Updating of an internal model without proprioception: a deafferentation study

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This study sought to determine whether intact proprioception is required to adapt to a novel kinematic environment. We compared adaptation with a rotated visual feedback between a deafferented patient and healthy participants. They performed reaching movements towards visible targets while vision of the cursor was rotated by 30° with respect to hand position. The patient adapted at the same rate and to the same extent as the controls when exposed to the rotated visual feedback. She also presented large aftereffects following removal of the perturbation. This suggests that proprioception is not an absolute requirement to update a kinematic internal model. Adaptation was likely mediated by a comparison between the sensory consequences of a movement as predicted by a forward model and the visual feedback from that movement. NeuroReport 17:1421–1425 © 2006 Lippincott Williams & Wilkins.

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Introduction

When reaching towards a visible object, one needs to transform visual information about the position of the object into the appropriate set of motor commands required to bring the hand to the object. Such a capacity to estimate the motor commands required to achieve a desired outcome is underlined by the concept of internal model [1], which represents the complex sensory transformations taking place between visual input and motor output. These transformations are flexible, as exemplified by our ability to reach accurately under perturbations of the visual input, such as when a virtual display of limb position is rotated with respect to actual limb position [2]. When exposed to such a shift, participants typically miss the target by an amount proportional to the magnitude of the induced rotation. After seeing the resultant reach as laterally displaced, participants are able to reduce the error on subsequent trials, such that their reaches again land on the target. This rapid adaptive behavior occurring during exposure through online visuo-motor control or strategic corrections reflects the flexible nature of the motor system [3]. Following removal of the perturbation, participants typically miss the target to the opposite side by an amount similar to the initial error. Such plastic changes in movement kinematics that occur following the period of exposure have been termed ‘aftereffects’. It is generally agreed that the presence of aftereffects results from a coordinative remapping between sensory representations, suggesting that an internal model has been updated. It is unclear, however, which sensory process leads to the adaptive state, and in particular which sensory modalities are necessary for an adaptation to occur.

Several studies have addressed this issue by investigating the adaptive capacities of deafferented patients, but results have been inconsistent. A first view, put forth by Guédon et al. [4], suggests that plastic changes in visuo-motor control take place as a consequence of the conflict between visual and proprioceptive information resulting from the induced distortion. These authors found that a deafferented patient (loss of proprioception below the neck) did not present aftereffects following a period of exposure to an altered visual–proprioceptive environment in a tracking task. They concluded that the absence of aftereffects resulted from the inability of the patient to detect any discrepancy between visual and proprioceptive cues, thus supporting the hypothesis that vision and proprioception are both critical parts of the adaptive process. In contrast, the same patient was found to adapt (in some conditions and controls) to an alteration in gain between final arm position and presentation of feedback cursor on a single-joint elbow extension task [5]. In line with these results, it has been suggested that adaptation would result from the discordance between the motor commands issued and the feedback obtained from a movement [6]. Importantly, as vision is sufficient to allow one to determine the outcome of a movement, proprioceptive feedback may not be necessary for adaptation to occur.
One difficulty in interpreting these conflictual findings may be due to the nature of the tasks that were used. In fact, the dependent measures in both studies were subject to online control, and hence might not have been best suited to investigate true visuo-motor adaptation, which is above all understood as a change in the planning of the movement.

Another potential confound in studies with deafferented patients is the extent of proprioceptive loss. Evidence for this was provided by Bard et al. [7], who showed that a deafferented patient below the neck adapted to a prismatic displacement as well as controls while a deafferented patient below the nose did not adapt at all. They suggested that neck proprioception was critical for adaptation as it allowed the eye–head sensorimotor system to be linked and recalibrated with the hand–head sensorimotor system following a change in visuo-manual mapping. Still, these latter results may not be directly comparable to the ones presented earlier [4,5], as the coordinative strategies deployed with prism goggles are thought to differ from those deployed with tasks using computer-generated representations of limb position [8].

In light of these equivocal findings, the goal of the present study was to reassess whether proprioceptive feedback is required for updating an internal model of simple reaching movements. This was achieved by comparing adaptation to a rotated visual feedback between a patient deafferented below the nose and healthy participants. In contrast to a rotated visual feedback between a patient deafferented below the neck, the latter results may not be directly comparable to the ones following a change in visuo-manual mapping. Still, these last results may not be directly comparable to the ones presented earlier [4,5], as the coordinative strategies deployed with prism goggles are thought to differ from those deployed with tasks using computer-generated representations of limb position [8].

