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RESEARCH ARTICLE

Sensorimotor adaptation in response to proprioceptive bias

Pierre-Michel Bernier · Romeo Chua ·
J. Timothy Inglis · Ian M. Franks

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Abstract Studies investigating visuo-motor adaptation typically introduce sensory conflicts by manipulating visual information (prisms, cursor gains). The purpose of the present study was to determine whether similar adaptation would be observed when a conflict is created through distortion of the proprioceptive sense, rather than through visual distortion. We used a coordinated movement task that required participants to release thumb and index finger at a specific elbow angle during passive elbow extension. Participants could not see their arm, but were shown a cursor representing the forearm on a video screen. In the proprioceptive group, a sensory conflict was introduced by vibrating the biceps brachii muscle, introducing a discrepancy of approximately 7.5° between the proprioceptively perceived and visually perceived elbow angle. In the visual group, a conflict of similar magnitude was obtained by introducing a gain of 7.5° to the cursor with respect to forearm position. Adaptation was assessed by the presence of plastic changes in release elbow angles following a period of exposure to the sensory conflict (i.e., aftereffects). Both groups showed high accuracy during exposure despite the sensory conflicts. More importantly, the visual group presented large and persistent aftereffects, while the proprioceptive group presented none. We suggest that the proprioceptive group's lack of adaptation was due to the artificial muscle spindle activity resulting from vibration, which prevented visual and proprioceptive signals to be merged into a common frame of reference.

Keywords Visuomotor adaptation · Vision · Proprioception · Vibration · Muscle spindle

Introduction

Our ability to execute accurate reaching movements depends on complex sensorimotor transformations that translate an object's location from its retinocentric coordinates into the pattern of motor commands necessary to achieve it. Authors have investigated the flexible nature of these transformations by exposing participants to novel visuo-motor environments, using displacing prisms (Welch 1978; Redding and Wallace 2002), or rotated virtual displays of limb position (Krakauer et al. 1999). Performance is generally poor early in the exposure period. Over repeated trials, however, participants adapt to the novel visuo-motor mapping and often reach levels of performance similar to those of pre-exposure. This rapid compensation to the visual shift taking place during the exposure period, often ascribed to as the strategic component of prism adaptation (Redding and Wallace 1996), does not necessarily imply that a genuine realignment has occurred. Such realignment is rather assessed by removing the visual perturbation and having participants perform reaching movements to visual targets without visual feedback of the hand or knowledge of results. This typically leads to directional errors similar but opposite to those observed during the exposure phase. Only these "aftereffects", and not performance while wearing the

P.-M. Bernier · R. Chua · J. T. Inglis · I. M. Franks (✉)
School of Human Kinetics,
The University of British Columbia,
210-6081 University Boulevard, Vancouver,
BC, Canada, V6T 1Z1
e-mail: ifranks@interchange.ubc.ca

P.-M. Bernier
UMR Mouvement et Perception,
CNRS and Université de la Méditerranée, Marseille, France

prisms, reveal that a plastic change took place in the transformation between visual-motor coordinates and proprioceptive-motor coordinates (Redding et al. 2005).

Most authors emphasize the importance of detecting a sensory misalignment as mediating adaptation. For example, Guédon et al. (1998) investigated the adaptive capacities of a deafferented patient, and found that aftereffects were almost nonexistent for the patient. They suggested that this absence of plastic changes would result from the fact that no discrepancy between visual and proprioceptive modalities can be detected by such patients. Similarly, Redding and Wallace (2002) showed that the detection of a conflict depends upon the comparison of a command signal and the achieved position, and that a coordinative remapping would not occur under situations in which these signals are not different.

A common feature in studies investigating visuomotor adaptation is that the discrepancy between sensory modalities is introduced by manipulating visual information. Hence, it is unclear whether similar recalibration would occur when a conflict is created through distortion of the proprioceptive sense, rather than through visual distortion. The goal of the present study was to address this issue by comparing adaptation to a proprioceptively induced and a visually induced sensory conflict.

We used a coordinated movement task requiring participants to release two fingers at a specific elbow angle during elbow extension. In experiment 1, participants were not permitted vision of their forearm, but instead were provided with vision of a virtual forearm on a monitor. In the proprioceptive conflict condition, we used tendon vibration to introduce a discrepancy between the proprioceptively perceived and visually perceived location of the effector. In the visual conflict condition, a conflict of similar magnitude was obtained by introducing a gain to the cursor with respect to forearm position. Adaptation was assessed by the presence of plastic changes in the participants' release elbow angle following removal of the perturbation in a posttest (i.e., aftereffects). Also reported in the present report is a second experiment in which vision of the virtual forearm was not permitted during the movement, but only following movement completion.

