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RESEARCH ARTICLE

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The role of proprioception and attention in a visuomotor adaptation task

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Abstract The role of proprioception in the control and adaptation of visuomotor relationships is still unclear. We have studied a deafferented subject, IW, and control subjects in a task in which they used single joint elbow extension to move to a visual target, with visual feedback of the terminal position provided by a cursor displayed in the plane of their movements. We report the differences in movement accuracy between the deafferented subject and controls in the normal task and when challenged with a cognitive load, counting backwards. All subjects were less accurate when counting; this was a small effect for the controls (<10% change) but much greater for the deafferented subject (>60% change). We also examined changes in movement kinematics when the instructed amplitude was altered via a changed gain between final arm position and presentation of the feedback cursor. The deafferented subject maintained temporal movement parameters stable and altered amplitude by scaling force (i.e. changed peak velocity), whereas the controls scaled both movement velocity and duration. Finally, we compared the subjects' adaptation of movement amplitude after a period of exposure to the changed visuomotor gain. The deafferented subject was able to adapt, but his adaptation was severely impaired by the counting task. These results suggest that proprioception is not an absolute requirement for adaptation to occur. Instead, proprioception has a more subtle role to play in the adjustment to visuomotor perturbations. It has an important role in the control of reaching movements, while in the absence of proprioception, attention appears necessary to monitor movements.

Key words Proprioception · Adaptation · Visuomotor control · Attention · Human

Introduction

Reaching to visual targets requires a complex transformation from the visual representation of the target to the required motor output, as well as integration of the resultant proprioceptive and visual information concerning the outcome of the movement. That these transformations are flexible has been demonstrated by the ability to reach accurately under various perturbations of the visual input caused by wearing spectacles or the wedge prisms used in many psychophysical studies, or by adaptation of the trajectory to other disturbances (e.g. Shadmehr and Mussa-Ivaldi 1994; Wolpert et al. 1994).

Adaptation studies have been used extensively in an effort to understand the factors affecting visuomotor transformations and as an aid to uncover the form and the location of the processes that lead to the adapted state. In principle, it seems likely that an internal signal representing the movement (either proprioceptive inputs or efference copy) could be compared to the perturbed visual feedback of the hand. Welch (1978) suggested that adaptation depends on the integration of a visual-to-proprioceptive mismatch across the learning period. Hence, there would seem to be a role for proprioception in adaptation. However, the details of this role are still unclear. For example, Taub and Goldberg (1974) studied prism

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adaptation in deafferented monkeys and found that not only did they adapt, but they adapted significantly more than control animals. This was attributed to a lesser discordance between the visual input and “proprioception”, where the latter was interpreted as being made up of both afferent and efferent information. In experiments with normal human subjects, Wallace and co-workers (Wallace and Garrett 1973, 1975; Wallace and Fisher 1979) reported that they could completely preclude prism adaptation by hypnotically anaesthetising the subject’s arm and so, hypothetically, removing proprioceptive feedback. However, these findings could not be replicated (Spanos et al. 1981; Spanos and Saad 1984). Bard et al. (1995) completed a short study of two human deafferented subjects and found that one subject (IW in the present study) adapted to the prisms while the other (GL) did not adapt at all. The difference was attributed to the level of proprioceptive loss: GL has no proprioception from the neck, whereas it is spared in IW.

One of the difficulties in interpreting these conflicting prism adaptation experiments is the multiple levels at which changes may occur. Different authors have reported changes in: felt direction of gaze (e.g. Craske 1967; Craske and Templeton 1968), egocentric specification of retinal loci (e.g. Cohen 1966; Crawshaw and Craske 1974; Howard 1970), head position (Kornheiser 1976; Lackner 1973, 1981), felt position of the arm (Hamilton 1964; Harris 1963, 1965) and the central control of sensorimotor coodination (Efstathiou et al. 1967; Hardt et al. 1971).

In the present study we aimed first to clarify the function of proprioception in motor adaptation. We tested a deafferented subject (IW) and control subjects in a single-joint movement task involving adaptation to a change in the display gain, similar to the classic oculomotor saccade adaptation paradigm (McLaughlin 1967) and used in other visuomotor studies (Bock 1992; Ojakangas and Ebner 1991, 1992, 1994; Kerr et al. 1993; Pine et al. 1996). In this task, the subject was required to compensate for an imposed increase in gain between movement amplitude and the visual feedback displayed in order to move accurately to targets. The advantage of this task is that it avoids the confounding factors of a prismatically induced visual shift. First, as the visual targets and visual field remain constant, adaptation could not result from “eye muscle potentiation” (Ebenholtz 1974), or any of the other visual changes detailed above. Second, as there is no recalibration of the visual system with respect to the neck or trunk position, it is unlikely that IW’s residual neck proprioception would play a significant role in his ability to adapt. Bard et al. (1995) had suggested that his neck proprioception was necessary in their task, to link the recalibration of the eye-head reference system to the head-hand reference system.

It is known that deafferented subjects require a great deal of concentration and cognitive effort to produce and monitor their movements even without an adaptive task (Cole and Sedgwick 1992). Hence, any failure to adapt might simply reflect the excessive cognitive demands placed on the deafferented subject. We have therefore also examined the contribution of attention to the adaptive process, by increasing the cognitive or attentional demands on subjects during the exposure period.

Furthermore, visuomotor adaptation requires a change in the ratio of visual input to motor output. As noted above, the visual input was constant in our task and thus successful adaptation required a change in movement kinematics. We therefore aimed to identify whether, devoid of proprioception, IW uses different kinematic strategies to control his movements.

A final important question is how the magnitude of the visuomotor discordance affects adaptation. In prism studies the optical displacement is usually introduced immediately, producing a large discordance (error) in the initial movements. If the prismatic displacement is introduced incrementally, small or even negligible errors are produced, but adaptation has still been observed (Howard 1968). Whether the gradual introduction facilitates or decreases the level of adaptation is unclear (Dewar 1971; Lackner and Lobovits 1978). Bock (1992) reported adaptation when a gain change was introduced gradually although he did not compare gradual and immediate schedules. Most recently, Kagerer et al. (1997) found greater adaptation to a rotation transformation when the change was introduced gradually; however, there may be fundamental differences between a rotation transformation and a gain change (e.g. rotation may make more demands on short-term working memory; Pine et al. 1996). Thus the final aim of our study was to clarify the effect of a gradual versus immediate gain change on the level of adaptation achieved. Moreover, since the two exposure conditions lead to visual errors of different magnitudes, we also compared the effect in control subjects with that found in the deafferented subject. This enabled us to further refine the role of proprioception in the perception and integration of the movement errors produced.

Our data suggest that proprioceptive feedback was not an absolute requirement for adaptation to occur in these tasks, in agreement with Bard et al.’s (1995) conclusion. Rather the pattern of our results indicates that proprioception has a more subtle role to play in the adjustment to a visuomotor perturbation. It has an important role in the control of reaching movements, while in the absence of proprioception, attention appears necessary to monitor movements.

Materials and methods

Subjects

Six control subjects (five males, one female, aged between 22 and 40 years) and one deafferented subject (IW, 43 years old) participated in this experiment with local ethics committee approval. All subjects gave their informed consent prior to their participation in the study. IW suffered an acute, large-fibre, sensory neuropathy when he was 19 years old, resulting in a complete loss of proprioception below the neck. For a more complete description of IW’s neuropathy, see Cole and Sedgewick (1992) and Cole (1995).

