

CALIBRATION OF PROPRIOCEPTION

By

PIERRE-MICHEL BERNIER

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Abstract

Although proprioceptive information allows accurate perception of limb movement in the absence of vision, its exact contribution to position coding when vision is also available is still debated (Gandevia et al., 1992). One view is that proprioceptive input would play a relatively minor role when vision is present (Hay et al., 1963). In fact, some have suggested that the processing and calibration of proprioceptive feedback would be masked by the processing of visual feedback (Tremblay and Proteau, 1998). The purpose of this thesis was to use a visuomotor adaptation paradigm to assess whether proprioception is concurrently calibrated with vision during visually guided movements.

In Experiment 1, a full vision group (FV) was given vision of a cursor representing hand position and was asked to aim towards visible targets. A no vision group (NV) performed the same task without vision of the cursor and was given knowledge of results (KR) after movement completion. A visual bias was introduced between the location of the cursor and the location of the hand in an adaptation phase, which resulted in participants deviating to the right of the intended target. Of interest was whether participants would still show rightward deviations in a post-test series of trials in which vision was removed (i.e. aftereffects). The NV group presented strong aftereffects. However, the FV group only showed modest aftereffects early in the post-test, which rapidly decayed over the course of the post-test. This suggests that proprioception was not calibrated when vision was concurrently available, and further analyses showed that the presence of those early aftereffects was rather due to an offline influence of vision on movement planning.

A similar protocol was used in Experiment 2, but instead of inducing a visual bias, a sensory conflict was rather created through distortion of the proprioceptive sense by means of tendon vibration. Participants were asked to release two fingers at a specific target angle while the right elbow was passively extended. The vibration created a discrepancy between the proprioceptively perceived and visually perceived location of the effector. In an adaptation phase, participants performed with full vision (FV group), or with only terminal KR (NV group) while being vibrated on every trial. Any recalibration of the sensory modalities would be expressed by the presence of significant overshooting following the removal of visual feedback and vibration in a post-test phase (i.e. aftereffects). Both groups showed aftereffects early in the post-test, but these decayed very quickly, such that participants rapidly resorted to their pre-exposure levels. We propose that a sensory recalibration took place for both groups, but that the passive nature of the task prevented persistent aftereffects from occurring.

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General Introduction

Proprioception is an important source of information used in movement planning and control. It has long been known to mediate spinal and cortical reflexive loops, either regulating the mechanical properties of muscles (Stein, 1982) or correcting for the effects of perturbations to movement trajectories (Marsden et al., 1976). It is also widely recognized that proprioception is necessary for movement planning by mediating the learning of internal models (Krakauer et al., 1999). In the absence of vision, proprioceptive feedback also contributes to the conscious coding of position and movement (Prochazka and Gorissini, 1998). However, its exact contribution to position coding when vision is also available is still debated (Gandevia et al., 1992). In fact, much evidence has been gained regarding the fact that proprioceptive information might play a relatively minor role when vision is present (Hay et al., 1963). Proponents of the specificity of practice hypothesis (Proteau, 1992) even suggest that this type of feedback would not be processed during visually guided aiming movements.

The Sense of Proprioception

The sense of proprioception consists of the integrated signal provided by an ensemble of receptors that inform the CNS about the position and movement of the limbs (Verschueren et al., 1998). This comprises cutaneous receptors, joint receptors, Golgi tendon organs and muscle spindles. Muscle spindles are thought to be the main sensory component of the motor system, contributing to the conscious awareness of limb kinematics (Goodwin et al., 1972). Specifically, the CNS would extract information regarding muscle length (and its related variable joint angle) mostly from muscle spindle

primary and secondary afferents. Microneurographic studies have revealed the importance of muscle spindles by showing that their firing patterns accurately represent velocity as well as static and dynamic positions of the joints (Vallbo, 1974). In static conditions, individual muscle spindles are thought to code for position through their steady-state firing rates (Botterman and Eldred, 1982), presenting a linear function between impulse frequency and joint angle in relaxed muscles. This simple relationship gets more complex when a position is actively achieved. This is due to the fusimotor drive that accompanies an active position holding, changing muscle spindle output in a way that abolishes position response of muscle spindles in the agonist (Vallbo et al., 1981). In fact, at moderate and fast velocities, spindles from an actively shortened muscle can even fall silent (Prochazca et al., 1979). This has led some authors to suggest that a greater role was played by the antagonist muscle not submitted to a fusimotor drive in providing position information to the CNS (Inglis and Frank, 1990).