Experiment 1

Materials and methods

Participants

A total of 16 right-handed (4 males, 12 females; 24 ± 2.1 years) participants took part in experiment 1. All were naïve to the hypothesis being tested and those in the proprioceptive group were not told about the specific illusory effects of tendon vibration. The study was conducted in accordance with the ethical guidelines set by the University of British Columbia.

Apparatus

Participants were seated on a height-adjustable chair in front of a horizontally rotating servo-controlled manipulandum, used to passively extend the right elbow. The task was to release thumb and index finger as the elbow rotated through a prescribed target angle. Position information of the servo motor (Mavilor DC Servo Motor MT–600) was measured by an optical encoder giving 10,000 counts per revolution. Finger release was measured using a fingertip switch made from two pieces of thin copper sheet metal attached to the participants' index finger and thumb with double-sided tape.

Procedure

While seated at a table, participants faced a video monitor, and an opaque screen covered the right arm (see Fig. 1). This setup allowed participants to see a cursor representing the forearm on the monitor but prevented them from seeing their actual arm. The monitor was positioned 1 m in front of participants. Motion of the forearm was represented by a red line (from herein called "cursor"; 2 mm in width and 25 cm long) rotating around a virtual elbow joint in a circular movement trajectory. Stationary black lines perpendicular to motion of the cursor indicated the target angles. The elbow was flexed at 90° at the starting position and passively rotated through one of three targets to a final angle of 160° (180° representing full elbow extension). The targets were presented in random order to prevent the implementation of stereotyped responses. They were located at 125°, 135° and 145° of elbow angle. Thus the distance from the starting angle to the target angle was 35°, 45° or 55°. The forearm was strapped into position on the manipulandum with the upper arm positioned 30° from horizontal. This restricted the movement mainly around the elbow joint, which was rotated at a constant velocity of 22°/s. Before every trial, a target appeared, concurrent with the sound of a tone. This informed participants that movement would begin in 2 s. The elbow was then passively extended until 1 s after finger release. Immediately on opening of the hand, the cursor stopped moving and turned from red to white. Following a trial, the arm was brought back to the starting position at a velocity of 10°/s.

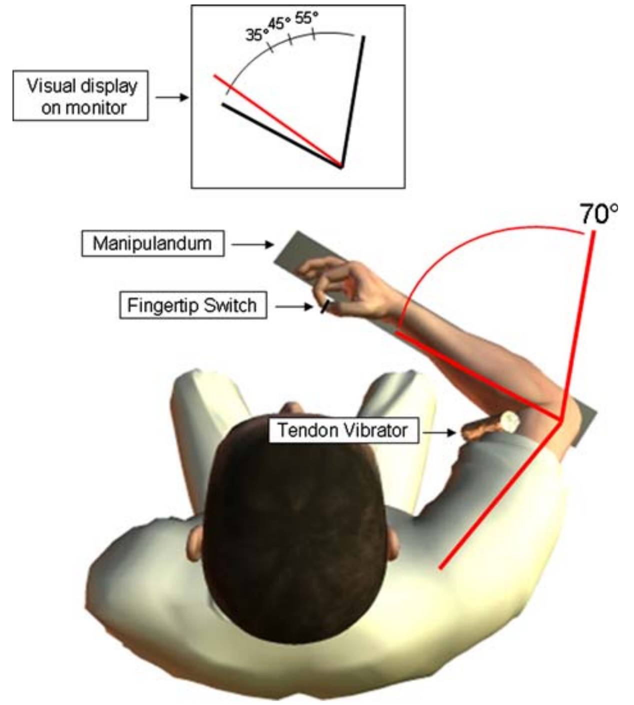


Fig. 1 Overhead view of the setup. The participant's right forearm rested on a manipulandum used to passively extend the elbow. A tendon vibrator was fixed over the right biceps brachii tendon, and a fingertip switch was used to measure the moment of finger release. Note that an opaque screen covered the arm. *Inset*: visual feedback of target and cursor shown on monitor (not to scale)

Consecutive trials were always separated by a minimum of 14 s.