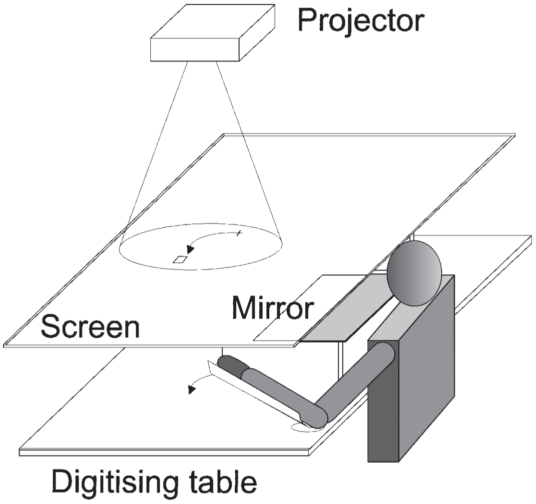


Fig. 1 Schematic diagram of experimental setup. Prior to the start of a session the subject was allowed a direct view of his own hand through a semi-silvered mirror. During the session the direct view of the hand was blocked, and the subject viewed a reflected image of the target and a cursor in the mirror

Experimental setup

A schematic representation of the experimental setup is presented in Fig. 1. The subject was seated in front of a large digitising table (GTCO RUD table, 80×100 cm, placed horizontally at a height of 90 cm from the floor). A detector pen was positioned at the subject's fingertips and sampled by the digitising table (at 133 Hz, 0.1 mm resolution). The pen was attached to the end of a freely rotating arm rest. The subject's left forearm (IW's preferred arm) was restrained in the arm support with Velcro straps, with the elbow located over a bearing joint. The resulting movements were therefore single-joint elbow extensions; the arm support had very low mass and negligible friction or inertia. Restricting the movements to the elbow allowed us to minimise the possibility that the deafferented subject received extraneous motion cues from upper arm or shoulder movement. The subject's head was stabilised by a chin rest.

A start position for the arm was provided by a padded wooden block located near the edge of the table to which the subject would move before each movement. At the start position the forearm was parallel to the frontal plane and slightly below the shoulder. The elbow was located 28 cm to the left of the midline (chin rest) and 19 cm in front of the chin rest. To display visual targets, the image from a liquid crystal display (LCD) projector was projected through a backprojection screen and viewed in a semi-silvered mirror (Fig. 1). The position of the mirror was adjusted so that the virtual image of the target appeared to be in the plane of the subject's fingers.

At the beginning of each session the subject would place his arm in the manipulandum and position it against the starting block before direct vision of the arm was precluded by a horizontal screen placed just below the semisilvered mirror. IW would use this time to visually position and thoroughly check his arm posture; he would then have a visual and cognitive map of where his arm was positioned at the start of the first movement. He was able to return to the starting block after each trial without vision, by gentle flexion of his elbow.

Experimental sessions

On each trial, subjects heard a tone which indicated that they were at the start position, and after a random time (1–2 s), a square target (1×1 cm) was illuminated at a position equivalent for each individual to an elbow extension of 30° or 40° from the start position. As the elbow position was fixed for all subjects, the position of the pen at the start position was used to determine the length of the subject's forearm and hence the radius of the arc on which to present both the targets and the visual feedback. This length was also used to transform the Cartesian coordinates of the pen position into angular values with respect to the elbow and the start position (i.e. start position was 0°). The subject was asked to make one comfortable movement to the target. When hand velocity was below a threshold (1 cm/s ~0.6°/s) for 150 ms, a second tone signalled the end of the movement. During the practice and exposure phases a static white cursor (a cross, length and width 1 cm) would then be displayed indicating the pen position (i.e. terminal visual feedback). The feedback cursor was erased as the subject returned to the starting block. During these sessions subjects were instructed to "try and get the cursor to land on the target". In contrast, during the pre- and postexposure trials the feedback cursor did not appear (i.e. the movements were performed visually open-loop), and the subjects were instructed to "move naturally to the visual target" and not to use any cognitive strategies to adjust their movements. Measuring the movements without any visual feedback is equivalent to measuring the negative aftereffect (Welch 1978) as the distortion (in this case the visual feedback) has been removed and subjects are not given any indication of their accuracy. The instruction not to use any cognitive strategies during the test phase was similar to that used by Bedford (1993). The end position of the movement and, for most subjects, the trajectory of the hand were recorded on computer.

During each session the subject first completed 20 practice trials with a veridical relationship between final hand position and visual feedback (unity display gain). Two different target amplitudes (30° and 40°) were used in a random order in the ratio of 3:7 to reduce habituation of specific motor responses. Subjects then completed ten pre-exposure test movements (without visual feedback) to the target at 40°. The exposure period movements were again to the two targets and were performed closed-loop (with terminal visual feedback). During this period the relationship between the terminal visual feedback and the actual terminal position of the hand was changed to a gain change of 1.5. This meant that the visual feedback cursor displayed at the end of a movement was presented at an angular position 50% further than the pen. Thus to compensate, the subject would have to produce smaller movements. Immediately after 80 exposure trials, 10 postexposure test movements (without feedback) were completed to the target at 40°. Trials were self-paced but on average took 3–4 s to complete including returning to the starting position.

Exposure conditions

Three different gain conditions were applied during the exposure trials:

- Immediate: a gain change to 1.5 was introduced on the first trial of the exposure period. Thus a 40° movement resulted in the feedback cursor appearing at 60° and successful adaptation required moving 26.67°.
- Gradual gain change: the gain was increased incrementally throughout the exposure period such that the final gain factor (1.5) was only reached on the last trial (Fig. 2).
- No gain change: this controlled for any fatigue effects but also allowed us to assess performance without the presence of any adaptive changes.

In order to assess the influence of attention on the adaptation process, subjects also completed the immediate, gradual and no change conditions while counting backwards in 7's, 13's or 17's. Subjects were not directly monitored for accuracy and regularity of their counting, although they were observed throughout the exposure period, to check that they did not pause at any time. Subjects were instructed to count continuously throughout a block of trials, including the intertrial periods. The pre- and post-exposure test movements were performed without counting.

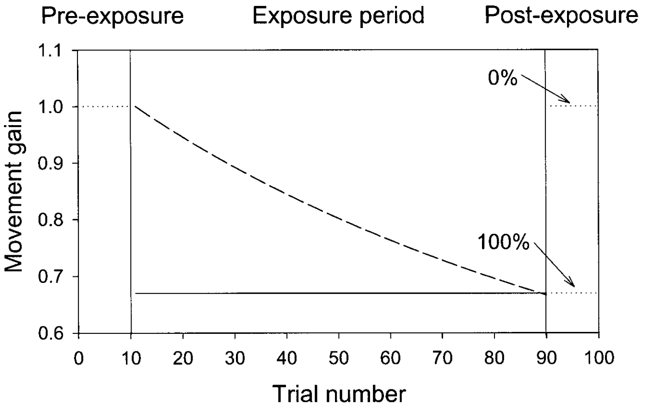


Fig. 2 Representation of experimental sessions. The movement gain (*abscissa*) represents the ratio between the desired response amplitude and the target amplitude. The left and right sections of each panel show the ten open-loop pre- and post-exposure movements respectively. The pre-exposure gain is expected to be around 1.0 while post-exposure gain could lie between 1.0 and 0.67, representing 0% and 100% adaptation as shown by *the upper and lower dotted lines*. The central sections (movements 11–90) indicate the exposure period. The required change in movement gain in each condition is given by *the solid* (immediate change) *and dashed* (gradual change) *lines*

The combination of three gain changes, with and without a cognitive load, resulted in the control subjects participating in six sessions over 4–7 days. These conditions were presented randomly both within and between subjects to cancel the effect of any sequential change in adaptation over successive sessions. The practice trials held at the beginning of every session also served to eliminate any residual adaptation between the sets: Kitazawa et al. (1997) and others have found complete deadaptation to prisms after only four or five movements with terminal feedback.

