Research Report

Dual adaptation to sensory conflicts during whole-body rotations

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A dual adaptation paradigm was used in order to study the adaptation to two conditions of conflicting visual and kinesthetic and vestibular information. Adaptation was induced in humans by modifying visual information during whole-body rotations with the help of a virtual reality set-up. Real rotations' amplitudes were factored by a gain of 0.5 or 1.5. The two conditions were associated to a visual context cue. The aim of the experiment was to provide support for either the feedback or the feedforward model of adaptive states switch. Results show that subjects could adapt to the two conditions of conflict during whole-body rotations. However, the two conflict situations have been found to differ both in their motor dynamics and in their susceptibility to adaptation, as it seems that the adaptation is more complete in the condition of gain 1.5, i.e., faster and more precise. Subjects could be divided into two groups according to their ability to use contextual information to switch between adaptive gains. The visual cues were sufficient for some subjects to switch adaptive state, which corresponds to a context-dependent dual adaptation, or feedforward model of switching. Other subjects showed a switch cost maintained across the experiment, corresponding with a stimulus-dependent adaptation, or feedback model of switching.

We are suggesting that the process enabling switching between adaptive states depends on subjects' abilities to use contextual cues of certain types, and thus on their "perceptive styles". This could explain the variability of results obtained in the literature.

1. Introduction

The construction of a coherent representation of the relationship between our body and the environment is a challenging task for the brain, given the existence of many sensory ambiguities in the information provided by our senses. A theory has been proposed to model this system. The sensory weighting model of multisensory integration consists of three processing layers (Zupan et al., 2002). Firstly, each sensory system provides the central nervous system with information regarding a specific physical variable. Secondly, because the information available from different sensory systems is qualitatively different, sensory estimates are converted to intermediate estimates that share the same 'units', a process referred to as 'promotion' by Landy et al. (1995). This conversion is based on internal models of the relationships between sensory systems. Thirdly, because several sensory systems may provide information about the same physical variable, the final estimate is computed as a weighted average of all available intermediate sensory estimates. An interesting
question concerning this model and similar ones rests on the capacity of the nervous system to build internal models. Internal models are explicit or implicit knowledge of body dynamics which enable the system to anticipate state changes before the corresponding sensory data have arrived. Is it possible to store two or more variations of an internal model at the same time?

The neural basis of adaptation to conflicting sensory inputs during motor tasks has been extensively studied (see for instance, review by Berthoz and Melvill Jones, 1985 for gaze control or review by Todrov, 2004 for sensorimotor control). However, most theories and models of adaptation to conflict, for instance adaptation to conflicting visual and proprioceptive-kineesthetic information during arm pointing movements, are based upon the idea that only one visuo-motor transformation, or internal model, can exist at any given time, and hence subjects need to adapt to a normal environment following an initial adaptation to an altered environment. Consistent with these theories, subjects make errors upon the return to the normal environment, opposite in direction to those observed when subjects were first exposed to the adaptive stimulus. These errors have been termed aftereffects (Harris, 1963).

However, another theory has been proposed. In 1993, Welch et al. (1993) introduced the notion of “dual adaptation”. According to this theory, individuals can concurrently store two or more visuo-motor transformations, or adaptive configurations of internal models. Such a dual adaptation can be induced by alternately switching back and forth between environments over blocks of trials (Cunningham and Welch, 1994; Donderi et al., 1985; Welch et al., 1993). This ability to adapt to a sensory rearrangement more rapidly and/or more completely after repeated experience with it has been demonstrated with a variety of adaptive stimuli, including wedge prisms (Donderi et al., 1985; Martin et al., 1996; Welch et al., 1993), rotated visual feedback (Cunningham and Welch, 1994), varying VOR gains (Kramer et al., 1998; Shelhamer et al., 1992, 2002; Tiliket et al., 1993; Welch et al., 1998; Yakushin et al., 2003), varying saccade gains (Shelhamer and Clendaniel, 2002a,b), microgravity (Baroni et al., 2001), modified scaling of visual feedback (Seidler et al., 2001), and force fields perturbing the direction of limb movement (Gandolfo et al., 1996).

An important question relating to dual adaptation is whether the dual adaptation can be associated to context cues, in such a manner that contextual information is sufficient to induce a change in adaptive state. In such a case, subjects would be trained to associate context to dual adaptation by associating two different adaptive states with two different states of a context cue, and the gain, for example, would switch between the two adapted states when the context cue changes state. Adaptation would thus be imposed by alternating context/adaptation states together over the course of an adaptation session.

Post and Welch (1998) offered two hypotheses for the role of contextual cues in switching between two adaptive configurations. On one hand, contextual cues could serve as “warning signals” and, in principle, allow the adaptive mechanism to make its switch before the adaptive stimuli are actually presented. On the other hand, the necessary condition for changing to the alternate adaptation could be one or an association of the visual, proprioceptive-kineesthetic, and vestibular feedbacks that occur from interacting with the alternate adaptive environment. In this case, the shift cannot occur until the feedback has arrived at its appropriate neural locus or loci, and the context information is not enough for the switch to the new adaptive state to take place. Thus, even very strongly dual-adapted participants will reveal a delay between the moment the adaptive environment has been changed and the initiation of the appropriate adaptation. Brown and colleagues (2002–2003) studied the adaptation of the VOR during short-radius centrifugation and have proposed two models corresponding to these two hypotheses. These models were adapted to the current experiment and are presented in Fig. 1. The “feedback” model supposes that an error must be made before the internal model can be updated, even if the

![Image](image)