Materials and methods
Participants
Five age-matched (three men, two women; ranging between 42 and 58 years old) right-handed healthy participants and one deafferented patient (GL) took part in the study. Patient GL suffered two episodes of sensory polyneuropathy affecting selectively the large myelinated sensory fibers, resulting in a complete loss of the senses of touch, vibration, pressure and kinesthesia [11]. The study was conducted in accordance with the ethical guidelines set by the University of British Columbia.

Materials
All participants performed the task while seated on a height-adjustable chair in front of a horizontal digitizing tablet (Calcomp Drawing Board III, GTCO Calcomp Inc, Columbia, Maryland, USA; sampling rate: 225 Hz), with their chin resting on a chinrest. A mirror was fixed horizontally 30 cm above the digitizing tablet. The visual stimuli were projected from a monitor installed above the setup and viewed by participants as a reflected image on the mirror. Participants controlled a cursor displayed on the mirror by manipulating a mouse across the surface of the digitizing tablet. The mouse had a plastic extension containing a cross-hair whose coordinates were registered by the tablet. This setup allowed participants to see a cursor representing their hand on the mirror but prevented them from seeing their arm.

Task
The target set consisted of five radially arrayed targets, separated by 72° and placed 10 cm from a common starting point (targets located at 0, 72, 144, 216 and 288°). The targets were represented as red circles of 0.7 cm in diameter, while the starting point consisted of a 0.5 cm × 0.5 cm black square. Once the cursor had been maintained stationary for 200 ms in the starting point, a target appeared, prompting participants to initiate their movement. They were asked to make straight uncorrected movements toward the targets as accurately as possible in a movement time of approximately 250 ms, and to bring the cursor back to the starting point afterwards. The task had no amplitude requirement, such that participants had to only ‘move through’ the targets. The five targets were presented in a pseudorandom order, forming a cycle. The cursor location was visible at all times on the surface of the mirror.

Procedure
All participants took part in a pretest, an adaptation phase and a posttest. In the pretest, they performed 15 cycles (75 trials) in which motion of the screen cursor was mapped normally to hand movement (right–left and forward–backward was identical for hand and cursor). This served to familiarize participants with the task. Subsequently, participants performed 30 cycles (150 trials) in which the cursor was rotated 30° counterclockwise around the origin, thus requiring participants to modify their movement kinematics to accurately guide the cursor to the targets (adaptation). Immediately following this adaptation phase, participants again performed 15 cycles (75 trials) in the normal visuo-motor mapping (posttest).

Data analysis
Movement initiation was defined as the point in time when the mouse moved 1 mm from the home position, whereas movement end point was the point in time at which the cursor crossed that target’s radius. For each movement, the spatial positions at peak tangential velocity and at movement end point were measured. We used the directional error at peak tangential velocity as a measure of rotation adaptation. This was calculated as the difference between the direction of the target from the initial hand position and the direction of the hand at peak tangential velocity from the initial hand position. To assess the course of adaptation to the imposed rotation, we computed the mean directional error over successive cycles of movements. The presence of aftereffects was assessed by calculating the change in directional error from cycles in the posttest compared with the mean directional error from cycles in the pretest. As this study compared the performance of a single patient with that of a larger number of controls, a typical analysis of variance (ANOVA) could not be performed. Rather, we assessed significance by determining whether GL’s data were comprised within a 0.95 confidence interval around the controls’ means.

Results
In line with the experimenter’s instructions, participants produced straight and uncorrected movements towards the targets. On cycles 8, 21 and 25 of the adaptation phase, GL’s hand accidentally, however, slipped outside the digitizing
The time to reach peak kinematic markers is presented in Table 1. On an average, the controls reached peak tangential velocity 156, 161 and 173 ms after movement onset in the pretest, the adaptation phase and the posttest, respectively. The data were submitted to a three (phase) repeated-measures ANOVA, which revealed a significant main effect, F(2,8)=5.1, P<0.05. Post-hoc analysis (Tukey’s honestly significant difference; P<0.05) revealed that participants took significantly longer time to reach peak tangential velocity in the posttest than in the pretest. Similarly, total movement time was slightly greater in the posttest (246 ms) than in the pretest (232 ms) and the adaptation phase (233 ms), but this effect did not reach significance (P=0.21). As for GL, the time taken to reach peak tangential velocity (150, 177 and 166 ms for pretest, adaptation phase and posttest, respectively) was within the 0.95 confidence interval around the controls’ means for all three phases. GL’s total movement time (183, 201 and 191 ms for pretest, adaptation phase and posttest, respectively) was also within the controls’ 0.95 confidence interval, except in the posttest, in which it was significantly lower than the controls.