IW completed nine sessions in total over two separate days of testing: he was tested twice in the immediate change condition, 3 times in the gradual change and once in all other conditions. IW was given many breaks between sessions, either resting, performing an unrelated wrist movement task or a weight estimation task, or taking refreshments. The minimum interval between sessions was 30 min.

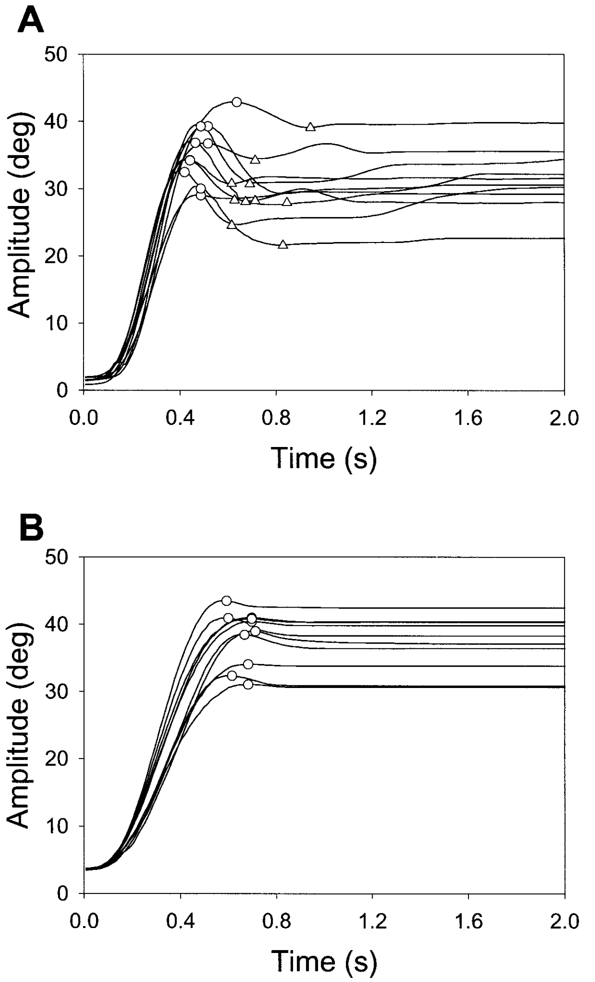


Fig. 3 Typical examples of IW's **(A)** and controls' **(B)** movement trajectories during closed-loop exposure trials. The records show ten consecutive trials in the no gain change condition. *The open circles* mark the first zero velocity points, taken to be the end of the movement for most of the analysis reported here. *The triangles* mark the second zero velocity points (**A** only), which when taken to indicate the end of the movement gave very similar results to those reported in the text

Movement analysis

IW had difficulty in holding steady the final static position of each movement because only a static visual feedback cursor was displayed. Thus, the positional records of his movement drift or oscillate somewhat at the end of each movement. Hence, movement amplitudes were measured to either the first point of zero velocity (the first peak in the movement amplitude profile, Fig. 3, open circles) or to the second point of zero velocity (the first trough in movement amplitude, Fig. 3, triangles). The amplitudes obtained from the first peak in the trajectory were significantly correlated with those obtained from the first trough (r=0.763, n=177, P<0.001). Hence for brevity we will only present those results obtained using the first peak in the trajectory.

Accuracy and variability analysis

Only the final 40 movements of the exposure condition (with terminal feedback) were assessed to ensure that movements were stable. Movement error was calculated as the difference between the target amplitude (T) and the movement amplitude (A) modified by the imposed gain (G). Thus, Error = $A \times G - T$. Zero error would indicate that subjects had compensated for the imposed gain and the cursor would have landed on the target.

The absolute error in the no gain change condition (gain=1.0) was used to assess the accuracy of normal movements, while the absolute errors in other conditions were used to assess any effect of condition on accuracy, and also to compare the accuracy of movements between IW and control subjects. The accuracy of IW's movements in the no gain change condition with and without counting were compared using an independent samples t-test. For control subjects, a Mixed Effects Analysis of Variance (a Mixed Effects ANOVA is equivalent to a Repeated Measures ANOVA but with more than one observation per factor combination) was performed with cognitive load (present, absent) as a fixed factor and subject as a random factor.

Movement variability was assessed by determining the standard deviation of the errors, again for the last 40 movements of each exposure period. The standard deviation was calculated for each subject and condition and averaged across the control group.

Kinematics analysis

To assess changes in movement kinematics with the instructed change in amplitude, velocity profiles for each movement made during the gradual gain-change, no counting, exposure period were plotted. The gradual gain-change condition was chosen because it gave a range of movement amplitudes. From these, we calculated the time to the peak velocity, the magnitude of the peak velocity, the deceleration time (time from peak velocity to first zero crossing of velocity profile) and the overall movement time. This was done for five of the six control subjects and for IW in his three repetitions of the gradual change condition. Each measure was then plotted against the movement amplitude. Linear regression lines were fitted to the data from the control subjects and IW separately. The slopes calculated from the regressions were compared using Student's *t*-test (p. 294, Armitage and Berry 1994).

Adaptation analysis

Adaptation was assessed by calculating the change in the amplitude of the ten post-exposure test movements from the average of the ten pre-exposure period test movements (all movements being made to the target at 40°). Adaptation was then expressed as a percentage of the maximum expected change. The adaptation results were analysed using a 2×3 Mixed Effects ANOVA in the SPSS statistics package. The Fixed factors were cognitive load and imposed gain change (immediate, gradual and no change). The different subjects were taken to be a random factor as they are assumed to be representative of the population.

IW's results were analysed using a 2×3 Mixed Effects ANOVA with the same fixed factors as for controls, but with the postexposure movement number within each condition (1–10) considered as a random factor. Trial-to-trial movements were considered as being taken from a larger population of similar movements.

The effect of a cognitive load on adaptation was further assessed in controls by performing a 2×3 Mixed Effects ANOVA on the absolute errors with fixed factors cognitive load (present, absent) and gain change (no change, immediate, gradual), and subject as a random factor. For IW a 2×3 Fixed Effects ANOVA was performed with factors cognitive load and gain change.

Results

Figures 3 and 4 show movement profiles for the deafferented subject and for a control subject. These data were recorded during the exposure phase of a session without a gain change, and represent typical movement profiles under these circumstances, where the subject makes a smooth movement to the target position, and then receives terminal visual feedback. The profile of movements in the test conditions (without terminal feedback) is essentially identical.

Accuracy analysis

Figure 5 illustrates the results obtained from the accuracy analyses of these exposure period movements for the control subjects (Fig. 5A) and for IW (Fig. 5B). These data are the means and SD of terminal errors calculated from the final 40 movements of the exposure period, with and without the counting condition. A 2×3 ANOVA with main factors of cognitive load and gain condition on the data from the control subjects showed a small but significant effect of an added cognitive load ($F_{(1,5)}$=9.650, P=0.027), but no effect of the gain change ($F_{(2,10)}$=1.696, P=0.232), nor a significant interaction term. Comparison of the errors in the two no gain change conditions – with and without the cognitive load – was not significant ($F_{(1,5)}$=1.292, P=0.307).