Typically, when lengthened, a muscle spindle first produces a brief, high-frequency burst, called "initial burst" (Cordo et al., 2002). This is followed by a pause and a gradual increase in firing rate ("ramp increase") as a function of position (Houk et al., 1981). The peak firing rate of the initial burst represents the starting position of movement with a precision comparable to that of the ramp increase (Cordo et al., 2002). Although the discharge pattern of a single muscle spindle is potentially complex enough to represent both velocity and position of the joint (Houk et al., 1981), there is now much evidence suggesting that those kinematics are derived from the ensemble of afferents responding to joint position. For example, it has been demonstrated (Cordo et al., 2002) that there is a very limited range of wrist joint angles at which individual muscle spindles

are position sensitive (15° on average over the entire 110° of wrist positions), suggesting that positional information used by the CNS is primarily based on the pattern of afferent recruitment rather than the firing patterns of individual receptors.

Tendon Vibration

The importance of muscle spindle input in the sense of proprioception has also been evidenced by the characteristic illusions evoked by tendon vibration. This technique has been used in the isometric limb to study the perceptions of position and velocity (Sittig et al., 1987) and in the moving limb to study endpoint control (Inglis and Frank, 1990; Inglis et al., 1991). Tendon vibration is known to be a powerful stimulus of activity in primary afferents by entraining their discharge rate (Roll and Vedel, 1982). Muscle spindle secondary afferents are less sensitive to vibration, and tendon organ Ib afferents are generally insensitive to vibration (Roll and Vedel, 1982). Vibration (1 to 100 Hz) applied over a muscle excites a subpopulation of muscle spindles, “locking” their firing pattern to the vibrating pattern, and thereby occluding those receptors to other forms of stimulation (Calvin-Figuière et al., 1999). During vibration, afferents insensitive to vibration and those only partly entrained continue to respond to natural forms of mechanical stimulation, such as joint rotation and muscle contraction (Roll et al., 1989). The artificial increase of primary input creates the illusion that the vibrated muscle is being stretched, resulting in an illusory limb movement corresponding to a joint rotation stretching the vibrated muscle. The nature of this interaction was initially thought to result from a *summation* of vibratory-evoked activity in proprioceptive afferents along with movement-evoked activity associated with static stretch of the muscle or with

increasing muscle length during slow movement (Sittig et al., 1985). This was supported by the finding that increasing the frequency of vibration increased the perceived displacement and velocity of rotation (Sittig et al., 1985, 1987). However, other effects of vibration, such as the illusion of muscle shortening evoked by low-frequency vibration on isometric joints, could not be explained by such a straightforward summation. Rather, it seems more likely that the influence of vibration results from an *interaction* between movement-evoked and vibration-evoked proprioceptive activity. As such, Cordo (1995) proposed that it is the difference between sensory input evoked by vibration and movement that mediates the direction of the illusion.

Tendon vibration studies have also provided evidence that the CNS uses information from an ensemble of muscle spindles to represent movement kinematics. Gilhodes et al. (1986) showed that when antagonist muscles were simultaneously vibrated at the same frequency, no illusory sensations of movement were evoked, and sensations of this kind could only be perceived when the muscles were vibrated at different frequencies. Similarly, Verschueren et al. (1998) have shown that the errors resulting from the vibration of a combination of synergistic muscles were larger than the errors produced by vibrating one of these muscles independently. This summation of errors suggests that the proprioceptive input from all muscles subtending a joint contributes to the perception of dynamic joint position and velocity.

This technique was also used to demonstrate that proprioceptive feedback could provide temporal cues about the actual time course of an evolving movement in which different muscle groups have to be serially activated (Cordo et al., 1994). Specifically, the movement sequence used by Cordo and colleagues involved a passive (Cordo et al.,

1995) or active (Cordo, 1990) rotation of the elbow, followed by a voluntary hand movement as the elbow passed through a prescribed joint angle. Using a wide range of velocities (16-69 °/s), they showed that the sense of joint position was extremely precise (0.7°-1.5°) and relatively independent of the speed of rotation. It was suggested that proprioceptive information about the dynamic position (position during movement) and velocity of a movement could be used to trigger discrete joint rotations during movement sequences (Cordo et al., 1994). Specifically, the CNS would use velocity information to predict future positions of the elbow and thereby compensate for the delays in sensorimotor transmission and processing. In contrast, dynamic position information would be used to track the limb position during movement and determine when the elbow reaches the appropriate triggering angle (Cordo et al., 1995).

The purpose of these studies that used tendon vibration was to examine how the CNS uses proprioceptive input to control movement. Therefore, a constant feature in this type of protocol has been to prevent participants from seeing their limbs, rendering proprioception as the only source of useful kinematic information with which to perform the tasks. While this has proven to lend great insight into the role of proprioception when solely available, it might not be reflective of many *visually*-guided movements that humans execute. In fact, it has been reported that visual regulation would prevent the processing of proprioceptive signals (Proteau, 1992).

