geq -1.53$, $P>0.05$], nor for the mean peak power in either tracking mode [$t(12)> -0.57$, $P>0.05$]. Hence the baseline performance of the two groups was equivalent.

Figure 3 shows the mean peak frequency for the two conditions plotted against time. Inspection of this figure suggests that there was a difference in mean frequency between the two experimental conditions (0 vs. 300 ms), and this difference was apparent for both display types (pursuit vs. compensatory). The figure clearly shows a strong downward change in mean frequency across time. A mixed three way (group × tracking mode × day) ANOVA showed significant main effects of group [$F(1,12)=68.3$, $P<0.0001$], and day [$F(4,48)=3.73$, $P=0.010$], while the effect of tracking mode was outside significance [$F(1,12)=4.20$ $P<0.063$]; the interaction between group and day was significant [$F(4,48)=2.86$, $P=0.033$]. Separate mixed two-way ANOVAs were then performed on the pursuit and compensatory data to determine whether there was a significant difference between the two groups across days 1 and 5. The ANOVA for pursuit data revealed a non-significant main effect of day [$F(2.24,26.9)=2.843$, $P=0.07$, Greenhouse–Giesser corrected]. A significant main effect of group was found [$F(1,12)=51.9$, $P<0.0001$]. Perhaps surprisingly, no significant interaction was found between day and group [$F(2.24,26.9)=2.143$, $P=0.09$]. For the compensatory tracking data, there was a significant main effect of group [$F(1,12)=47.2$, $P<0.0001$]; the effect of day and the interaction between day and group were not significant [$F(2.3,19.8)\leq 2.155$, $P>0.130$].

Figure 4 shows the change in mean power for the two experimental groups over time. This measure represents the magnitude of intermittent tracking across time. The test group (300 ms condition) shows a strong downward trend while the controls remain unchanged over time. To confirm this statistically we first carried out a mixed three way (group × tracking mode × day) ANOVA. This showed significant main effects of group [$F(1,12)=4.95$, $P=0.046$], tracking mode [$F(1,12)=11.76$, $P=0.005$], day [$F(4,48)=5.225$, $P=0.001$], and interaction between group and day [$F(1,12)=4.1$, $P=0.006$]. Hence the

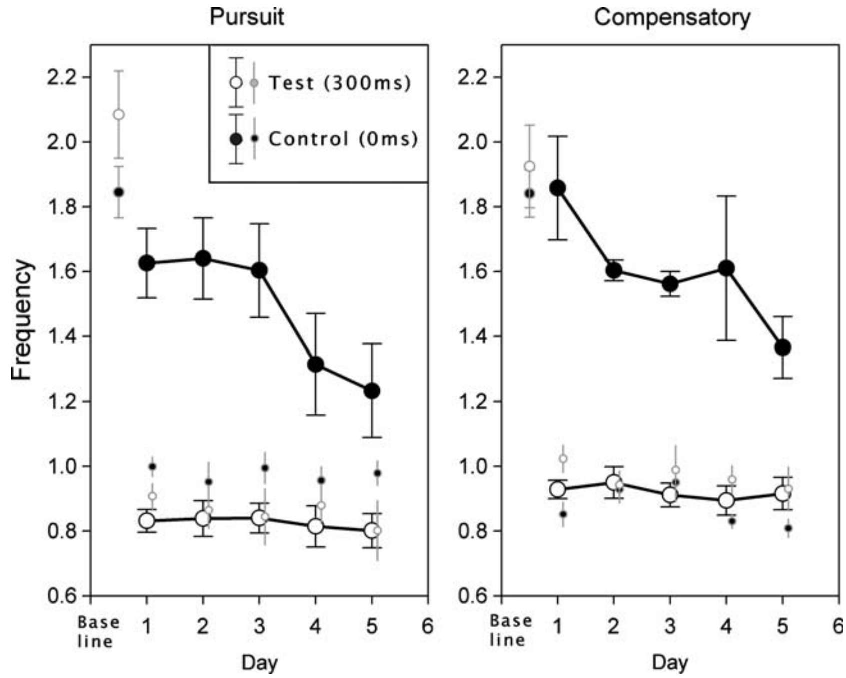

Fig. 3 Mean frequencies ±1 SE of the main response component in the noise power spectra for unperturbed (*large symbols*) and catch trial (*small symbols*) for the two subject groups against time. **A** Data from the pursuit display task. **b** Data from the compensatory display task. The format is the same as in Fig. 2

experimental group showed a strong decline in power over the 5 days, whereas the control group did not. The tracking mode did not influence this decline (all interactions between mode and group and day were far from significant).