Participants took part in three experimental phases: a pre-test, an adaptation phase and a post-test. Prior to data collection, participants completed a practice session to familiarize themselves with the task, in which their arm was passively moved out and back ten times, with vision of the cursor. No targets were present in the practice session; hence no finger release was performed. Following this, participants took part in a pre-test. For the proprioceptive group, the pre-test consisted of ten trials performed without vibration (pre-test 1), immediately followed by ten trials with vibration (pre-test 2). This allowed us to evaluate the magnitude of the proprioceptive shift induced by vibration for every participant. The pre-test was identical for the visual group, with the exception that vibration was not applied on pre-test 2. For both groups, only the 45° target was used during the pre-test, and all movements were executed without vision and knowledge of results. In the adaptation phase, participants performed 45 trials (15 towards each of the three targets presented randomly) with full vision of the cursor during the movement. For the proprioceptive group ($n = 8$), vibration was applied on every trial during this phase. Similarly, for the visual group ($n = 8$), the cursor gain was present on every trial during this phase. Finally, all participants took part in a post-test, which was identical to the pre-test. That is, the proprioceptive group performed ten trials without vibration (post-test 1), immediately followed by ten trials with vibration (post-test 2), while the visual group performed both post-test 1 and post-test 2 without vibration. Again, only the 45° target was used, and all movements were executed without vision or knowledge of results.

Proprioceptively derived conflict (proprioceptive group)

The proprioceptive conflict was induced through vibration of the right biceps brachii muscle. We used a custom tendon vibrator, consisting of a low voltage DC motor with a rotating counterweight in a cylindrical plastic case, which was positioned over the biceps brachii tendon. The vibrator was controlled through an adjustable power supply to provide a 90 Hz pulse with peak-to-peak amplitude of 2 mm. This vibratory frequency has previously been shown to evoke strong lengthening illusions in antagonist muscles (Inglis and Frank 1990). Vibration was applied on initiation of movement and continued for 1 s after finger release.

Visually derived conflict (visual group)

The visual conflict was created by the introduction of a gradual gain to the cursor with respect to forearm position. Importantly, in order to validate any comparison between the groups, we had to make sure that the magnitude of the visual conflict be similar to that of the proprioceptive conflict. Hence, we purposely collected the proprioceptive group's data prior to that of the visual group. We then calculated the magnitude of the proprioceptive shift experienced by that group (i.e., 7.5°; see Results section), allowing us to determine the required magnitude of the visual gain that would be given to the visual group. Specifically, the cursor gain we introduced was such that it would lead the forearm by 7.5° when reaching the target. The cursor gain was introduced gradually only during the initial 15° of elbow rotation. This was done by moving the cursor at a constant angular velocity of 33°/s during the first 0.68 s of the movement (i.e., until the forearm, being moved at a velocity of 22°/s, had traveled 15°). From 15° of elbow rotation to the end of the movement, both the forearm and the cursor moved at a constant velocity of 22°/s, with the cursor leading the forearm by 7.5°.

Analysis

The elbow angle at which participants released the fingers was recorded. Undershoots were expressed as negative errors, while overshoots were expressed as positive errors. Constant errors (for each participant) as well as variable errors (intra-individual standard deviation values for each participant) were calculated for each experimental phase. In order to assess the presence of aftereffects for both groups, we compared the constant errors at finger release in the pre-test (pre-test 1, pre-test 2) to those in the post-test (post-test 1, post-test 2). For the analysis, we also included the last ten trials from the adaptation phase. Importantly, we chose to use only the last ten trials from the adaptation phase that were directed towards the 45° target (from herein called "Late Adaptation"). This caution was driven by the fact that the pre- and post-tests were solely directed towards that target. This resulted in a 2 (group) × 5 (phase) repeated-measures ANOVA.

Results

We first assessed the magnitude of the shift in perceived arm position induced by vibration for the proprioceptive group. This was done by comparing the average elbow angle at hand opening during pre-test 2 (with vibration) to that of pre-test 1 (without vibration). On average, participants released the fingers 7.2 ± 3.8° earlier in pre-test 2 than in pre-test 1. The effect of vibration was also observable in the post-tests, as the difference between post-test 2 and post-test 1 was 7.6 ± 5.0°. From these data we estimated the proprioceptive shift to be approximately equal to 7.5°, which is the magnitude of the conflict we induced to the visual group.