Specificity of Practice Hypothesis

The reliance on sources of afferent information has been examined in a series of studies leading to the specificity of practice hypothesis (Proteau, 1992). It is typically

reported that learning is specific to the sources of afferent information used to guide one's movement during practice. In an early study, Proteau et al. (1987) had participants practice an aiming movement for 200 or 2,000 trials under a full vision condition or a condition in which they could only see the target to be reached (no vision condition). Not surprisingly, by the end of practice, participants who had performed under the full vision condition were more accurate than participants who had trained under the no vision condition. More interesting results were obtained in a transfer test performed by all participants in the no vision condition without knowledge of results (KR). The results of the transfer test revealed an important increase in error and variability for participants who had trained in the full vision condition, who, regardless of the amount of practice, became significantly less accurate than participants who practiced in the no vision condition. This led Proteau and colleagues to suggest that learning appears to be specific to the sources of afferent information used to ensure optimal accuracy during practice. When that information is withdrawn in a transfer test, performance suffers because the individual has no reliable source of reference with which to evaluate his movement. Therefore, in the context of manual aiming movements in which accuracy demands are high, vision would quickly be determined to be a more efficient source of information than proprioception. Thus, during practice, one would not attend to proprioceptive afferent information, but would only process visual afferent information (Proteau and Isabelle, 2002). It has even been suggested that the processing of vision would mask the processing and calibration of proprioceptive feedback (Tremblay and Proteau, 1998). Although the evidence presented by Proteau and colleagues is convincing with regards to the fact that vision is preferentially used when available, their claim that its processing

masks the processing of proprioceptive feedback is somewhat debatable. In fact, it stems from the observation that endpoint error and endpoint variability both increase when one is transferred from a full vision to a no vision condition. However, such increases do not *necessarily* imply that proprioceptive feedback was not being processed. As such, Vindras and Viviani (1998) proposed that the larger pointing errors found in a no vision condition would rather be attributable to transformation errors that occur when the representation of the target is transformed from its allocentric frame of reference to an egocentric frame of reference. This is because when vision of the effector is not permitted, the location of the target is coded within an allocentric frame of reference, whereas the location of the effector is coded within an egocentric (proprioceptive) frame of reference (Jeannerod, 1988). Errors would occur when one would transform the location of the target from its allocentric frame of reference to an egocentric frame of reference. This is different from a normal visual context, in which both the effector and the target are coded within an allocentric (visual) frame of reference, and in which errors can easily be detected and corrected.

With the aim of clarifying these issues, we used a visuomotor adaptation paradigm in Experiment 1 to determine whether proprioception is calibrated during visually guided movements. This protocol allowed us to assess the processing of proprioceptive feedback by analyzing not only endpoint *variability*, but also the *spatial location* of movement endpoints. Specifically, we induced a directional bias between the position of a cursor representing hand position and the actual hand. After practicing a manual aiming task with the biased visual feedback in an adaptation phase, participants were transferred to a no vision condition. The presence of the bias in the adaptation phase

resulted in the participant's hand consistently deviating to the right of the target by an amount equal to that of the induced bias. Of interest was whether participants would still show rightward hand deviations after the removal of vision in a post-test (i.e. aftereffects), suggesting that proprioceptive feedback had been processed and calibrated during the adaptation phase.

A visuomotor adaptation paradigm was also used in experiment 2 to determine whether limb position information provided by proprioceptive feedback is processed by the CNS while vision is used to coordinate an action. However, instead of inducing a visual bias, a proprioceptive illusion was introduced by means of tendon vibration. Similar to Cordo and colleagues' investigations, participants were asked to open the hand at a specific target location while the right elbow was passively extended. It was hypothesized that the vibration would create a discrepancy between the proprioceptively perceived elbow angle and the visually perceived elbow angle. If participants did process proprioceptive input regarding elbow angle while vision was also available, then they should show systematic biases (i.e. aftereffects) when vision is removed in the post-test. This would result from a coordinative remapping (calibration) between vision and proprioception, suggesting that the target had been correctly transformed from its allocentric (visual) frame of reference to an egocentric (elbow angle) frame of reference during the visually mediated trials.

Experiment 1

The calibration of proprioception during visually guided movements

Vision and proprioception are both primary sources of information that can be used when planning and controlling goal-directed movements. Movement planning involves computing an inverse model that consists of the specification of target location as well as location of effector. It has been shown that when the hand is visible prior to movement, both vision and proprioception are combined in a very efficient way by the CNS to plan the movement (Desmurget et al., 1995). However, such an interplay between both modalities is seldom reported for the online control of movement. Specifically, the increased precision afforded by visual regulation appears to encourage the use of this feedback source over and above other sources that may be available. When practicing with vision, participants learn to use this source of information in an online manner rapidly and efficiently (Elliott et al., 1998). It has even been suggested that participants become dependent on vision for movement accuracy (Proteau and Isabelle, 2002). Conversely, when movement unfolds without visual regulation participants typically develop less feedback-dependent strategies (Elliott et al., 1998) and therefore performance relies essentially on the accuracy of motor planning.