In order to assess that movement trajectories were straight, we correlated the direction error at peak tangential velocity with that at movement end point for every trial of each participant (Table 2). For the analysis, we averaged the squared correlation coefficients (R^2) of all trials performed by each participant into a single value. The reasoning is that if directional error at movement end point is explained by directional error at peak tangential velocity, then the coefficient of determination (R^2) will be high. In contrast, if the trajectories were amended online and deviate from linearity, then that coefficient would be low [12]. The controls presented high R^2 (global mean=0.94), highlighting the linearity of the trajectories. GL’s average R^2 of 0.94 was within the controls’ 0.95 confidence interval, suggesting that her movement paths were also very straight.

We assessed the presence of aftereffects for the five controls by comparing their mean directional error in the pretest to that in the posttest, which is represented in Fig. 1. The data were submitted to a two (phase) repeated-measures ANOVA, which revealed a significant main effect F(1,4)=313.6, P<0.001. Hence the period of adaptation significantly altered the participants’ visual-to-motor transformations, as evidenced by the important aftereffects. We then sought to determine whether GL presented aftereffects of similar magnitude as the controls. To do this, we compared GL’s change in directional error between the pretest and posttest to that of the controls. This measurement captured the total difference in directional error, without regard to each participant’s initial directional bias. On an average, the control participants presented an 8.4° clockwise shift in the posttest compared with the pretest, with a 0.95 confidence interval spanning between 7.0 and 9.9°. With a clockwise shift of 8.0° between pretest and posttest, GL was within the confidence interval, leading to the conclusion that she presented similar aftereffects as the controls.

Finally, we assessed the rate at which participants adapted to the perturbation across the exposure period. This is presented in Fig. 2, which provides an overall picture of the participants’ adaptation to the perturbation during the exposure period, and GL’s performance. From the figure, it appears that GL’s adaptation to the perturbation followed a similar time course to those of the controls. We fitted a logarithmic curve through the 30 data points (30 cycles) of the adaptation phase, and compared the mean value of the obtained slope for the controls to that of GL. The mean slope for the controls was 7.6, with a 0.95 confidence interval spanning between 6.4 and 8.7 (R^2 ranging from 0.78 to 0.96). Again, GL was within the confidence interval, with a slope of 6.8 (R^2 of 0.75), suggesting that she compensated to the induced bias in a similar gradual manner as the controls.

**Table 1** Time-to-peak kinematic markers (ms) for the five controls and GL during the pretest, the adaptation phase and the posttest.

<table>
<thead>
<tr>
<th></th>
<th>S1</th>
<th>S2</th>
<th>S3</th>
<th>S4</th>
<th>S5</th>
<th>Mean (± 0.95 range)</th>
</tr>
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<tbody>
<tr>
<td>Time-to-peak tangential velocity</td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Pretest</td>
<td>150</td>
<td>145</td>
<td>172</td>
<td>168</td>
<td>145</td>
<td>156 (140–172)</td>
</tr>
<tr>
<td>Adaptation</td>
<td>164</td>
<td>157</td>
<td>180</td>
<td>180</td>
<td>125</td>
<td>161 (133–189)</td>
</tr>
<tr>
<td>Posttest</td>
<td>165</td>
<td>174</td>
<td>186</td>
<td>186</td>
<td>156</td>
<td>173 (157–188)</td>
</tr>
<tr>
<td>Total movement time</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pretest</td>
<td>210</td>
<td>229</td>
<td>302</td>
<td>208</td>
<td>212</td>
<td>232 (182–282)</td>
</tr>
<tr>
<td>Adaptation</td>
<td>218</td>
<td>237</td>
<td>301</td>
<td>213</td>
<td>195</td>
<td>233 (182–284)</td>
</tr>
<tr>
<td>Posttest</td>
<td>220</td>
<td>255</td>
<td>300</td>
<td>207</td>
<td>243</td>
<td>246 (200–288)</td>
</tr>
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</table>

**Table 2** Mean squared correlation coefficients (R^2) between the directional error at peak tangential velocity and the directional error at movement endpoint for the five controls and GL.

<table>
<thead>
<tr>
<th></th>
<th>S1</th>
<th>S2</th>
<th>S3</th>
<th>S4</th>
<th>S5</th>
<th>Mean (± 0.95 range)</th>
</tr>
</thead>
<tbody>
<tr>
<td>R^2</td>
<td>0.92</td>
<td>0.92</td>
<td>0.96</td>
<td>0.98</td>
<td>0.94</td>
<td>0.94 (0.91–0.94)</td>
</tr>
</tbody>
</table>

Values represent the mean squared coefficient of all trials from a participant.