Fig. 1 - Dual context adaptation. $G_{0.5}$ and $G_{1.5}$ are the two control laws corresponding to the two conflict conditions; $a$ is the amplitude of the body rotation to execute. In the case of a feedforward model (top), the control strategy is chosen as soon as the new context is recognized, and before any stimulus occurs. The external context cue which is associated with a particular control law enables the switch to the adequate control law for the movement, leading to a visual motion in the counter direction ($-x$) of the same amplitude as the rotation which was initially planned ($x = a$). In the case of a feedback model, an error must be made before the model can be updated. An error signal resulting from the first movement is generated by a comparison between the amplitude of rotation initially planned ($a$) and the amplitude of the resulting visual motion in counter direction ($x$). This error signal is analyzed in order to determine the appropriate new control law to employ (Berthoz and Melvill Jones, 1985). Only then can the switch occur. In the case of alternating conflict situations of gain 0.5 and gain 1.5, this means that subjects put in the context of gain 1.5 would always use the control law of the previous context, $G_{0.5}$, for their first movement, before switching to the adequate control law $G_{1.5}$. They would thus make a greater error in the first movement ($a$) than in the following ones.
updating is restricted to the selection of the appropriate stored sensory-motor control program, or adaptive state. The error signal serves as a cue that the environment has changed and that the associated change in adaptation state must now also occur. According to this model, a well-adapted subject requires at least one exposure to the context-specific stimulus in order to switch between adaptive states. Young and colleagues (2003) called such a model “stimulus-dependent adaptation”. Alternately, in the “feedforward” model proposed by Brown et al. (2002–2003) the recognition of the context serves directly as a cue for the switch in adaptive state, before any stimulation occurs. In this case, a change of context cue leads directly to a switch in adaptive configuration. Young et al. (2003) consider that such a model would correspond to a “context-dependent adaptation”.

Welch et al. (1993) suggested that dual adaptation was greatly facilitated by the association of stable sensorimotor cues to the different adaptation conditions. This hypothesis corresponds to a feedforward model, or context-dependent adaptation. Cunningham and Welch (1994) compared the effectiveness of auditory and visual cues to facilitate the switching between multiple adaptive configurations. Their results demonstrated only weak effects for both auditory and visual signals, with the cues appearing to be effective for switching between some but not all blocks. There are further conflicting results as to whether visual cues can be associated with acquired adaptations. Donderi and colleagues (1985) demonstrated color-contingent aftereffects following prism exposure. Seidler and colleagues (2001) compared the effectiveness of different types of cues for dual adaptation in a task of arm pointing. Their results showed that cues that can be efficiently associated with an adaptive state are those that are intrinsic to the task. In their experiment, head position was a cue which was more efficiently linked to the adaptation than the position of the opposite arm or the target orientation. Shelhamer and colleagues (1992, 1994, 2005) exposed subjects to alternating periods of vestibulo-ocular reflex (VOR) gain, shifting the angle of gaze with each change in gain. Their results show that eye position can be effectively associated with multiple gains of the VOR. Gandolfo et al. (1996) had subjects adapt to a force field opposing their movement, with a force magnitude proportional to the velocity of the moving limb. Subjects alternated between clockwise and a counterclockwise-directed opposing force field. The use of different posture to grasp the manipulandum, and thus different muscle requirements to execute the movement, was effectively associated with the different adaptive configurations.

These data suggest that contextual cues intrinsic to the task are effectively associated with multiple adaptive states. Martin and colleagues (1996) suggest that almost any type of cue can become effectively associated with multiple mapping following extensive alternating training periods. They demonstrated that subjects could switch automatically between clockwise and a counterclockwise-directing prism and without after 6 weeks of training sessions, with the only trigger being the presence or the absence of the lenses. Subjects pointed accurately from the first trial in a new context/adaptive state. Thus, less salient contextual conditions can be associated with adaptive states over longer periods of alternating exposures. These results support the feedforward model, or context-dependent adaptation, as the context cues can be associated with the adaptive states, and are sufficient to trigger the switch from one adaptive state to the other.

In other cases, however, the context cue may not be sufficient for the switch between adaptive states to occur, because an error signal feedback is necessary. For example, in an adaptation of reaching movements under prism displacement of vision, it was found by Welch and colleagues (1993) that the context state was only determined when the error of an initial movement was sensed. Gandolfo et al. (1996) demonstrated that subjects could not associate a change in the color of the ambient room lighting with different perturbing force fields. Young and colleagues (2003) conducted an experiment on dual state adaptation of vestibular responses to rotating and non-rotating contexts. Their results suggested that the sensory conflict resulting from the first head movement conducted within the rotating environment provided feedback necessary for the transition to the appropriate gravito-inertial internal program. These results are in favor of a stimulus-dependent adaptation, rather than a general context-dependent adaptation.

The aim of the present experiment was to further investigate the issue of the control of switching between adaptive states, rather than the adaptation of the response itself. Both models proposed in the literature are supported by experimental data, and we aimed to extend the research in this field to whole-body rotations in situations of conflict between visual and idiographic and vestibular information. We investigated whether subjects’ behavior following a period of adaptation corresponded to the predictions of the feedback or feedforward model. The analysis of subjects’ behavior was based on their movement parameters, such as mean velocity error or mean squared jerk. According to the hypothesis of a stimulus-dependent adaptation, subjects’ performance should be temporarily worsened each time the context state changes, as subjects need to process an error signal in order to determine that a change in context state has occurred. According to the hypothesis of a feedback model, or context-dependent adaptation, subjects’ performance should reach a stable level after adaptation, and there should not be an effect of switching context state.

2. Results

2.1. Hypotheses

Four hypotheses were investigated by studying the variations of the different movement parameters during the experiment. The first hypothesis (Conflict Hypothesis) is that an effect of conflict will be observed, showing that execution of whole-body rotations can be disrupted by changing the gain between proprioceptive and vestibular signals on one hand and visual signals on the other hand, in a virtual reality paradigm. According to this hypothesis, there should be significant differences at the beginning of the experiment between the conflict gains and the normal gain 1. The second hypothesis (Adaptation Hypothesis) is that subjects will adapt to the situations of conflict. According to this hypothesis, we should
observe a reduction of the effect of conflict during the experiment. If the experiment is long enough for subjects to adapt completely, there should be no difference between the movement parameters in the conflict gains and the normal gain at the end of the experiment. The last two hypotheses concern the type of model that could be involved in switching between two adaptive states. The Feedback Hypothesis predicts that subjects will need to make a first erroneous trial before being able to switch to the adequate configuration of internal model. According to this model, there should be a cost of switch gain all along the experiment, even at the end of the experiment when subjects have adapted to the conflict. This would lead to a main effect of turnblock. The Feedforward Hypothesis predicts that contextual cues will enable subjects to switch to the adequate configuration of internal model.