Spectral analysis of the catch trials

Mixed three way (group × tracking mode × day) ANOVA on the peak frequency data and on the mean power data showed only significant main effects of group [$F(1,12) \geq 4.80$, $P \leq 0.049$]. All other effects and interactions were well outside significance ($P \geq 0.11$). Thus there was no evidence of any change in spectral components with training (Figs. 3, 4). To confirm this, a set of regression analyses were performed on the mean peak frequency and power scores; none of the regression lines had a slope significantly different from zero.

Discussion

Our aim was to investigate adaptation to visual feedback delays in both pursuit and compensatory tracking over

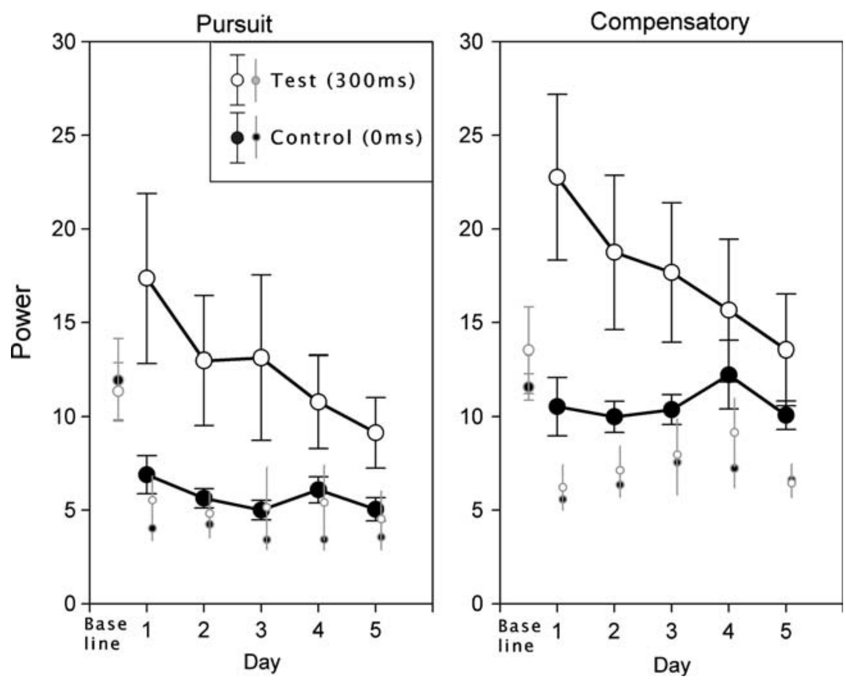

Fig. 4 Mean peak power ±1 SE of the main response component in the noise power spectra for unperturbed (*large symbols*) and catch trial (*small symbols*) for the two subject groups against time. **a** Data from the pursuit display task. **b** Data from the compensatory display task. The format is the same as in Fig. 2

the course of five days. We confirmed that subjects performed with less error during pursuit displays compared to compensatory displays. Adding a 300 ms visual feedback delay significantly impaired tracking performance. Importantly, subjects showed clear evidence of adaptation to this imposed delay, with decreases in mean error scores and in the mean spectral power over time. However, we failed to find consistent changes in the mean peak frequency over time that were predicted by the hypothesized Smith Predictor control strategy (Miall et al. 1993b). Furthermore, analyses of the data from catch trials (0 ms delay) produced an unexpected result, with evidence of decreases in error scores with increased training, and of limited or no change in spectral content of the response traces. These findings are discussed below.

Firstly, the error data from the two experimental conditions was consistent with findings from previous studies (Miall et al. 1985, 1986; Foulkes and Miall 2000). Subjects in the test group display a greater tracking error compared to subjects in the control condition, and also, when exposed to visual feedback delays for an hour a day over 5 days, they show clear improvements in tracking behaviour, suggesting that adaptation has occurred (Foulkes and Miall 2000). Our analysis revealed a significant interaction between experimental group and time in the pursuit mode only. However, this is probably because there was a trend towards reduced errors in the control group during compensatory tracking (Fig. 2b), suggesting that there was some learning in this relatively difficult task, even in the absence of imposed feedback delay.