The average course of adaptation to the bias is shown in Fig. 2 for the proprioceptive group and in Fig. 3 for the visual group. The data represent the angular constant error at finger release. Clearly, both groups adapted very quickly to the bias, as expressed by their ability to perform accurately on the first trial of the adaptation phase.

These constant error data were submitted to a 2 (group) × 5 (phase) repeated-measures ANOVA. The interaction was significant [$F(4,56) = 6.8$, $P < 0.001$; Greenhouse-Geisser adjusted]. Post hoc analysis (Tukey's LSD; $P < 0.05$) revealed that vibration caused the proprioceptive group to release the fingers significantly earlier in pre-test 2 and post-test 2 (with vibration) than in pre-test 1 and post-test 1 (without vibration), respectively. More importantly, however, no aftereffects were present for this group, as the mean elbow angles at finger release were not significantly different between pre- and post-tests. A different picture emerged for the visual group, for which the release angles were found to be significantly lower in Late Adaptation, post-test 1 and post-test 2 than in both pre-test 1 and pre-test 2. Furthermore, the opening angles in post-test 1 and post-test 2 were not significantly different than in Late Adaptation. Hence this suggests the presence of aftereffects that persisted during the entire course of the post-test.

Finally, we wanted to confirm that vibration was not causing a disruption of proprioceptive sense, but was simply shifting participants' perception of limb position. Hence we compared the proprioceptive group's variable error (i.e., intra-individual variability) in the pre-test to that in the post-test (see intra-individual standard deviation values in Table 1). The variable error data were submitted to a 4 (phase) repeated-measures ANOVA which revealed a main effect [$F(3,21) = 3.3$, $P < 0.05$]. Surprisingly, post hoc analysis revealed that variable error in post-test 2 (with vibration) was significantly lower than that in pre-test 1 (without vibration). No other comparison was significant. Note that this analysis was not performed for the visual group because they were not exposed to vibration.

Discussion

The purpose of experiment 1 was to determine whether a sensory conflict induced through proprioceptive distortion would lead to a recalibration similar

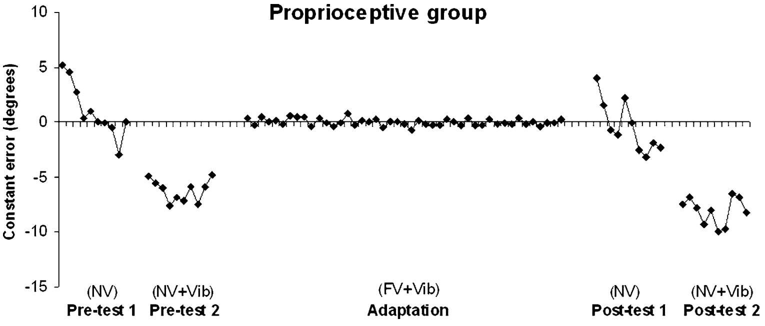


Fig. 2 Constant error in elbow angle at finger release for the proprioceptive group during the pre-test, the adaptation phase, and the post-test. Labeled above the experimental phase is the visual condition (*NV* no vision, *FV* full vision) and the presence of vibration (*Vib* vibration)

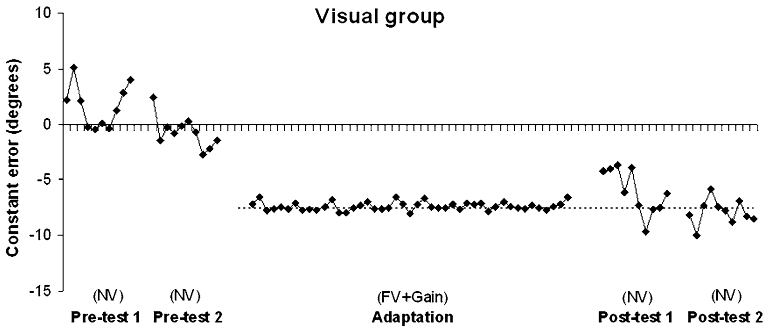


Fig. 3 Constant error in elbow angle at finger release for the visual group during the pre-test, the adaptation phase, and the post-test. Labeled above the experimental phase is the visual condition (*NV* no vision, *FV* full vision) and the presence of a cursor gain (gain = cursor gain) [note that because of the cursor gain, participants had to release the fingers 7.5° prior to reaching a target in order to correctly align the cursor with the visual target (indicated by the *dotted line* at −7.5°)]