2.2. Qualitative description of the results

2.2.1. Orientation
The average orientation profiles were plotted as a function of the amplitude of the turns, the gain, and the navigation block (Fig. 2). The rotation occurred over approximately 3.5 s. Gain 0.5 showed profiles with an overestimation and then a correction to attain the correct orientation after the turn. The amplitude of the overestimation as well as the amplitude of the correction was reduced as the navigation block increased. The profiles for the last navigation block showed little overestimation, but still attained the final orientation quicker than in gain 1. In the condition of gain 1.5, the profiles of orientation do not show corrective movements. The profiles for the amplitudes 45° and 135° were similar, with variations towards more similarity to gain 1 as the navigation block increased. The inverse pattern was observed with the amplitude of 90°, the orientation seemed to become more different from the gain 1 profile.

2.2.2. Angular velocity
Average angular velocity profiles were plotted as a function of gain, amplitude of the turn, and navigation block (Fig. 3). In the condition of gain 1, the peak velocity increased with the amplitude of the turn, from 45°/s at 45°, to 73°/s at 90° and 84°/s at 135°. The profiles suggested delayed corrective sub-movements in the opposite direction for the amplitudes of 45° and 90° whereas the reduced right slope at 135° suggests an overlapping sub-movement.

In the condition of gain 0.5, the peak velocity was greater than in gain 1, although we could see a reduction as the navigation group increased. The peak of velocity never reached the level of gain 1, and in the orientation profile, this is shown by the fact that the final orientation was reached quicker in...
gain 0.5 than in gain 1. Delayed sub-movements could be observed and their amplitude diminished with the navigation block. In the condition of gain 1.5, the peaks of velocity were smaller than in the condition of gain 1, but reached a level very close to that of gain 1 in the amplitudes of 90° and 135°. The angular velocity profiles did not show the corrective sub-movement observed in gain 1 for 45° and 90°, and the profiles suggested the presence of overlapping sub-movements. For 135°, the profiles are very close to that of gain 1.

Decomposing the angular velocity profile in single peaks can provide some information about the difference between the two conflict conditions. We fitted fourth order polynomial curves to the angular velocity profiles of a turn made by one randomly chosen subject in the two conflict conditions at the beginning of the adaptation. The results showed that typically, whereas in condition of gain 1.5—when subjects have to turn more than in a normal environment—sub-movements were of the overlapping type (Fig. 4a), in condition of gain 0.5—when subjects have to turn less than in a normal environment—sub-movements are of the delayed type (Fig. 4b). In the gain 0.5 condition, subjects tend to overshoot, thus they have to make a movement in the other direction to compensate. This leads to series of sub-movements of the delayed type, as subjects realize too late that the movement they planned was too large. In the gain 1.5 condition, on the contrary, subjects tend to make a rotation which is too small, but they can realize this while doing the movement and send a motor command to execute a prolonged rotation, which is shown on a velocity profile by overlapping sub-movements.

2.3. Orientation at peak of angular velocity

In the case of a canonical symmetrical bell-shaped angular velocity plot, the orientation at the peak of angular velocity corresponds to half of the complete rotation. It thus depends directly on the amplitude of the turn, leading to main effects of angles in analyses done on this movement parameter.

In the condition of Gain 1, the only significant effect was an increase of the orientation at peak of angular velocity with the angle of the turn ($F(2,16) = 85.0, P < 0.01$), all pairwise comparisons were significant ($P < 0.01$, means (45°,90°,135°): 21.3 < 39.9 < 56.6°). For each angle, there was an underestimation (i.e., the values correspond to less than half of the rotation). This underestimation seems to increase with the amplitude of the turn (underestimation of 1.2, 5.1, and 11.4°).

Conflict Hypothesis: the orientation was significantly bigger in gain 0.5 than gain 1, and smaller in gain 1.5 than gain 1 in the first four navigations of the experiment (Table 1). Thus, the two types of conflict were found to affect the orientation at the peak of angular velocity at the beginning of the experiment. Adaptation Hypothesis: no difference was observed between the last turnblock of the last navblock of the conflict conditions and the gain 1 reference (Table 1). Thus, the effect of conflict had disappeared at the end of the experiment. Feedback/Feedforward Hypotheses: an interaction between gain and turnblock was observed. In gain 0.5, there was a main effect of turnblock, which was found significant in post hoc tests only in the first navigation block. In gain 1.5, no significant effect was found (Table 2). Thus, an effect of turnblock was present in the condition of gain 0.5 at the beginning of the experiment but then disappeared, which supports the Feedforward Hypothesis.

2.4. Peak angular velocity

It could be argued that adapted subjects should have the same velocity profile in the conflict conditions than in the control gain 1 condition. We investigated how the peak angular velocity varied across the experiment.

Gain 1 showed an effect of angle ($F(2,16) = 191.9, P < 0.001$), with the angular velocity increasing with the amplitude of the rotation. All pairwise comparisons were found to be significant ($P < 0.01$, means (45°,90°,135°): 43.1 < 72.2 < 84.6°/s). Conflict Hypothesis: the peak of angular velocity was significantly
greater in gain 0.5 than gain 1, and smaller in gain 1.5 than gain 1 (Table 1), showing an effect of conflict on the peak angular velocity at the beginning of the experiment. Adaptation Hypothesis: there was no significant difference between the last turnblock of the last navblock of the conflict conditions and the gain 1 reference (Table 1). Thus, the effect of conflict found at the beginning of the experiment was not found at the end. Feedback/Feedforward Hypotheses: there was an interaction between gain and turnblock, with a decrease in angular velocity in gain 0.5 and an increase in gain 1.5. In gain 0.5, there was an effect of turnblock maintained across the experiment (except navblock 3), though the interaction navblock × turnblock was significant (effect of navblock in the first turnblock only). In gain 1.5, there was an effect of turnblock only, which was maintained across the experiment. In both cases, the effect of turnblock corresponded to a significant difference between the first turnblock and the second and third, a decrease in gain 0.5, and an increase in gain 1.5 (Table 2). Thus, in both gains, there was an effect of turnblock maintained across the experiment, which supports the Feedback Hypothesis.