**Discussion**

The goal of the present study was to determine whether proprioceptive feedback is required to update an internal model, by comparing the adaptive capacities of a deaf-dull patient to that of healthy participants. We found that GL not only adapted at a similar rate as the controls to the visual rotation during the phase of exposure, but also presented very similar aftereffects in the posttest. These results strongly suggest that proprioceptive input was not absolutely necessary to adapt to the rotated visual feedback. Rather, adaptation likely resulted from a comparison between the sensory consequences of a movement as predicted by a forward model and the visual feedback obtained from the movement. Despite the lack of proprioception, GL was still capable of predicting the outcome of a given motor command through an efference copy and compare it with the visual feedback of her hand position [13].
Several studies [14,4] have reported faster adaptation for deafferented patients than controls during the early stages of exposure to a visual–proprioceptive conflict. This facilitation is generally attributed to the absence of discordance between visual and proprioceptive cues for such patients [15,7]. This was not, however, reflected in our data as GL’s rate of adaptation was similar to that of the controls during the adaptation phase (see Fig. 2). The nature of the tasks used in these studies probably accounts for the differential findings. In fact, Lajoie and colleagues [14] used a mirror drawing task, while Guédon and colleagues [4] used a visuo-manual tracking task. The continuous nature of such actions requires participants to control the limb extensively in an online manner, through visual and/or proprioceptive feedback loops. Obviously, when a conflict is introduced, the visual and proprioceptive maps do not match, such that proprioception of the moving limb interferes greatly with its visual representation. These tasks can be thought of as being less problematic for deafferented patients because they do not have limb proprioception to hamper online visual guidance. Hence, the faster adaptation rates for the patients witnessed in these studies likely resulted from the greater ease with which they can use visual feedback in an online manner to guide the limb. Conversely, the outcome of our task was the result of feedforward processes, whereby a visuo-proprioceptive conflict could be detected only after the movement, or at least too late to interfere with its execution. GL could thus not benefit from her lack of sensory conflict to easily visually guide the cursor to the target. Furthermore, the dependent measure used in the present study (i.e. directional error at peak tangential velocity) was blind to online visual modulations, as it is thought to reflect solely the preplanning processes. We believe that such a measure is more appropriate to investigate the updating of an internal model, which is understood as a modification of the planning of the movement, rather than a change in its online control. In this scope, our results provide clear evidence that the modification of the motor plan taking place during exposure occurs in a similar gradual manner for the patient and the controls.

Recently, authors addressing issues related to movement planning have distinguished between kinematic internal models and dynamic internal models [2]. Initially, the visually defined object to be reached is transformed from its retinocentric coordinates into intrinsic coordinates, such as joint angles. This transformation would be mediated by a kinematic internal model, and would need to be updated to adapt to a rotated visual feedback such as in the present study. Then one would transform the planned displacement, coded in intrinsic coordinates, into the required pattern of motor commands necessary to achieve it. This estimation of the required muscle activation pattern would be mediated by a dynamic internal model, and would need to be updated whenever a given limb displacement requires a new pattern of force to be achieved (i.e. following a muscle lesion; following a change in external forces). Krakauer and colleagues [2], who first suggested a distinction between kinematic and dynamic internal models, examined consolidation when adapting to a novel spatial (kinematic model) and inertial (dynamic model) perturbation. They found that the learning of novel intersegmental dynamics did not interfere with the learning of a novel kinematic transformation, and that the two could be learned simultaneously at the same rate as in isolation. Importantly, they proposed that the independence of kinematic and dynamic internal models might result from the fact that they are mediated by different sensory modalities. On the other hand, proprioception would be crucial to update a dynamic internal model, which requires an estimation of the limb’s inertia and intersegmental torques. This has been supported by studies with deafferented patients showing that such patients make direction-dependent errors reflecting their failure to take into account the complex biomechanical properties of the moving limbs [16]. On the other hand, Krakauer and colleagues [2] suggested that proprioception might not be necessary to update a kinematic internal model, which would rather be mediated by vision. In this respect, our finding that the lack of proprioception did not prevent GL from adapting to the rotated visual feedback (i.e. updating a kinematic internal model) provides strong support for this type of model.

**Conclusion**

In conclusion, one needs to be cautious when making comparisons between healthy participants and GL. It could be argued that GL has developed compensatory strategies because of her neuropathy to regain a certain level of...
autonomy. These strategies may not necessarily be required for the normal control of movement. Nonetheless, our finding that the rate and magnitude of adaptation was highly similar for GL and the controls indirectly suggests that the same mechanisms were mediating adaptation for everyone. If this holds true, our results support the idea that proprioception plays a minimal role (if at all) in kinematic transformations. Its role in movement planning is more likely at the level of the mechanics and dynamics of motion.

References