Secondly, in agreement with Weir et al. (1989) findings, we found that subjects performed with less error on the pursuit display compared to the compensatory display. Our findings support Weir et al. (1989) assumption that subjects make use of two distinct modes of tracking. One, used during pursuit tracking, relies on visual feedforward (predictive) signals about the target's motion, which leads to smoother less intermittent tracking behaviour. In contrast, subjects tracking in a compensatory display are more reliant on negative visual feedback control, as no explicit positional information of the target is available. For this reason disruption of feedback, by introducing visual feedback delays, results in highly intermittent tracking behaviour (Weir et al. 1989). However, as our subjects adapted to the delay, all our measures of performance in both pursuit and compensatory modes changed qualitatively equally (Figs. 2, 3, 4, 5). This suggests that the major change underlying their adaptation was on the forward path of the control, rather than on the feedback path. We return to this point later on.

Analyses of the post adaptation trials (400 ms delay) provided further evidence for adaptation. This result is consistent with the finding of Foulkes and Miall (2000) who found that the introduction of a large visual feedback delay (400 ms) resulted in different levels of post-adaptation error in groups trained with different levels of visual feedback delay (0, 200 and 300 ms). Our results demonstrated that there was a significant increase in post-adaptation error in both conditions (0 and 300 ms condition), however, the effect of the 400 ms perturbation was far greater in the control (0 ms) condition compared to the 300 ms condition, especially in pursuit mode. This suggests that subjects in the test condition who have received previous exposure to visual feedback delays find it easier to extend their existing control under the 300 ms delay to the novel 400 ms delay, whereas controls find very difficult to move from 0 to a 400 ms delay.

The results from the analysis of the mean peak power in the tracking data agree with the error data and provide further evidence that adaptation occurred in the test condition. This is evident by the significant interaction observed between day and group indicating a significant downward trend in the mean power over time in the test condition, with no significant change in the control condition. Hence, the magnitude of intermittent tracking decreased during exposure to the visual feedback delays, suggesting that adaptation was occurring, leading to the improved performance shown in Fig. 2.

We predicted that as subjects adapt to a visual feedback delay, there would be an initial reduction in the mean frequency of the spectral peak, followed by an adaptive increase (Foulkes and Miall 2000). While the initial reduction was very obvious, we failed to observe any subsequent change in mean frequency over time for the test group. This finding is consistent with a result reported by Foulkes and Miall (2000) who also failed to observe a adaptive shift in spectral frequency following training on a pursuit tracking task.

The results from the regression analyses of catch trial data (either in terms of RMS error, peak frequency or peak power) provide no evidence that the performance of subjects in the test condition changed over time for either pursuit or compensatory displays. These results contradict our hypotheses, as we predicted that subjects in the test condition would initially show no negative after effect, but that this effect would develop as learning progresses. This prediction was also not supported by the significant difference found between the error data for the baseline trials and the catch trials on day one, despite both having zero feedback delay. Negative after effect should only occur after adaptation has taken place (Cunningham et al. 2001; Foulkes and Miall 2000). Our data, in addition to that of Foulkes and Miall (2000) using a similar task, suggest that adaptation requires hours of practice over several days. So why in the present study do we observe a negative after effect on day 1? We suspect that this is the consequence of the strategy adopted during the very early exposure to the delay. Subjects typically immediately slow their responses (and this is clearly seen in the dramatic drop in the mean frequencies in Fig. 3, dropping from the baseline level of around 1.8–2.0 to 0.8 Hz. In the catch trials they continue to respond sluggishly, and so the catch trial frequencies remain at about 0.8 Hz, while the catch trial peak power levels are very low (Fig. 4). Hence the RMS tracking errors are higher than baseline (Fig. 2).

The second interesting change seen across the training sessions is the reduction in mean peak frequencies seen in the control group (Fig. 3). Here there is a dramatic reduction in frequency, dropping by about 50% from the baseline level over the 5 days if training. This is achieved despite very limited change in mean power (Fig. 4), and only modest reduction in tracking error (Fig. 2). Hence we suspect this reflects an important tuning of the visuomotor control loop to the task demands. The average frequency of tracking responses can be influenced by target speed (Miall 1996), and the changes seen in our study may reflect adaptive tuning of these responses to reflect increased knowledge of the average speed and frequency content of the target trajectories. In other words, a key change in performance with extended experience in this task was the reduction in rate of corrective, intermittent changes in position, such that each corrective action intercepted the target more accurately. Figure 1a shows small, frequent overshoot of the target even in the absence of added delay, typical of performance on day 1. For the test group, however, there is also a marked reduction in power across the 5 days (Fig. 4). So while they are unable to increase the rate of movement, as hypothesized, they do adjust their intermittent corrective movements to reduce their initial large overshoot of the target (Fig. 1b, c). This implies that the most important change in performance is more appropriate feedforward control of each intermittent corrective action in order to intercept the target (Miall et al. 1988), despite the delay in cursor motion.