2.5. Mean angular velocity error

This value is a measure of how different the velocity profile at a turn is from the gain 1 template. Adapted subjects should show a velocity profile similar to the velocity profile for gain 1. Contrary to the previous two variables, this measure is a mean of the absolute difference between the velocity profile and the template, and thus adaptation should be observed as a decrease in the mean angular velocity error in both gains, instead of changes in opposite directions for gain 0.5 and gain 1.5. Moreover, as the data from gain 1 is already used to calculate the mean angular velocity error, it was not possible to test the Conflict Hypothesis. The Adaptation Hypothesis was investigated by testing whether there was a decrease in mean angular velocity error corresponding to subjects’ adaptation. A main effect of navblock was found, showing a decrease in the mean velocity error when the navblock increased. Post hoc comparisons were not significant. Feedback/Feedforward Hypotheses: there was a main effect of gain, with a greater mean angular velocity error in gain 0.5 than gain 1.5, but no interaction with gain was found, thus the two conflict gains were analyzed together. There was a main effect of turnblock and a navblock by turnblock interaction. The effect of turnblock was a decrease in mean angular velocity error between the first and second turnblocks and was significant only in the first two navblocks. The effect of navblock was a decrease in mean angular velocity error as well, and was significant only in the first turnblock (Table 2). Thus, an initial effect of turnblock disappeared after the second navblock, which supports the Feedforward Hypothesis.

2.6. Mean squared jerk

Jerk is a second time derivative of the velocity. Increases in jerk can be caused by general increases in velocity as well as by increases in the irregularity of movement due to discrete corrective sub-movements. For each turn, the value of mean squared jerk was calculated by taking half of the mean value of the squared jerk on 200 data points around the peak of angular velocity (~3.4 s). A bad adaptation or the use of the wrong internal model would have as a consequence a less smooth movement, with more corrections, and thus a bigger mean squared jerk. An increase in angular velocity would also lead to a bigger mean squared jerk. Gain 1 showed an effect of angle (F[2,16] = 62.3, P < 0.001), with a significantly bigger mean squared jerk for rotations of 90° and 135° than 45° (P < 0.001, means (45°,90°,135°): 0.45 < 0.89 = 1.01). Conflict Hypothesis: the mean squared jerk was significantly greater in condition of gain 0.5 than gain 1, but not significantly different between gains 1.5 and 1 (Table 1). Only gain 0.5 was investigated further. Adaptation Hypothesis: the difference between gain 0.5 and gain 1 is smaller but still significant at the end of the experiment (Table 1). Feedback/Feedforward Hypotheses: a main effect of turnblock and an interaction between navblock and turnblock were found. The effect of turnblock is found in the first and last navblock, with a significant decrease in mean squared jerk as the turnblock increased. Navblock showed a significant effect in the first turnblock (Table 2). Thus, there is an effect of turnblock at the beginning of the experiment, which disappears in navblocks 2 and 3, and is significant again, but to a lesser extent, in the last navblock. These results do not clearly support the Feedforward or Feedback Hypotheses.

2.7. Differences between subjects

Plotting the orientation as a function of turnblock in the second half of the experiment for each participant seemed to show a distinction between two groups of subjects in the gain 0.5 condition. One group (group A, 4 subjects) seemed to show little or no effect of turnblock, while the other (group B, 5 subjects) showed a bigger orientation in the first group of turn. We decided to investigate how this difference could have affected the results of the previous analyses. The method used

<table>
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<tr>
<th>Table 1 – Initial effect of conflict, and effect of adaptation</th>
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<td>Orientation at peak of angular velocity (°)</td>
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<td>Peak of angular velocity (/s)</td>
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<td>Mean squared jerk</td>
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Results of the paired t tests performed between gain 1 and the conflicts gains. Start: tests done on the beginning of the experiment, i.e., between the average gain 1 and the first four navigations of the conflicts conditions. End: tests done on the end of the experiment, between the average gain 1 and the last turnblock of the last navblock of the conflicts conditions.

* P < 0.05.
** P < 0.01.
*** P < 0.001.
was to add a between subject factor called group to the Repeated Measures ANOVAs. When an interaction effect with group was found significant, we investigated the effect further. The hypothesis was that we would consistently find an interaction of group with the factors of interest turnblock and navblock. We aimed at testing whether group A showed an effect of turnblock maintained across the experiment, while group B would not show an effect of turnblock at the end of the experiment.

The analysis of the peak orientation showed an interaction effect in the full Repeated Measures ANOVA: gain × navB × TurnB × group (F(6,42) = 2.6, P < 0.05). An interaction between turnblock and group was found to be significant in the gain 0.5 only. Group A showed a main effect of turnblock, with a decrease in the orientation at the peak of angular velocity when the turnblock increased (Fig. 5). Group B showed no effect of turnblock (Table 3).

In the analysis of the peak angular velocity, there was an interaction between navblock and group in the full Repeated Measures ANOVA (F(3,21) = 5.4, P < 0.01). There was no interaction with gain, and it was hypothesized that the effect of adaptation was in the same direction for both conflict gains, thus data were collapsed across gains. In group A, there was a significant effect of turnblock, showing a decrease in the peak of angular velocity from the first to the third block of turns. Group B showed an interaction between navblock and turnblock. The effect of turnblock was significant in the first two navblocks only, with in both cases a significant decrease between the first and third turnblocks (Table 3, Fig. 5).

No interaction with group was found when comparing the last turnblock of the last navblock with the reference gain 1 in all the analyses, which show that the groups were differing only in the earlier turnblocks, as suggested by the previous analyses (shown in Table 3).