In contrast, IW revealed a significant main effect of the cognitive load on his movement errors (Fixed effects ANOVA, $F_{(1,354)}$=24.442, P<0.001), a significant main effect of the gain change condition ($F_{(2,354)}$=77.342, P<0.001), and also a significant interaction ($F_{(2,354)}$=4.344, P=0.014). An independent sample *t*-test on the two sets of data from IW in the non-adaptive condition revealed a significant difference between the counting and no counting conditions ($t_{(64.7)}$=2.881, P=0.005; normality was implied from the Kolmogorov-Smirnov statistic for each condition but variances were unequal, so the degrees of freedom have been adjusted).

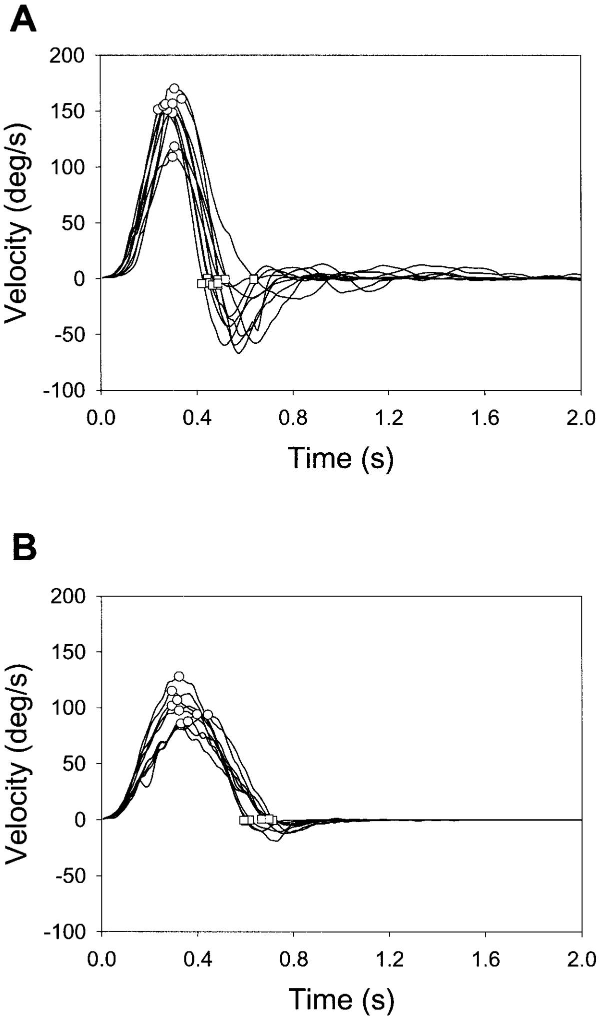


Fig. 4A,B Velocity profiles for the movements presented in Fig. 3. These were recorded during the closed-loop exposure trials for the deafferented subject **(A)** and a control subject **(B)**. *The open circles* represent the point of peak velocity and *the squares* indicate the end of the primary movement (used to determine the total movement time)

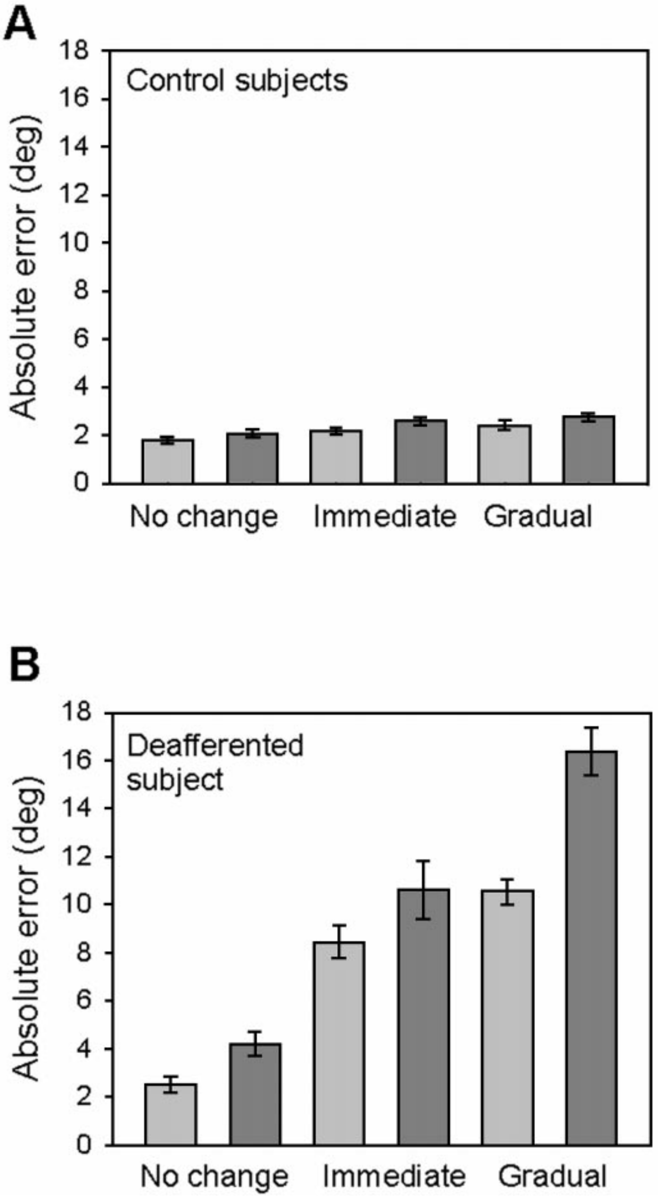


Fig. 5 Comparison of movement accuracy of control subjects **(A)** and IW **(B)** across the six experimental conditions. Data are the mean absolute error (±1 SE) of the final 40 movements of the 80 movement exposure period of each condition. *The light bars* indicate the no counting condition, and *the darker bars* indicate the counting condition

Thus in IW there was a strong and significant increase in movement error when counting, with a much weaker effect in control subjects. This indicates that in the absence of proprioception (i.e. for IW), greater mental resources are required to maintain accuracy even in ordinary movements without an adaptive demand. Furthermore, the additional requirement to alter his movement amplitude also reduced his accuracy, while it had no significant effect on the control subjects. Combining counting and adaptation was therefore most difficult for IW, and significantly higher errors were recorded.

Kinematics

Investigating the kinematics of movements made during the exposure period of the gradual gain change condition revealed marked differences between IW's movement characteristics and that of control subjects.

For the control subjects there were significant linear correlations between all measured kinematic variables and the corresponding movement amplitudes (Fig. 6). This has been shown previously for movement of the wrist (Hoffman and Strick 1986) and elbow (Gottlieb et al. 1989). In contrast only IW's peak velocity against movement amplitude showed a significant regression (Fig. 6A). The timing variables of his movements (time to peak velocity, deceleration time and total movement time) did not show a significant correlation with movement amplitude.