Finally, and most importantly, we can see no evidence in the spectral content of the tracking responses for the increase in average tracking frequency that is suggested from the Smith Predictor model (Miall et al. 1993b). In this model, adaptation of the internal representation of the feedback loop delay should allow increased feedback gain, reduction in tracking error, and increased corrective response frequencies. Hence we predicted an increase in the frequency curves shown in Fig. 3 for the unperturbed training conditions, across the 5 days, and a corresponding decrease in the mean frequencies and mean performance in the catch trials. Neither has been seen. We suggest this argues against the Smith Predictor as a model of human visually guided tracking. Other evidence against this model has been presented for discrete reaching movements (Bhushan and Shadmehr 1999) and for control of coordinated lifting actions (Flanagan et al. 2003). The Smith Predictor strategy is incompatible with these other data sets because it uses a single adaptive forward model both for forward modelling—for predicting the consequences of actions—and for control. While our present data fail to provide evidence for Smith Prediction in the adaptation of movements, they do show clear evidence of adaptation or tuning of performance. Thus one needs to consider a separation of prediction from the control. This is consistent with Bhushan and Shadmehr's model (1999), in which they argue for inverse model control supplemented by forward model-assisted feedback. It is also compatible with the MOSAIC model (Haruno et al. 2001), in which forward models are used to select appropriate inverse models for control, but the MOSAIC model has not been simulated in conditions with feedback.

In conclusion, our results indicate that humans are able to adapt to changes in the timing of visual feedback over the course of several hours. For the test group, faced with a 300 ms feedback delay, this process involved reduction in the mean power of their tracking responses, hence achieving smoother tracking performance with lower RMS errors, but without the predicted increase in response frequencies that would imply a tracking strategy based on the concept of Smith Prediction of the feedback delay. For the control group, with no additional delay, the change is seen as a reduction in frequency without change in power, tuning their responses to the task demands.

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References

Bhushan N, Shadmehr R (1999) Computational nature of human adaptive control during learning of reaching movements in force fields. Biol Cybern 81:39–60

Cunningham DW, Chatziastros A, Heyde M, Bulthoff HH (2001) Driving in the future: temporal visuomotor adaptation and generalization. J Vis 1:88–98

Flanagan JR, Vetter P, Johansson RS, Wolpert DM (2003) Prediction precedes control in motor learning. Curr Biol 13:146–150

Foulkes AJ, Miall RC (2000) Adaptation to visual feedback delays in a human manual tracking task. Exp Brain Res 131:101–110

Haruno M, Wolpert DM, Kawato M (2001) Mosaic model for sensorimotor learning and control. Neural Comp 13:2201–2220

Miall RC (1996) Task-dependent changes in visual feedback control: a frequency analysis of human manual tracking. J Motor Behav 28:125–135

Miall RC, Weir DJ, Stein JF (1985) Visuomotor tracking with delayed visual feedback. Neuroscience 16:511–520

Miall RC, Weir DJ, Stein JF (1986) Manual tracking of visual targets by trained monkeys. Behav Brain Res 20:185–201

Miall RC, Weir DJ, Stein JF (1988) Planning of movement parameters in a visual tracking task. Behav Brain Res 27:1–8

Miall RC, Weir DJ, Stein JF (1993a) Intermittency in human manual tracking tasks. J Motor Behav 25:53–63

Miall RC, Weir DJ, Wolpert DM, Stein JF (1993b) Is the cerebellum a Smith predictor? J Motor Behav 25:203–216

Pew RW, Duffendack JC, Fensch LK (1967) Temporal limitations in human motor control. Psychonomic Society, Human Performanance Centre, University of Michigan

Poulton EC (1974) Tracking skill and manual control. Academic, London

Smith OJM (1959) A controller to overcome dead time. ISA J 6:28–33

Weir DJ, Stein JF, Miall RC (1989) Cues and control strategies in visually guided tracking. J Motor Behav 21(3):185–204