2.8. Test of adaptation after effects

Seven out of the nine subjects completed the navigation of 2 extra corridors at the end of the task. During these two

<p>| Table 2 – Results of the analysis of movement parameters: investigation of the switch cost |
|---------------------------------------------|---------------------------------------------|---------------------------------------------|</p>
<table>
<thead>
<tr>
<th>Gain x Angle x NavB x TurnB Repeated Measures ANOVA</th>
<th>Further analyses</th>
<th>Gain x Angle x NavB x TurnB Repeated Measures ANOVA</th>
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<tbody>
<tr>
<td>Orientation at peak of angular velocity</td>
<td>Gain F(1,8) = 61.0***</td>
<td>Gain F(1,8) = 4.5*</td>
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<td>---------------------------------------------</td>
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<tr>
<td>Peak of angular velocity</td>
<td>Gain F(1,8) = 86.2***</td>
<td>Gain F(1,8) = 27.5***</td>
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<tr>
<td>Mean angular velocity error</td>
<td>Gain F(1,8) = 53.4***</td>
<td>Gain F(1,8) = 27.5***</td>
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<tr>
<td>Mean squared jerk</td>
<td>Gain F(1,8) = 73.5***</td>
<td>Gain F(1,8) = 27.9***</td>
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</table>

The first column shows the results of gain (2) × angle (3) × navblock (4) × turnblock (3) Repeated Measures ANOVAs performed on the data of the conflict conditions. Further analyses investigated the effects of turnblock, navblock, and their interaction. In dark grey are results showing a cost of switching present during the whole experiment, which support the Feedback Hypothesis, in light grey are results showing a switch cost at the beginning of the experiment but not at the end, supporting the Feedforward Hypothesis.

* P < 0.05.
** P < 0.01.
*** P < 0.001.
navigations, the gain was returned to 1, but the color of the corridors continued to alternate between the colors associated with gains of 0.5 and 1.5. If subjects were adapted to the conflict gains, then they should show an after effect of the adaptation when returned to gain 1. This could be shown by an effect of the color of the corridors.

2.8.1. Orientation at peak of velocity
A Repeated Measures ANOVA with 3 factors, color (associated with gain 0.5, 1 and 1.5) × angle (3) × turnblock (3), was run on the logarithm of the orientation at the peak of velocity. Results showed a main effect of color \(F(2,12) = 6.5, P < 0.05\), a main effect of angle \(F(2,12) = 152.6, P < 0.001\), and a color × angle × turnblock interaction \(F(8,48) = 2.3, P < 0.05\).

A possible reason for this interaction effect is the fact that the test of after effect was performed in only one corridor for each conflict gain. There was no averaging across the four different corridors as in the rest of the analysis. In this case, the first turn was either 90° corresponding to gain 0.5 and 135° corresponding to gain 1.5, or the reverse. As there was a main effect of angle, this was likely to have affected the results. Looking at the results for these two angles, at 90° there was a main effect of color \(F(2,12) = 4.4, P < 0.05\) and a color × turnblock interaction \(F(4,24) = 2.9, P < 0.05\). Post hoc comparisons showed a marginally significant difference between the colors associated with gain 0.5 and 1 at the first level of turnblock only (\(P = 0.055\)), but no difference between the color associated to gain 1.5 and that of gain 1. The variations were in the hypothesized direction, that is to say in the corridor with a color associated with gain 0.5, subjects had a smaller orientation than the reference gain 1, while the orientation was greater in gain 1.5 than in the reference gain 1. At 135°, there was no significant effect.

3. Discussion
This experiment aimed at investigating dual adaptation to conflict between kinesthetic, vestibular, and visual information during a navigation task in virtual reality. In particular, we wanted to provide experimental support concerning the two hypotheses concerning switching between adaptive states. In a feedforward model, the contextual information is sufficient to make the switch, while in the feedback model, error feedback is necessary before the switch can happen.

Subjects were exposed to a conflict between kinesthetic, vestibular, and visual information during whole-body rotations. In the condition of gain 0.5, subjects had to turn less than in the normal world to achieve the task (staying in the middle of the corridor), while in the condition of gain 1.5, subjects had to turn more than in the normal world. The color of the corridor’s walls (red or blue) provided contextual information. Dual adaptation was imposed by alternating context and gain together over the course of the experiment. Decomposing the movements into submovements, as suggested by Novak et al. (2002), for two typical turns of a subject enabled us to sketch the dynamical differences of the movement in the two conflict conditions. We decomposed the angular velocity profiles of one subject at the beginning of the adaptation in simple velocity peaks described by polynomial equations of the fourth order. The
results of this decomposition showed that in the condition of gain 0.5 the subject used “delayed sub-movements”, that is to say sub-movements initiated after the completion of the previous sub-movement. However, in condition of gain 1.5, the subject used, in addition, “overlapping sub-movements”, the motor command of which is sent before the end of the previous sub-movements (Novak et al., 2002). When subjects turn in gain 0.5, they have a tendency to overshoot, and then make a correction by turning in the opposite direction. This corrective turn is also too large, and subjects start a new rotation in the direction of the turn, and this goes on until the subjects finally reach the correct orientation in the virtual corridor. In the condition of gain 1.5, subjects can realize while they are still turning that their turn will not be large enough and thus continue their rotation until they reach the correct orientation. This difference in response to the two conditions of conflict is important to the interpretation of the results of the analyses of the movement, as they affect measures such as the mean angular velocity error and the mean squared jerk.