to that observed when visual feedback is manipulated. During the adaptation phase, participants in the proprioceptive group were provided with online visual feedback of their movement while being vibrated on every trial. Despite vibration, this group showed very high levels of accuracy throughout that phase. As suggested by Pisella et al. (2004), this was likely due to online visual guidance. Importantly, vibration created the illusion that the elbow was extended approximately 7.5° further than its visually perceived position (see Results section). Of interest was whether participants correctly associated the visually perceived target angle to the appropriate proprioceptively derived elbow angle. Had this occurred, we would have expected participants to systematically overshoot the target by about 7.5° in post-test 1, while showing error levels near 0° in post-test 2 (aftereffects). Clearly this was not the case, as this group immediately reverted to its pre-exposure levels, even on the first trial of post-test 1. A different picture emerged for the visual group, for which a sensory bias was created by introducing a gradual gain to the cursor with respect to forearm position. Participants in this group were very accurate during the period of exposure, but most importantly, they presented large and persistent aftereffects in the post-test.

A potential explanation for the absence of aftereffects for the proprioceptive group might be due to the labile nature of the vibratory illusion. In fact, it is thought that vibratory illusions of limb position might disappear when vision of the limb is also permitted (Roll et al. 1980). This was the case for the proprioceptive group during the adaptation phase, as participants in this group were seeing a representation of their vibrated limb. Hence there was a distinct possibility that participants attended to the cursor, disregarding proprioceptive signals. A visuo-proprioceptive conflict might not have been registered, leading to an absence of aftereffects. To test this hypothesis, we undertook a second experiment in which vision of the cursor was not provided during the movement, but only after movement completion as a form of knowledge of results (proprioceptive-no-vision group). This condition would force participants to rely solely on proprioceptive signals to indicate the moment of finger release. Since vibration was still applied during the movement, participants needed to monitor the sensory conflict and modify their proprioceptively derived elbow angle at finger release to perform the task accurately.

Experiment 2

Methods

Participants

Eight right-handed participants (4 males, 4 females; 23 ± 3.5 years) took part in experiment 2.

Table 1 Constant error in elbow angle at finger release for the proprioceptive group, the visual group and the proprioceptive-no-vision group during the pre-test and post-test (degrees)

	Pre-test 1	Pre-test 2	Pre-test 1	Pre-test 2
Proprioceptive group	1.0 ± 4.5	−6.2 ± 3.6	−0.4 ± 3.8	−8.1 ± 3.0
Visual group	1.3 ± 4.9	−0.7 ± 4.1	−6.0 ± 3.9	−7.9 ± 3.2
Proprioceptive-no-vision group	−5.0 ± 4.1	−12.0 ± 3.3	0.3 ± 4.6	−7.9 ± 4.6

Values are mean constant errors ± mean intra-individual standard deviations

Apparatus

The apparatus was identical to that used in experiment 1.

Procedure

The task was identical to the one used for the proprioceptive group in experiment 1, the only difference being that in the adaptation phase, participants were not given vision of the cursor during the course of the movement, forcing them to rely on proprioception to indicate the moment of finger release. Instead the cursor only appeared following movement completion to indicate the angle at which the fingers were released. Hence this provided participants with a visual indication of where they opened the hand in relation to the target angle. The cursor appeared immediately upon finger release in the form of a static line positioned exactly where the fingers were released. It consisted of a white line (2 mm in width and 25 cm long), and was presented for 1 s following hand opening.

Proprioceptively derived conflict (proprioceptive-no-vision group)

Identical to the proprioceptive group in experiment 1, the sensory conflict in experiment 2 (proprioceptive-no-vision group) was induced through vibration of the right biceps brachii muscle. We used the same tendon vibrator which provided a 90 Hz pulse with peak-to-peak amplitude of 2 mm.

Analysis

The dependent measures were identical to those of experiment 1.

Results

The proprioceptive-no-vision group initially presented an undershoot bias, releasing on average 5.0° prior to reaching the target in pre-test 1. Nonetheless, the influence of vibration on the perception of limb position was very consistent with that witnessed in experiment 1. In fact, participants released the finger 7.0° ± 2.3° earlier in pre-test 2 than in pre-test 1. The same trend was present in the post-test, where the finger release occurred 8.1° ± 3.0° earlier in post-test 2 than in post-test 1.