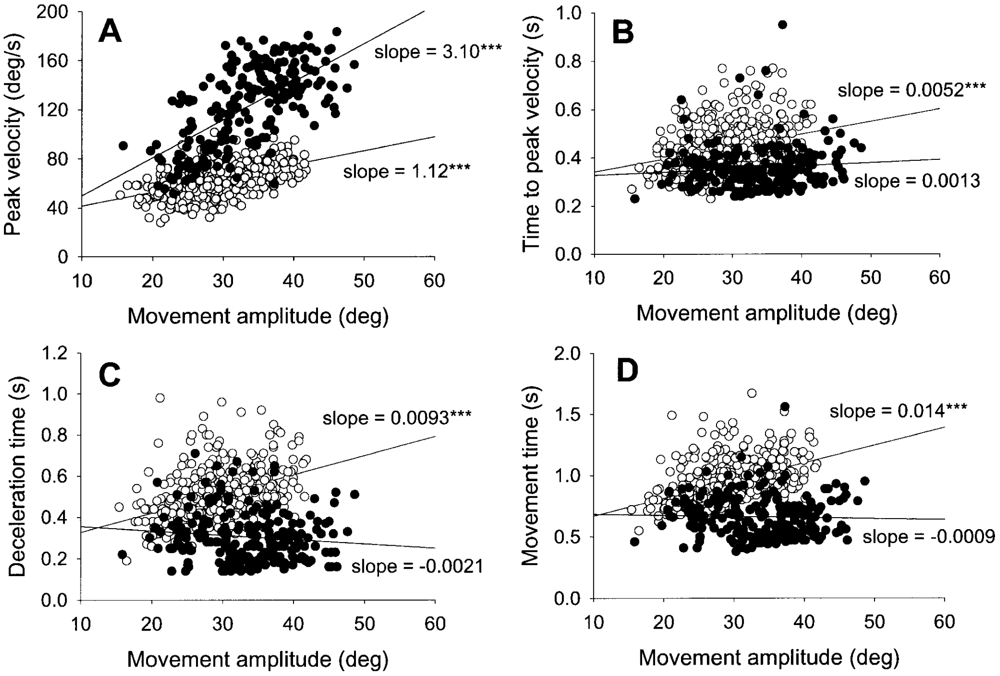
IW's peak velocity was higher than control subjects over almost all movement amplitudes and with a much greater slope (comparison of slopes: $t_{(607)}=8.48$, $P<0.001$; Fig. 6A). For example, for a movement amplitude of 40°, IW had a peak velocity approximately twice that of control subjects. Figure 6B shows that control subjects scaled the time to peak velocity with the movement amplitude (slope significantly greater than zero), while IW did not. IW kept his time to peak velocity nearly constant despite moving different distances. Thus there was a significant difference between the two slopes ($t_{(607)}=3.01$, $P=0.003$). Note that the *t*-test used to compare the regression slopes takes into account the errors associated with each estimate; hence it is valid despite there being an insignificant regression for IW's data, i.e. a slope not significantly different from zero. IW was also more constant in his deceleration time than the control subjects ($t_{(607)}=7.15$, $P<0.001$; Fig. 6C) and similarly for the total movement time ($t_{(607)}=7.03$, $P<0.001$; Fig. 6D). Taken together, these data imply that IW modulated his movement amplitude mainly by varying the initial acceleration and peak velocity of the arm and kept the timing of his movements relatively constant. In contrast, the control subjects appeared to modify the amplitude of their movements by scaling all the measured variables.

Adaptation analysis

The course of a typical experimental session with gain adaptation is shown in Fig. 7 for a typical control subject (A) and the deafferented subject (B). We have presented the data as normalised movement gains that represent the ratio of the response amplitudes to the target amplitudes. This was to enable data from movements to the two targets – 30° and 40° – used during the exposure period to be presented on the one graph.

During the immediate change condition the control subject adjusted to the change in gain very quickly (white squares, Fig. 7A); whereas during the gradual change the subject continually adjusted his movements as the gain was incrementally changed (black circles). In

Fig. 6A–D Change in movement kinematics with amplitude. *Each panel* plots data from the gradual change conditions for the deafferented subject IW (n=212; *filled circles*) and from five control subjects (n=399; *open circles*). Separate linear regression lines are drawn for the control group and for IW. The regression slope and its statistical significance (*** P<0.001) are indicated. **A** Magnitude of peak velocity against movement amplitude. **B** Time to peak velocity against movement amplitude. **C** Deceleration time against movement amplitude. **D** Total movement time against movement amplitude



both conditions the final movements made during the exposure period were close to the required value of 0.67.

The effect of the exposure period can be seen in the difference between the gain of the pre- and post-exposure test movements, especially in the gradual gain change condition (black circles, left and right sections of Fig. 7A). In this instance there appears to be a slight deadaptation over the ten post-exposure trials; however, all ten individual post-exposure movements were considered in the analysis, so any decay would be taken into consideration in the statistics.

The deafferented subject was able to perform the task in all the conditions tested. Figure 7B shows that he was able to adjust to the imposed change but not as well as controls and with much greater variability. The variability of his movements was higher than that of control subjects across all conditions, and at least in the two sessions illustrated in Fig. 7B there was little overall difference in his responses during the exposure period between the immediate and the gradual gain change conditions (see also Fig. 5B).

The levels of adaptation seen in control subjects across the six different conditions are shown in Fig. 8A. As expected there was no adaptation in the two no gain change conditions, either with or without a cognitive load. Control subjects showed adaptation in all other

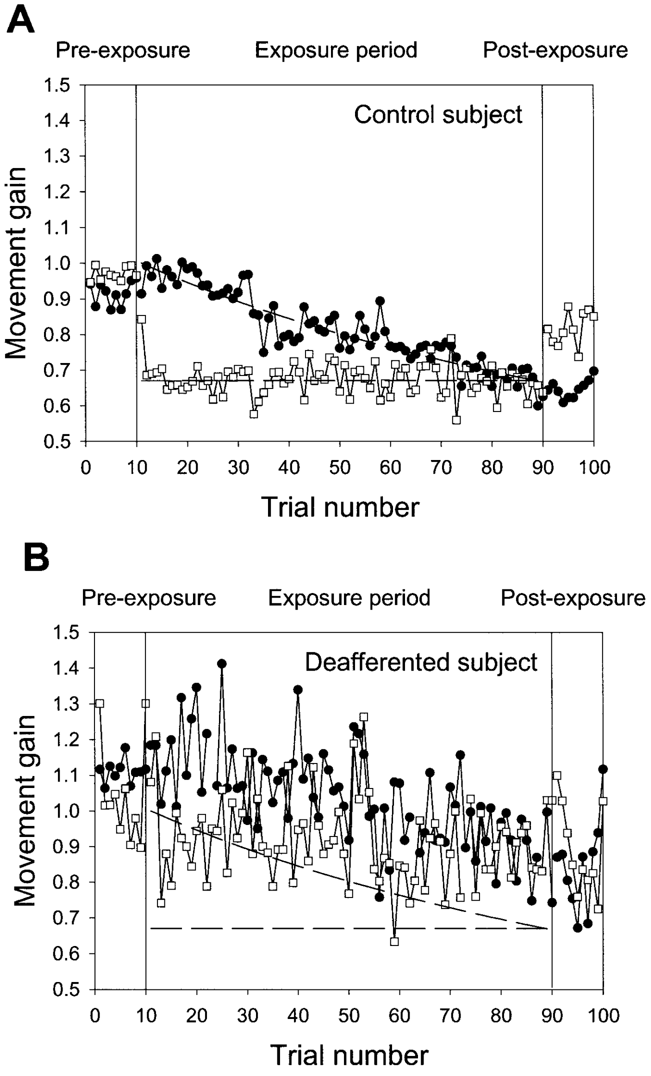


Fig. 7 An immediate gain change (*open squares*) and gradual gain change (*filled circles*) adaptation session for a typical control subject **(A)** and the deafferented subject **(B)**. The gain represents the ratio between the response amplitude and the target amplitude. *The left and right sections of each panel* show the ten open-loop pre- and post-exposure movements. The central sections (*movements 11–90*) illustrate the exposure period movements in response to the change in gain. The imposed gain in each condition is shown by *the dashed lines*

conditions, with the gradual no counting condition showing the greatest level (62.3%). Hence, in a 2×3 ANOVA considering cognitive load and gain conditions they showed a significant main effect of the gain change condition on the level of adaptation (immediate, gradual or no change; $F_{(2,10)}=21.133$, $P<0.001$). A pairwise comparison (using Tamhane's T3 test, which does not assume equal variances; Levenne's test of Equality of Variances was significant) revealed that all three imposed gain change conditions were significantly different from each other (immediate vs gradual, $P=0.008$; immediate vs no change, $P<0.001$; gradual vs no change, $P<0.001$). Cognitively loading the control subjects with the counting task during the exposure period led to a reduction in the amount of adaptation (21.4% compared to 47.2% for the immediate gain change; 30.0% compared to 62.3% for the gradual change). The main effect of the cognitive load on the level of adaptation across all three gain conditions was just outside the significance threshold ($F_{(1,5)}=6.372$, $P=0.053$); there was no significant interaction between cognitive load and gain condition ($F_{(2,10)}=1.635$, $P=0.243$).