The results of the movement analysis suggest that adaptation was achieved. When an effect of conflict was observed at the beginning of the experiment, it disappeared at the end. The comparisons between the average for gain 1 and the average for each conflict of the last block of turn of the last navigation block showed no significant differences. Some differences were observed in the adaptation to the two gains, however. From the beginning of the experiment, the mean velocity error was generally smaller in gain 1.5 than gain 0.5, and there was no difference in squared jerk between gain 1.5 and 1 while this difference was significant with gain 0.5. These differences can be in part explained by the differences in type of corrective movements. Delayed sub-movements, especially when in the opposite direction to the overall movement, lead to a greater difference between the angular velocity trace in the condition of gain 0.5 compared to the template gain 1. It also leads to bigger peaks of angular velocity as well as a reduced smoothness of the movement, which both increases the mean squared jerk value. The results suggesting differences between the two conflict gains could be compared to those of Seidler et al. (2001) who observed, in a task of dual adaptation of arm pointing with computer visual feedback, that context association was made in the condition of visual feedback with a gain 0.5, that is to say when the movement presented to the screen was a 0.5 scaling of the movement made by the subjects, while it was not when the scaling was 1.5.

The movement data were first analyzed using the whole group of subjects, and the results were not clear concerning the Feedforward/Feedback Hypotheses. On one hand, the analyses of the orientation at peak and the mean angular velocity error provided support for the feedforward hypothesis, as an effect of turn block which was observed at the beginning of the experiment disappeared later on. On the other hand, the analyses of peak angular velocity and mean squared jerk provided support for the Feedback Hypothesis, as the effect of the turn block was maintained across the whole experiment, suggesting that an error signal feedback was necessary for the switch of adaptive states to occur.

The data concerning orientation at peak suggested a difference between subjects. Two groups were distinguished according to the difference between the value for the first and the second block of turns in the second half of the experiment. Group A (4 participants) corresponded to subjects showing an orientation further away from the mean gain 1 in the first block of turn than in the second. Group B was made of the 5 other participants. The new analyses run with a between subjects factor group showed clearer results. There was an interaction with group of all measures in gain 0.5, and in gain

### Table 3 – Difference between groups in the variation of the movement parameters

<table>
<thead>
<tr>
<th>(TurnB x NavB) x Group</th>
<th>Group A Turn x NavB Repeated Measures ANOVA</th>
<th>Group B post-hoc, effect of TurnB</th>
</tr>
</thead>
<tbody>
<tr>
<td>Orientation at peak of angular velocity</td>
<td>Gain 0.5 TurnB x Group F(2,14) = 3.8*</td>
<td>n.s. TurnB F(2,14) = 6.3*</td>
</tr>
<tr>
<td>Peak of angular velocity</td>
<td>Gain 0.5 NavB x TurnB x Group F(6,42) = 2.4*</td>
<td>TurnB F(2,6) = 16.6** 1 &gt; *</td>
</tr>
<tr>
<td>Mean Angular Velocity Error</td>
<td>Both gains collapsed NavB x Group F(3,21) = 5.4**</td>
<td>TurnB F(2,6) = 37.9*** 1 &gt; 2*, 1 &gt; 3*</td>
</tr>
<tr>
<td>Mean squared jerk</td>
<td>Gain 0.5 NavB x TurnB x Group F(6,42) = 2.6*</td>
<td>TurnB F(2,6) = 16.5*</td>
</tr>
</tbody>
</table>

Interactions effects with Group were found for all movement parameters when doing the full Gain × Angle × Navblock × Turnblock Repeated Measures ANOVA with Group as a between subject factor. Interaction effects with Group were found significant in the condition of gain 0.5 only, for all the movement parameters except the Mean Angular Velocity Error. This was investigated further by doing Turnblock × Navblock Repeated Measures ANOVAs for each group separately. Group A showed significant main effects of Turnblock, suggesting that the cost of switching gain was maintained during the whole experiment. Results supporting the Feedback Hypothesis are in dark grey cells. Group B showed interactions between Navblock and Turnblock, linked in at least two variables to an absence of Turnblock effect after the second navblock. This suggests a reduction in the cost of switching gain at the end of the experiment. Results supporting the Feedforward Hypothesis are in light grey cells.}

* P < 0.05. ** P < 0.01. *** P < 0.001.
1.5 as well for the mean velocity error. There was a reliable difference between the groups concerning the navigation block × turnblock interaction. In general, group A showed an effect of turnblock, but no interaction with the navigation block. The effect of turnblock, showing a difference between the first two blocks of turns but not between the second and the third, was maintained across the experiment. Group B, however, showed an interaction effect with the navigation block. The effect of turnblock, similar to the one observed in group A, was significant in the first and sometimes the second navigation block, and then disappeared.

A possible explanation of the difference between the groups might be that participants of group A were slower in adapting to the conflict gains, and the effect of turn block observed in those subjects could have disappeared over a longer period of adaptation. However, there was no interaction with group when looking at the effect of gain in the last group of turns of the last navigation block (compared to average gain 1), suggesting that all participants had adapted to the same level. Another possibility is that the two groups of subjects differed in their ability to associate contextual information to the adaptive states. Subjects in group B could use the contextual information and show no switch cost when the gain changes. Subjects in group A could not use the contextual information and needed an error feedback signal to make the switch between gains.

Lambrey and Berthoz (2003) observed differences between subjects in a paradigm using similar type of exposure to conflict. They observed that 5 subjects placed more weight on visual than non-visual information, while 5 other subjects placed more weight on non-visual than visual information. Lambrey and Berthoz suggested that subjects used conflicting visual and non-visual information differently according to individual “perceptive styles”. Such inter-individual variability has also been demonstrated in studies investigating the visual contribution to body orientation and postural balance (Collins and De Luca, 1995; Cremieux and Mesure, 1994; Isableu et al., 1997, 1998). Golomer et al. (1999) studied the degree of dependence on vision, for postural control and for perception, among male adult dancers and untrained subjects. They showed that professional physical training might shift the sensorimotor dominance from vision to proprioception. This study suggests that the more a sensory modality is used and/or useful, the greater its weight becomes. Individual sensory experiences could, therefore, be responsible for influencing “perceptive styles” in multisensory processing. In the present experiment, differences in “perceptive styles” could have enabled subjects of the group B to use more extensively the contextual visual information. Further studies comparing the use of different types of cues in such a paradigm would be interesting to investigate how “perceptive styles” might influence the strength of different types of contextual cue for different subjects.