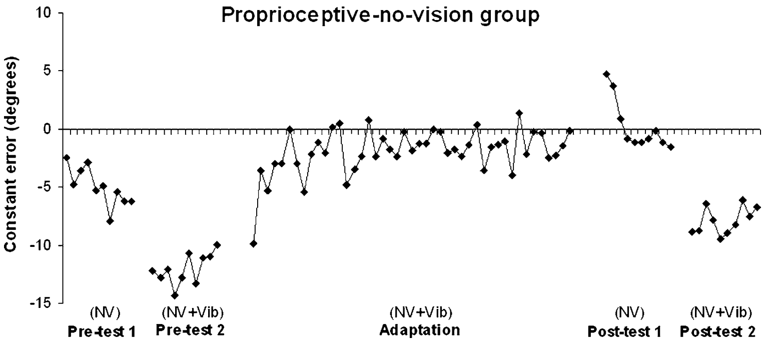
The time course of adaptation for the proprioceptive-no-vision group is presented in Fig. 4. Not surprisingly, vibration caused participants to largely undershoot the target early in the adaptation phase. This can be attributed to the absence of vision of the cursor on the monitor, preventing participants from visually guiding the cursor to the target. Instead, this task forced participants to estimate limb position on the sole basis of proprioception to signal the moment of finger release, rendering them sensitive to the illusion. Nonetheless, knowledge of results was provided after every movement, allowing participants to gradually improve their performance throughout that phase of the study. Hence they were able to release the fingers within 2°–3° of the target despite vibration in the late stages of the adaptation phase. To assess the presence of aftereffects, a 5 (phase) repeated-measures ANOVA was performed on the constant error data, revealing a main effect [$F(4,28) = 11.3$, $P < 0.001$; Greenhouse-Geisser adjusted]. Post hoc analysis (Tukey's LSD; $P < 0.05$) revealed that this group released the fingers significantly earlier in pre-test 2 and post-test 2 than in pre-test 1 and post-test 1, respectively. Furthermore, the release angles in Late Adaptation were significantly greater than in pre-test 2 and post-test 2. More importantly, similar to the proprioceptive group in experiment 1, no aftereffects were present as the opening angles were not different between pre- and post-tests. Despite the absence of statistical significance, it appears from visual inspection of Fig. 4 that the post-test values are shifted with respect to the pre-test values. However, this apparent shift is most likely due to sampling error, as six out of eight participants of this group had an undershoot bias in the pre-test, pulling the baseline levels down.

We finally compared the intra-individual variability in the pre-test to that in the post-test (see intra-individual standard deviation values in Table 1), to confirm that vibration was not causing a disruption of the proprioceptive sense. The variable error data were submitted to a 4 (phase) repeated-measures ANOVA which was not significant ($P = 0.3$). Hence in line with the findings of experiment 1, the vibratory stimulus did not result in a loss of proprioceptive acuity, but rather introduced a consistent shift.

Discussion

The purpose of experiment 2 was to test the hypothesis that the absence of aftereffects found for the proprioceptive group in experiment 1 was due to fact that this group did not register a sensory conflict during adaptation. Vision of the moving limb might have greatly attenuated the illusory effects of vibration, leading to

Fig. 4 Constant error in elbow angle at finger release for the proprioceptive-no-vision group during the pre-test, the adaptation phase, and the post-test. Labeled above the experimental phase is the visual condition (*NV* no vision) and the presence of vibration (*Vib* vibration)



the lack of sensory recalibration. Hence we devised a second experiment (proprioceptive-no-vision group) in which no vision of the cursor was permitted during the course of the movement in the adaptation phase, forcing participants to attend to proprioception of the limb. Using a similar task, Cordo et al. (1994) confirmed that in the absence of vision, participants do use proprioceptive information related to velocity and position of the elbow to trigger the hand opening.