IW's adaptation results are displayed in Fig. 8B. In the no gain change condition without counting he showed apparent negative adaptation of more than 40%. However, this condition had been the first session tested and at the end of the session IW reported that he felt unstable in his chair. This meant that he was not able to concentrate fully on the task, as indicated by the large errors in his movements even during the exposure period (Fig. 5B, second column). Furthermore he was found to have been severely undershooting the 40° target during the pre-exposure test period, with an average amplitude of only 31.6°. His mean movement amplitude in the postexposure period was 36.9°, close to the target of 40°. The difference, then, between the pre- and postexposure led to the apparent negative adaptation. In contrast, and as expected, IW showed no adaptation in the no gain change condition coupled with a cognitive load, and also no adaptation in a subsequent no gain change session in which we tested him with only 40 exposure movements. Hence we feel confident to reject these anomalous "negative adaptation" data. When they were excluded, there was a significant effect of the imposed gain (immediate, gradual or no change; $F_{(2,18)}=4.154$, $P=0.033$). As the variances for the different factors were equal, post hoc tests for the simple main effect of the gain condition were completed using Tukey's Honestly Significant Difference test. Overall, the no gain condition was significantly different from the immediate condition ($P=0.038$), and from the gradual condition ($P=0.020$); however, there was no overall difference between the immediate and gradual change conditions ($P=0.954$).

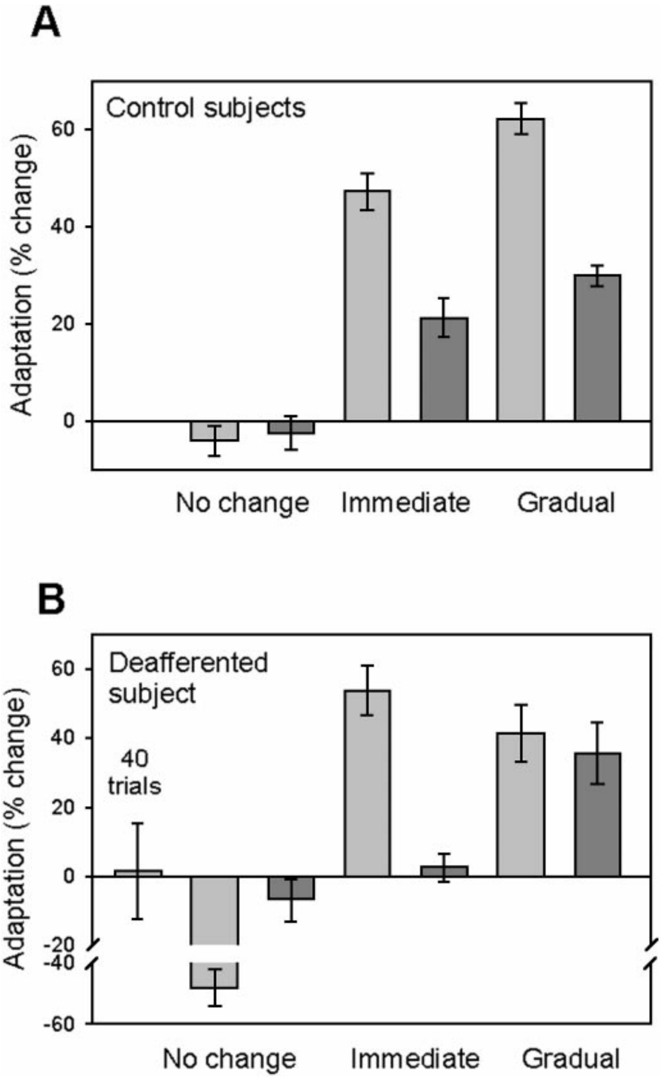


Fig. 8 Adaptation results for control subjects **(A)** and IW **(B)**. For the control subjects, each point represents the mean change in amplitude across six subjects (±1 SE, $n=60$). For IW each point represents the mean change in amplitude (±1 SE, $n=10$). *Lighter fill* indicates conditions without counting; *darker fill* indicates conditions with counting. In **B** an additional column is included, collected in a separate no gain change condition using only 40 exposure trials (*left column*). This is to demonstrate the atypical result observed in the second column, due to the deafferented subjects' poor positioning at the table

IW also showed a significant effect of cognitive load ($F_{(1,9)}=12.59$, $P=0.006$), with the added task of counting reducing his level of adaptation in both the immediate gain condition (54% to 2%) and the gradual gain condition (42% to 36%). Strikingly in the immediate condition adaptation was reduced to almost zero. Hence, there was also a significant interaction between gain condition and cognitive load ($F_{(1,9)}=37.82$, $P<0.001$). This arose from the different effect of the cognitive load between the immediate and the gradual change conditions. A paired comparison of IW's adaptation in the no counting conditions with immediate or gradual gain change was not significant ($t_{(18)}=1.050$, $P=0.299$), while the comparison in the counting conditions was significant ($t_{(18)}=3.376$, $P=0.003$), indicating the source of the significant interaction.

In summary, these data indicate that IW was able to adapt his movement amplitude, and in the immediate condition he adapted as much as the control subjects

(54% for IW compared to 47.2% for controls). Control subjects showed greater adaptation in the gradual condition compared to their immediate condition, while IW showed no significant difference between the two conditions. A cognitive load reduced adaptation in all subjects in all conditions.

Discussion

This study has tested the role that proprioception plays in the control and adaptation of single-joint arm movements to visual targets. We have shown first that, without proprioception, movement accuracy is severely reduced. Second, without proprioception, significant mental resources are necessary to monitor movements such that an added cognitive task impairs performance. Third, without proprioception, the deafferented subject employs different kinematic strategies when adjusting his movement amplitude. However, we have also shown that within this task the deafferented subject can adapt to a visuomotor perturbation, and can in some conditions adapt to the same level as control subjects. We have shown there is an attentional or mental resource requirement in this adaptation task as an added cognitive load reduced adaptation in all subjects and all conditions; thus the combination of moving without proprioception coupled with an added cognitive task reduced adaptation in the deafferented subject to almost zero. Finally we found that a gradual introduction of the gain change facilitated adaptation in the control subjects with respect to an immediate change, whereas it had no significant effect on adaptation for the deafferented subject. These results help define the role of proprioception in visuomotor adaptation.

The role of proprioception in control

We should make clear at the outset that inferring the role of proprioception by comparing IW and control subjects is difficult because IW has spent 20 years developing compensatory strategies to control his movements. A more appropriate test of deafferentation would have been to observe IW soon after his neuropathy and before his rehabilitation, but these experiments would have been impossible then, as he had very little movement control. However, his remaining deficits do serve to highlight where proprioception remains necessary.