Shellhamer et al. (2005) found in an experiment which imposed dual adaptation to two different saccade gains that 1-min rest breaks inserted between each change in context/adaptation state resulted in a dramatically improved context-specific adaptation. They suggested it resembled consolidation of motor learning, which, however, occurs over much longer time spans. Thus, the results may have reflected the operation of a novel “short-term” motor consolidation process. It would be interesting to implement such breaks in the current experiment to test whether this would improve the association of contextual information to adaptive states for all subjects.

Among the different types of movement analyses used in this experiment, the orientation at the peak of angular velocity seemed to be the measure that was most sensitive to the effect.

Fig. 6 - Experimental set-up. (a) The tracker position in the magnetic field is transmitted to the control unit which forwards information to the host computer. The computer then updates the images projected in the helmet as a function of the subject’s rotation movements. Vertical movements and horizontal translations are not taken into account. (b) Example of what a subject can see through the virtual reality helmet: corridor with striped walls and a 135° left turn at the end of the segment.
of conflict, as it showed a strong effect of the gain 1.5, which was found more weakly in the analysis of the peak of angular velocity and not found in the mean squared jerk data. However, the adaptation of this component of the movement seemed very fast for the gain 1.5, as no effect of turnblock was found in this condition. Thus, to study the variations of the switch cost during the experiment, the measure of mean angular velocity error seemed more adequate, as it showed similar effects for both gains, even though the error was generally smaller in gain 0.5.

The question of the possibility of maintaining context-dependent adaptation to two environments could find application in the domain of space research, as it would be a great advantage for astronauts to be able to learn and maintain the adaptation to different gravity and pressure environment, and be able to switch adaptive states as soon as they reached a new environment.

This field of research could be put in relation to task switching experiments. Rogers and Monsell (1995) observed in 1995 that the first trial after a task switch was slower than later trials, even when the switch was predictable and subjects had more than a second to prepare for it. They attributed this cost to a component of reconfiguration which would be triggered exogenously, i.e., only by a stimulus relevant to the task. It is the stimulus that enables the task set reconfiguration to be completed. This hypothesis was supported by results showing that switch-costs increased when there was an overlap between the stimuli of both tasks. In this respect, the model put forward by Rogers and Monsell resembles the stimulus-dependent dual adaptation, or feedback model.

The present experiment shows that dual adaptation to conflicts between visual and idiothetic and vestibular information is possible for active rotations of the whole body. This adaptation seems fast, but varies according to the type of conflict imposed on the subjects. Two groups of subjects were identified, whose movement data corresponded in one case to the feedback model proposed by Brown et al. (2002–2003) or stimulus-dependent adaptation (Young et al., 2003) and in the other case to the feedforward model or context-dependent adaptation. The results suggest that subjects differ in their use of contextual information, and this could be a reason for the variety of results found in the literature, where support for both models can be found. It seems that the use of contextual information in the switch between adaptive states could be depending on the “perceptive style” of the subjects. In the current experiment, the contextual cues were visual, so subjects relying preferably on visual information could learn to associate the contextual information to the adaptive states after a few alternations and then the contextual cues were sufficient for the switch of adaptive states. Subjects relying preferably on proprioceptive information may not have learned the contextual association, making visual feedback necessary for a change of adaptive state to occur. This would be consistent with the existence of a switch cost throughout the experiment.

4. Experimental procedures

4.1. Subjects and task

Nine subjects (3 females) who were not susceptible to sea-sickness participated in this experiment (23.6 years old, SD = 1.2). After hearing an explanation of the experiment, the subjects decided whether they wanted to volunteer. If they did, they provided written informed consent.

The participants stood in the middle of a safety hoop at waist level and wore a virtual reality helmet (Fig. 6a). Through this helmet, they viewed a virtual reality scene (a corridor), with an added linear motion as it occurs during walking at a normal speed. The participants performed a series of navigations in virtual corridors. Each navigation included 9 turns divided into 3 blocks of turns (turnblocks), each including a 45, a 90, and a 135° angle. The experimental protocol is shown in Fig. 7.

**Fig. 7** – Experimental protocol. On the left: subjects first performed 4 navigations with a gain of 1 in green corridors (white box); then they performed 24 navigations where the gain alternated between 0.5 and 1.5, and where the color of the corridors was associated with the gain (red or blue = grey or black box). These 24 navigations were divided into four blocks called navblocks. Finally, subjects performed two additional navigations (post-test) where the color of the corridors continued to alternate as before, but the gain was returned to 1. This aimed at testing the contextual cue association. In the middle: each navigation included 9 turns (α1–α9) divided into 3 blocks of turns (turnblocks), each including a 45, a 90, and a 135° angle. On the right, a map of one of the corridors is drawn.
speed (approximately 1 m/s). The scene showed in addition left and right turns of the corridor (Fig. 6b), for which subjects were asked to actively rotate their whole body. Thus, the task of the subjects was to stay still during linear segments of the corridor, and to rotate their body during turns, in order to maintain their position in the middle of the corridor, facing the direction of the linear motion imposed by the computer.

Normally occurring visual motion feedback during such turns would have a gain of unity, i.e., an $R^\circ$ body rotation is associated with an equal amount of visual motion in counter direction relative to the subject’s head, $-R^\circ$. In our experiment, the visual motion feedback was provided by the virtual reality head-mounted display and was set at a gain $(G) = 1$ (normal gain), 0.5, or 1.5. This can be summarized in the following equation: $R_{\text{V}} = -G \times R_{\text{R}}$, $R_{\text{V}}$ being the amplitude of the visual rotation provided by the helmet and $R_{\text{R}}$ the body rotation in the real world.

In the cases of gains 0.5 and 1.5, a sensory conflict between visual and kinesthetic and vestibular cues arises during the body turn. For instance, with an initially seen 90° rightward turn in the 0.5 visual gain condition, subjects would need to make only a 45° rightward turn to fulfill the visual criterion for a correct 90° turn, whereas one would require a complete 90° rightward turn to fulfill the proprioceptive and vestibular criteria for a correct turn. The software did not allow subjects to cross walls, and in the event of collisions, the trajectory ran along the wall.