The results of the proprioceptive-no-vision group corroborate those of the proprioceptive group (experiment 1) in the sense that there were no aftereffects following the period of exposure to vibration. This might appear counter-intuitive as participants did show a capacity to release the fingers with relative accuracy (within 2°–3° of the target) late in the adaptation phase despite the absence of vision. This suggests that they attended to proprioceptive feedback and correctly associated the visually defined target angles with their corresponding proprioceptive signals. Nonetheless their performance rapidly decayed in the post-test and reverted to near pre-exposure levels. This is especially surprising considering that the sensory modality (i.e., proprioception) relied upon to perform the task accurately in the adaptation phase was the same as in the pre- and post-tests. In fact, post-test 2 was performed in identical conditions as the adaptation phase (with vibration but without vision), with the only difference being that knowledge of results was provided following trials in the latter but not the former phase. Our findings thus provide evidence that the proprioceptive control of a coordinative sequence task decays if not "refreshed" by knowledge of results. Part of this decay might be attributable to the vibratory stimulus. As such, it is known that sensory information is a necessary substrate for the establishment of a memory trace that emerges from practice (Cruse et al. 1990). In this regard, Fleury et al. (1999) measured the retention capacities of a deafferented patient in a coincidence-anticipation task. It was found that the retention interval resulted in a greater deterioration in spatial accuracy for the patient than for control participants, suggesting that the absence of proprioception does not allow the establishment of a durable mnemonic trace. By extension, it is also possible that vibration interfered with the development of strong memory trace during exposure, leading to the decaying aftereffects in our study.

General discussion

While adaptation to visually derived conflicts has been widely investigated, to our knowledge this constitutes the first account of adaptation to a proprioceptively derived conflict. Our data indicate that aftereffects only occurred in response to a change in visual gain, but not in response to a proprioceptive shift. Importantly, this was observed despite the fact that the magnitude of the sensory conflict was similar for the visual and proprioceptive groups. It suggests that adaptation does not simply result from detecting a conflict between sensory modalities, but that it is mediated by the nature of that conflict.

One could argue that the absence of aftereffects for the proprioceptive groups stems from the distorting effect of the vibratory stimulus. Vibration might have rendered proprioceptive input unreliable, rather than inducing a consistent directional shift in the participants' perception of limb position. However, our analysis of variable error does not support this hypothesis. Specifically, we compared the intra-individual standard deviations in elbow angle at finger release in the pre-test and post-test. We hypothesized that if vibration did render proprioceptive input unreliable, then participants should have been more variable in pre-test 2 and post-test 2 (both *with* vibration) than in pre-test 1 and post-test 1 (both *without* vibration). This was not the case, as participants of both proprioceptive groups actually showed lower variability when vibration was present than when it was not (see intra-individual standard deviation values in Table 1). These results corroborate those of Inglis and Frank (1990), who also did not find differences in intra-individual standard deviation values across vibratory conditions. Consistent with our position, these authors concluded that vibration led to a directional effect on position sense rather than to a loss of limb position sense.

This interpretation raises an interesting question. If the altered proprioceptive input had a major perceptual influence, then why was it not merged with the visual signals to produce persistent adaptation? One possibility is that by introducing some level of artificiality in the muscle spindles' signal, vibration might have prevented the sensory error detection process to take place, which constitutes a crucial step for adaptation to occur. To that matter, microneurographic studies have revealed that the natural discharge pattern of muscle spindles is highly specific, accurately representing velocity as well as static and dynamic positions of the joints (Vallbo 1974). In response to a stretch, spindles first produce a brief, high-frequency "initial burst" (Cordo et al. 2002), which is followed by a pause and a gradual increase in firing rate ("ramp increase") as a function of position (Houk et al. 1981). Cordo et al. (2002) showed that the peak firing rate of the initial burst codes for the starting position of movement with a precision comparable to that of the ramp increase. This highlights an important feature of movement-evoked activity, namely that the muscle spindles' firing rate constantly changes with respect to muscle length and rate of change of muscle length. This information is lost when vibration is applied. By being a powerful stimulus of activity in primary afferents, vibration entrains the spindles' discharge rate (Roll and Vedel 1982). Thus, the firing pattern of a subpopulation of receptors becomes "locked" to the vibratory frequency. For instance, stimulating a tendon or a muscle at 80 Hz synchronizes a substantial part of the receptor population to a frequency of 80 Hz. In turn, these entrained muscle spindles become occluded to other forms of stimulation (Calvin-Figuière et al. 1999), such that they can no longer code for movement through their firing pattern (Roll et al. 1989). Although we did not record the actual firing rates of spindles in the current study, our vibratory stimulus produced large perceptual effects. Hence we are confident that at least a subpopulation of muscle spindles' signal reaching the brain was being altered by vibration. It is therefore plausible that this artificial sensory inflow prevented the proper merging of the signals of both modalities. This process is thought to take place in the posterior parietal cortex (PPC), which receives efferent input from the motor commands (Kalaska et al. 1983), as well as proprioceptive and visual input from the performed movement (Rushworth et al. 1998). Its role would be particularly important in the early acquisition of a visuo-motor transformation, allowing the establishment of stable relationships between sensory cues, which are coded in different coordinate frames. The detection of a sensory discrepancy would ultimately lead to the development of an internal model in the cerebellum, whose activity is thought to increase during learning of a visuo-motor transformation (Graydon et al. 2005). One potentially crucial premise for this sensory matching process to occur is that the sensory signals be realistic (hence meaningful). Obviously, this was not the case of at least a portion of the muscle spindles' firing pattern in the present study. This might have prevented the merging of the arm-related visual signals with the flow of arm-related proprioceptive signals into a common frame of reference, hence making adaptation impossible. Similar findings were recently reported by Pipereit et al. (2006), who investigated sensorimotor adaptation while concurrently vibrating antagonist muscles. Interestingly, they found that adaptation to a mechanical perturbation was considerably impaired by vibration, and concluded that this could be due to the fact that vibration masked the spindles' signal. In line with our position, this proprioceptive degradation would have affected the multisensory representation of the body that is thought to be represented in the parietal cortex (Maravita et al. 2003).