Turning first to the effect of the cognitive task, counting backwards is often used as a strong attention demanding exercise (Toole and Lucariello 1984) and can thus emphasise the cognitive demands of various tasks (Nicholson and Fawcett 1990; Lindberg and Garling 1982). By assessing its effect on the accuracy of movements in the exposure phase of the no gain change task, we can highlight the role of proprioception in movement control. It has been noted previously that IW has to attend closely to his movements but his attentional demand has not been quantified for normal reaching movements. For example, Cole and Sedgwick (1992) tested this subject in a repetitive force matching task and found that his performance deteriorated quickly while he was counting backwards. However, they found that control subjects also showed some deterioration in that task. Lajoie et al. (1996) tested the cognitive demands placed on IW when walking and found that during the double-support phase he had to allocate much more attention to his posture than did control subjects. In our study we found that for single joint arm movements made with terminal visual feedback, but without any required change in gain, a cognitive load significantly reduced IW's accuracy while it did not significantly affect the accuracy of the control subjects. There was a small increase in errors for the control subjects, however, so that the effect of the cognitive load was significant when tested across all three conditions tested. However, for IW it was a significant effect even when he was not challenged with a gain change. This implies that proprioception allows subjects to monitor movements without the need of significant cognitive resources. In the absence of proprioception, cognitive resources are required even for what normal subjects find quite simple movements.

Turning next to the voluntary change in movement amplitude required by our task, all subjects, including IW, were able to scale their movements appropriately to compensate for the imposed gain of 1.5. It was clear that this further reduced IW's accuracy (Fig. 5B), whilst for the control subjects, the slight increase in errors recorded was not significant.

An analysis of the kinematics indicated that IW mainly altered the magnitude of the velocity, acceleration and deceleration of his movement but not their timing in order to scale his movements: to move a shorter distance he reduced movement speed. In contrast control subjects tended to alter both the velocity and the duration of their movements. A similar result in normal subjects was observed in Hoffman and Strick's (1986) kinematic analysis of wrist tracking. They found that both the magnitude of velocity, acceleration or jerk, and the duration of the movement were used to specify the movement amplitude. Fitts (1954; Fitts and Peterson 1964) also recognised that subjects scaled their movement time with amplitude as well as velocity.

However, IW's tendency to keep his execution timing constant may serve to reduce the temporal degrees of freedom for his movements and therefore improve his control over them. Ojakangas and Ebner (1991) found that neurologically intact monkeys used a similar strategy in keeping the time to peak velocity constant while scaling the magnitude of peak velocity as they adapted to a change in the gain, similar to this task.

A related result has been reported by Gordon et al. (1995) in their multijoint movements to visual targets. They found that their deafferented subjects tended to confine their movements to a single joint: reducing movements to the external rotation of the shoulder. These subjects also tended to use a similar interjoint coordination pattern for movements of different distances.

Lajoie et al. (1996) found a similar result when they were assessing IW's gait: they reported that one strategy he used to achieve a secure gait was to reduce his degrees of freedom by freezing the knee articulations during the stance phase. Thus, in multijoint movements, the control is simplified by reducing the number of active joints, while for a single joint movement reduction of the temporal complexity is used.

Although his movement duration was more constant than that of the controls, IW moved with a higher average peak velocity than control subjects and correspondingly completed his movement in less time. This is somewhat surprising as usually moving faster makes movement more variable (Fitts 1954; Fitts and Peterson 1964; Schmidt et al. 1979; Meyer et al. 1982). However, this may reflect the fact that IW has no need to incorporate proprioceptive feedback into his movements (Miall et al. 1995).

Visuomotor adaptation with proprioception

We now turn to the question of visuomotor adaptation by the control subjects. By the end of the exposure period all subjects had appropriately scaled their movement amplitude to compensate for the gain change (see Fig. 7). However, this scaling did not entirely persist into the open-loop testing phase. Hence, we did not see complete adaptation (42–64%). However, the levels of adaptation measured in this experiment are within the range of levels (20–80%) previously reported for prism adaptation (e.g. Lackner and Lobovits 1978; Bard et al. 1995; Taub and Goldberg 1973; Redding and Wallace 1988; Kitizawa et al. 1995). They are also close to the 43% level of adaptation reported by Bock (1992) in his gain change study using terminal feedback.

The control subjects' adaptation was cut by about half in the immediate change condition when they were required to count backwards. We are not able to say exactly what mechanism or resource is affected by counting backwards. However, as subjects did not count during the pre- or post-exposure test phases, there are three possibilities. First, counting backwards could have disrupted their performance during the exposure period, and this might also have affected their performance in the testing phase, independent of any change in the visuomotor mapping. The counting task did have a statistically significant effect on their performance, but it was small (Fig. 5A). Second, counting backwards could have disrupted performance of the task and hence the change in gain might have been masked by increased errors in the exposure phase; this cannot be the case for the control subjects because the average increase in errors when counting was only 0.6° (Fig. 5A), much smaller than the imposed 13.3° change, and also much smaller than their typical errors in the no gain change condition (average 2°). Finally their performance of the movement task may not have been affected but, due to the extra cognitive load, subjects may either not have fully registered the discrepancy, or else, despite fully registering the discrepancy, the recalibration of the two systems was affected and hence they adapted less.

In an earlier study Redding et al. (1985) investigated the effect of a cognitive load on prism adaptation when subjects were involved in hallway walking. They showed a reduced negative aftereffect when performing mental arithmetic and explained this result as the effect of cognitive interference on a limited central processing capacity that maintained the directional linkage between the discordant sensory and motor systems. In a later study, the opposite result was obtained: terminal errors in pointing were affected while adaptation was not (Redding et al 1992). They therefore argue that it may be the detection of the discordance between the sensory and motor systems (a necessary prerequisite for adaptation) which is affected by the cognitive task, whilst the subsequent adaptation is an automatic process.

Performance and adaptation were both affected in our study, consistent with Redding et al.'s (1992) idea. However, the effect on performance was small, implying that, for our task, performance can be more easily maintained by the controls, but the detection of the discordance required for adaptation then suffers. In contrast to our study, Redding et al. used actual prisms and hence the discordance between vision and proprioception could be deduced by a variety of other cues; in our task, there were no other sources of useful information other than from the position of the terminal feedback cursor, compared with the subject's expected position of the feedback.

Of course, this explanation does not consider how detection of the discordance or realignment of the discordant systems was affected by counting backwards. One possibility is that the systems responsible have a limited capacity and counting backwards uses some of these resources (whatever they may be), reducing the amount that can be applied to detection or realignment (Heuer and Wing 1984; Redding et al. 1992). Alternatively there might be a cost of concurrence, i.e. a cost associated with having to both simultaneously detect/realign and count backwards (Heuer and Wing 1984).

Adaptation was not completely lost, however, for control subjects. Thus, counting backwards may not fully occupy the attentional channels involved in monitoring and adapting visually guided movements. Alternatively, counting backwards may demand the subject's full attention but there could be other attention-independent (i.e. automatic) processes that are able to produce some adaptation (cf. Redding et al. 1992).

Further insight into how counting could have affected adaptation is provided by the amount of adaptation measured in this task, calculated from the post-exposure movements made without terminal feedback: typically about 50%. This incomplete adaptation, despite accurate movements made over the final half of the exposure period, probably reflects the fact that subject's initially adopt a cognitive strategy to cope with the gain change, but then abandon this in the test period. These "coping" strategies should not have been used during the open-loop movements, as subjects were instructed to move "naturally" to where they saw the target and not to make any cognitive adjustments to their movements. We would contend that the 42–64% adaptation measured represents a genuine reflection of a change in the subjects' underlying visuomotor mapping. Comparing the counting and no-counting conditions, it is clear that the amount of adaptation was reduced (Fig. 8A). If the counting conflicted with the adoption of a "coping" strategy, and yet the subjects had still correctly adjusted their movement amplitude in the exposure phase, then we would expect more, rather than less, adaptation measured in the post-exposure period. Therefore the cognitive task appears to conflict mainly with the detection or realignment processes.