4.2. Virtual environment

Four corridors were used in this experiment. For each, the graphic model consisted of a striped pattern on the floor, a plain colored ceiling, and black stripes evenly spaced on the walls (Fig. 6b). Each corridor consisted of 9 turns, divided into 3 sets of 45, 90, and 135° turns. The walls of the corridors could have three possible colors: green in the condition of gain 1, blue or red (counterbalanced) in the condition of gain 0.5 and 1.5.

The virtual reality apparatus included an LCD display (Kaiser Electro Optics’ Proview™ 60, Carlsbad, CA) which had a monocular field of view of 48° by 36° and was refreshed at 30 Hz. The refresh rate did not induce any noticeable flicker or eyestrain. The orientation of the subject’s head on the horizontal plane was measured by a magnetic system (Flock of Birds, Burlington, VT) with a report rate of 50 Hz, with an electromagnetic tracker of movement (Ascension Technology Corporation). The image generator (O2, Silicon Graphics) recorded the head angular position provided by the tracker and transmitted the corresponding image to the display, with a 30 Hz update rate.

4.3. Experimental protocol

Before the experiment, subjects were instructed not to move their head in relation to their trunk when turning, and to try to stay in the middle of the corridor. Subjects were provided with a contextual cue, the color of the walls of the corridors, which was not explicitly mentioned. A particular gain was always experienced in corridors of a particular color. Thus, it was possible for subjects to infer (consciously or not) what gain they would be exposed to, as soon as they entered a new corridor. We refer to a walk through a corridor as a navigation.

Subjects first performed 4 navigations (one in each of the corridors) with a gain 1, in green corridors. These four navigations served as a reference in the analysis. Subjects then performed 24 navigations where the gain alternated between 0.5 and 1.5, and where the color of the corridors was associated with the gain (red or blue). These 24 navigations were divided in 4 blocks, called navigations. Finally, subjects performed 2 additional navigations where the color of the corridors continued to alternate (red/blue) as before, but the gain was returned to 1. This aimed at testing the contextual cue association. Navigations were divided into 3 blocks of turns (turn-blocks), each including a 45, a 90, and a 135° angle (Fig. 7).

After every 6 navigations, subjects had a break lasting 5 min. The experimental session lasted approximately 2 h.

4.4. Data analysis

Raw data consisted of the head orientation in the virtual world over time. It was transformed into angular velocity over time via a fourth order Savitzky Golay filter with a mask width of 22. Derivatives of velocity including acceleration and jerk were calculated through numerical differentiation.

Fig. 8 – Examples of recordings of orientation and angular velocity. The data correspond, for each gain, to the first turn of the first navigation in corridor 2 by one of the subjects. The traces were aligned according to the peak of angular velocity (time 0 s). The top graph gives the orientation of the subject, while the bottom graph gives the angular velocity. Gain 0.5 is represented by full dots, gain 1.5 by empty dots, and gain 1 by squares at each data point. The peak of angular velocity was analyzed, as well as the corresponding value of orientation, which in a symmetric movement should amount to half of the complete rotation. These recordings correspond to an early time in the adaptation and the consequences of the gain imposed on the subject’s rotations can be observed. In gain 1.5, the angular speed was reduced compared to gain 1, and the subject underestimated the amplitude of the turn, as can be seen on the orientation plot. In gain 0.5, the angular speed was increased compared to gain 1, and the subject overestimated the amplitude of the turn, and had to perform at least four corrective sub-movements to reach the correct orientation.
It has been proposed, in particular for arm movements (Novak et al., 2002), that movements can be decomposed into chunks called sub-movements corresponding to small adjustments and/or corrections. In Novak and colleagues’ study, the movements were hand actions on a joystick. They could be decomposed into an initial primary movement sometimes followed by corrective sub-movements, when the amplitude of the primary movements was too large or too small. These corrective movements can be performed at the same time as the primary movement (overlapping) or after (delayed). When the primary movement is exact, it is not followed by delayed sub-movements. According to Novak et al., exact primary movements have characteristic stereotypic kinematics observed in other arm movement tasks: such movements are smooth and the velocity has a symmetric bell-shaped profile. We analyzed two turns with this approach, decomposing the angular velocity profile in peaks fitted by fourth order polynomial equations. This was used to give cues for the interpretation of the results of the other analyses.

Subjects' movement data were separated in each turn. It was then aligned to the peak angular velocity (time zero) and the analyses were performed over 200 measure points, i.e., 3.4 s before and after the peak (–7 s in total).

Different measures adapted from Novak et al.’s experiment (Novak et al., 2003) were used to monitor performance as the subjects adapted to the perturbations and then to monitor how subjects switched from one conflict condition to the other. These included the orientation at the peak of angular velocity, the peak of angular velocity (Fig. 8), the mean squared jerk, and the mean velocity error. The orientation at the peak of angular velocity should correspond to half of the complete rotation in the case of a symmetric movement. This measure can provide information on the primary movement. The peak of angular velocity was investigated to see if there were differences between the conditions and after adaptation. The mean squared jerk was calculated as one-half of the mean value of the squared jerk over the duration of the turn. The velocity error was computed by using a template for each subject corresponding to his mean velocity profile in gain 1, at each amplitude of rotation. The velocity error was the mean magnitude of the difference between the measured velocity and the velocity template at each turn.

4.5. Statistical analysis

Significant changes in movement parameters were determined with Repeated Measures ANOVA. In all cases, the distribution of the data was positively skewed so a logarithmic transformation was used. Reported means correspond to the exponential of the logarithmic means.

First, when possible, effects of navigation (first two navigations/last two navigations), turnblock, and angle were tested in logarithmic means.

With Repeated Measures ANOVA. In all cases, the distribution of the data was positively skewed so a logarithmic transformation was used. Reported means correspond to the exponential of the logarithmic means.

Significant differences in the means were evaluated with post hoc analyses using Bonferroni correction, correcting for the number of comparisons done for a given variable.

Acknowledgments

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REFERENCES