Despite the fact that muscle spindles have long been thought to be the main sensory component of the motor system, it is known that movement kinematics are derived from the *ensemble* of afferents responding to joint position (Verschueren et al. 1998). In fact, any contribution of muscle spindles from synergist muscles to the biceps brachii (such as the brachioradialis) as well as Golgi tendon organs, joint receptors and cutaneous receptors, cannot be ruled out. To that matter, it has been shown that cutaneous receptors are capable of conveying high-fidelity information (Edin 1992) and play a significant role in proprioception and motor control even at distant limbs such as the elbow and the knee (Collins et al. 2005). Similar to muscle spindles, the firing patterns of cutaneous receptors located directly underneath the vibrator is influenced by the stimulus. However, joint motion is accurately represented by activity from receptors located on a wide perimeter around the joint (Edin 2001). Hence it is likely that an important part of these receptors was unaffected by vibration and kept providing the CNS with genuine limb position information despite vibration. This pattern of activity, consistent with the actual position of the limb and concordant with its visually derived position, might have prevented any sensory remapping from being required.

A long-standing debate in the visuo-motor adaptation literature has been concerned with the underlying sensory mechanisms that mediate the presence of aftereffects, which are thought to result from spatial adjustments in eye–arm coordination (Welch 1978; Redding and Wallace 1997). In the present study we did not perform the classical tests used in the prism literature (i.e., proprioceptive straight-ahead, visual straight-ahead) that have been used to tease out whether the aftereffects are of visual or proprioceptive nature. Hence the current data do not allow us to come to a firm conclusion on that matter. Nonetheless, the availability of continuous visual feedback during movement typically leads to proprioceptive recalibration. It is thus plausible that the visual group's aftereffects likely resulted from a change in the relationship between a visually derived arm posture and its corresponding muscle spindle signal during the movement (Baraduc and Wolpert 2002). Still, it should be noted that passive movements are generally thought to be non-conducive of such spatial realignment (Held and Hein 1958; Held and Bossom 1961), although some have shown that passive exposure can still produce significant adaptation (Pick and Hay 1965). Despite these considerations, one should keep in mind that the theoretical framework in which prismatic adaptation is understood may not be directly applicable to the study of adaptation to computer-generated representations of limb position, such as in the present study (Clower and Boussaoud 2000). For example, the integration of visual and proprioceptive cues is thought to be influenced by the perception of a physical coincidence between the limb and its representation, which is typically the case with prisms but not in the present task (Carey and Allan 1996; Lackner and Shenker 1985). Still this does not lessen the main finding of the present study, namely that a sensory conflict induced through tendon vibration did not lead to adaptation similar to when a conflict is introduced visually.

In conclusion, while the flow of entrained muscle spindle activity shifted participants' perception of limb position, it prevented multisensory integration processes to take place.

These results suggest that a dissociation might exist between the proprioceptive signals mediating perception and those mediating visuo-motor transformations, and highlight the need to discriminate between various levels at which these signals are processed.

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