Turning next to the gradual gain change data, we, like Kagerer et al. (1997), found that for control subjects adaptation was facilitated by gradual introduction of the perturbation. Like them, we would suggest that in the gradual condition the terminal visual errors presented to the subjects in the exposure period were very nearly the same magnitude as they would see as a result of their normal intermovement variability without any additional gain change. Therefore these small errors may be more often attributed to small inaccuracies in the relationship (the "visuomotor map") between the visual target position and the appropriate motor response. Hence the subjects would not be forced to adopt a new strategy to correct their performance, and yet would still use these small errors to recalibrate the movement required to reach the target. Therefore, even in the post-exposure phase the adaptation was still present and larger than in the immediate gain change condition. Adaptation still did not reach 100%, however, perhaps because the gradual perturbation meant that subjects were only exposed to the full gain change for the single, final, trial. In contrast, in the immediate condition the initial visual errors are too large to be attributed simply to an inaccurate visuomotor map, and subjects are more able to realise that a perturbation has been introduced. In this case they adopt a cognitive adjustment to enable them to move accurately to the target, and then when they are instructed not to use such adjustments in the post-exposure period the level of adaptation is smaller. However, despite this strategy, they do automatically adjust the underlying visuomotor relationship, so that adaptation of about 50% is achieved over 80 trials.

Finally, the cognitive task appears to have reduced adaptation for the control subjects in the immediate and gradual conditions by an equal amount. If we accept the arguments just outlined, then the reduction in adaptation during the gradual condition means that the counting task must have affected one or both of the processes responsible for detecting the discordance and recalibrating the visuomotor map, but not the process responsible for adopting a strategy. Hence, all the data from our control subjects are consistent with this explanation.

Visuomotor adaptation without proprioception

Considering now the adaptation achieved by the deafferented subject, it is clear that his movements are much more variable than the controls (Fig. 5B) but also that he did manage to reduce his average movement amplitude appropriately over the exposure phase in most sessions (Fig. 7). He also maintained this altered relationship into the post-exposure test period, such that in the immediate gain change condition IW showed the same magnitude of adaptation as the control subjects. This implies that proprioception is not necessary to adapt under these conditions. Moreover, the significant adaptation he showed in our study is in accord with his ability to adapt during continuous feedback pointing with wedge prisms (Bard et al. 1995). In that study, his adaptation was thought to be dependent on surviving proprioception from his neck, allowing a change in the eye-head reference system to then recalibrate the head-hand system. In our study, the position of the subject's head and the entire visual field remained unchanged. Thus despite the eye-head reference system remaining constant, and without any involvement of head/hand realignment, IW was able to modify his motor output.

Recently Guédon et al. (1998) had not been able to show a strong adaptive change in IW in a visually guided tracking task. Their task relied heavily on online visual feedback to correct tracking errors and imposed strong timing constraints. In our study only terminal feedback was presented after self-paced, discrete, movement and IW was required to process, integrate and correct for his errors from one trial to the next, based only on that information. Considering terminal feedback as essentially a form of distributed practice (Taub and Goldberg 1974), IW may have had more time in our task to integrate the movement errors into his plan for subsequent movements and hence produce larger and more longer-lasting change than seen by Guédon et al. Schmidt and Wulf (1997) have recently shown greater adaptation with terminal feedback than with continuous feedback, consistent with this view.

Hence, considering that we have shown that IW needs to attend carefully to his movements, we would expect that his level of adaptation would be severely reduced when he was required to count backwards. This was indeed the case with the immediate gain change: when a cognitive load was introduced IW's adaptation was reduced to almost zero. Furthermore, IW did not show a significant difference in his adaptation between the immediate and gradual conditions. This may be because of his much greater reliance on visual cues to adjust his movements, and because he has no access to a proprioceptive discordance signal. Hence, he may need to access and recalibrate his visuomotor map on the basis of all movements, and without a proprioceptive discordance signal he may integrate even the very large initial errors experienced in the immediate condition. In contrast, the control subjects discounted the immediate condition errors, and adopted a strategy to avoid them that reduced their impact on the adaptive process.

If this argument holds true, then we would not expect IW to adapt in the gradual gain change condition when counting. In this condition, he would still attend to the trial-by-trial errors, but his attention would be shared with the competing cognitive task; and yet he did show some adaptation (Fig. 8B, rightmost column). We found this surprising, especially as he had performed noticeably worse during the exposure period for this condition than in all others, with very large errors during the exposure period (column 6 of Fig. 5B). In fact, his mean absolute errors in this condition were as large as the imposed gain change. In contrast, when he was not required to count, IW's movement amplitudes reduced in accord with the gradually imposed gain change throughout the exposure period, even though with a high variance (Fig. 7B). Clearly this result will require additional testing. The only speculation we would give to account for this is to suggest that IW can allocate his considerable mental efforts to only a limited number of mental processes. Hence, he can control his movement accuracy during the exposure phase, he can adapt his visuomotor mapping on the basis of terminal feedback errors, and he can count backwards, but he may not be able to do all three at the same time. It may be that in the gradual gain change condition with counting, unlike the immediate condition, he relaxed his efforts to maintain high movement accuracy (column 6 of Fig. 5B), and as a result more of his resources were allocated to adaptation.

Hence, with this curious exception, our results provide a coherent framework. First, there is a strong attentional demand to adapting visually controlled movements, and all subjects were affected by sharing their attention between a counting task and the movement task. However, proprioception provided sufficient additional information so that, for controls, normal movements were unaffected by this added cognitive load. For IW, his accuracy was greatly reduced. Second, the magnitude of the visual errors, and their plausibility, affect adaptation. For the controls, the larger errors seen at the onset of the immediate gain change were not plausible, because with the benefit of proprioception they produced smaller variance in movement end points and also had a strong visual-to-proprioceptive discordance signal. Hence, it seems likely that they adopted a strategy during the exposure period which they then discarded for the postexposure test. Thus their adaptation was small. In contrast, IW's errors in the gradual and immediate conditions were roughly similar, and his level of adaptation was also roughly similar. Finally, the lack of proprioceptive information has led IW to develop unusual kinematic relationships in his movements. These are consistent with him controlling his movement amplitude by maintaining the temporal aspects quite constant, but varying the level of forces used to accelerate and brake his movements. Therefore, without proprioception, IW appears to adopt simplifying strategies to accurately control his movements. Even with these strategies, accurate and reproducible movements are difficult for IW in a perturbed environment. Proprioception allows for the automation of normal movements, maintaining movement accuracy, and for small adjustments to movement as a result of differing external conditions, without the need for cognitive attention. Mental attention can, however, be used to adjust movement on demand and appears to be necessary in controls to adapt to an imposed perturbation in the visuomotor relationship. IW's success in adapting to this perturbation shows that proprioception is not essential or necessary for this adjustment, and if sufficient attention to the task is allowed, IW can adapt to the same level as control subjects. However, his poor performance with mental arithmetic suggests that, without proprioception, this adjustment requires considerable attentional capacities. IW often describes anecdotally his tasks of daily living after more than 20 years without proprioception – for instance he says that walking on flat, well lit, windless ground still requires around 50% of his mental capacities, but that uneven, busy places continue to need 100%. We have gone some way to quantifying the effect of his cognitive control of movement by revealing how his performance deteriorates with an additional mental task.

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