Evidence thus suggests that proficiency at using the available feedback sources mediates the way movements are controlled. Although proprioception might allow accurate perception of limb movement in the absence of vision, it seems to play a relatively minor role when vision is present (Hay et al., 1963). Based on a number of specificity of practice studies, Proteau and Isabelle (2002) have suggested that the

reliance on vision is such that one would not pay attention to proprioceptive information during movement. In fact, the processing and calibration of proprioceptive feedback would be masked by the processing of visual feedback (Tremblay and Proteau, 1998). However, Proteau and colleagues have always used aiming protocols in which a veridical mapping existed between the hand and the cursor representing it. Since calibration is the process that establishes the present conditions of the task-work space, and is necessary to adapt to a change in these conditions (Redding and Wallace, 2001), a more appropriate way to determine whether calibration takes place would be to look at how participants adapt to visuomotor discrepancies. Thus, the goal of the present study was to assess whether proprioception is concurrently calibrated with vision during visually guided movements. This was done by introducing a bias between vision and proprioception in an adaptation phase of the experiment. This phase was preceded and followed by sessions completed without visual feedback (pre- and post-test). Of interest was whether participants would show plastic changes in their kinematics in the post-test compared to the pre-test. Measuring the movements without any visual feedback is equivalent to measuring the aftereffects (Welch, 1978), and it is the presence of those aftereffects that reflects proper calibration (Mather and Lackner, 1981). We thus hypothesized that if proprioception is calibrated along with the biased visual feedback, then the movements should still be biased after the removal of vision (i.e. aftereffects).

Materials and methods

Participants

Fourteen healthy subjects between 22 and 29 years of age participated in the experiment. All subjects signed informed consent statements, and the study was conducted in accordance with the ethical guidelines set by the University of British Columbia.

Task and Apparatus

The task was to move a mouse on a horizontal digitizing tablet towards one of three target locations. Participants were seated at a table in front of the tablet (31 cm x 46 cm, DrawingBoard III, GTCO Calcomp model no. 34180; sampling rate: 225 Hz). A white opaque cardboard was fixed horizontally 15 cm above the tablet. A 3M MP8020 projector (refresh rate: 60 Hz) attached to the wall one meter directly above the cardboard projected the corresponding trace of the performed movements onto the cardboard screen. This setup allowed participants to see the cursor representing their movement path but prevented them from seeing their hand. The mouse had a plastic extension containing a cross-hair whose coordinates were registered by the tablet. The home position consisted of a 0.5 cm x 0.5 cm square, while the three targets were represented as red circles of 1 cm in diameter. They were located on a radius 30 cm away from the home position. The central target was directly in line with the starting position, with the other two targets located 10° to either side of it. Participants sat on an adjustable chair with their chin resting on a chinrest.

Procedure

Participants were randomly divided into two groups (Full vision, No vision). For the Full vision group (FV), a cursor representing hand path was presented on the screen during movement execution. For the No vision group (NV), the cursor disappeared as soon as it left the starting base, and visual knowledge of results (KR) regarding the path adopted was presented after each trial. Participants were asked to fixate on the target and following an auditory tone, to initiate their movement when ready. The task had no amplitude requirement, such that participants only had to “move through” the target as smoothly and accurately as possible. Movement time (MT) was fixed from 400 ms to 600 ms, and KR regarding MT was given after every trial.

Participants all took part in three experimental sessions: a pre-test, an adaptation phase and a post-test. In the pre-test, they executed 20 trials with no vision and no KR towards the central target. This allowed us to establish a baseline value for each participant's perceived central target position. They were then exposed to a visuomotor bias during the adaptation phase. Specifically, a 2.5 cm gradual rightward bias was induced between the mouse location and the cursor representing it. Thus, in order to accurately guide the cursor to a target, the participant's hand (mouse) had to pass 2.5 cm to the right of that target. The same bias was also induced on the KR given to the NV group. Participants executed 80 trials towards each of the three targets during that phase. Following that, participants took part in a post-test, during which they executed 20 trials with no vision and no KR towards the central target (as was the case in the pre-test).

Data reduction

Movement initiation was defined as the point in time when the mouse moved 1 mm from the home position. Movements were considered to be complete when the cursor crossed the arc subtended by the three targets. The displacement data of the mouse over time were first smoothed using a fourth order recursive Butterworth filter with a cut-off frequency set at 5 Hz. The smoothed data were then differentiated using a central finite difference technique to obtain the velocity profiles. We measured the position of the mouse at four landmarks (25%, 50%, 75% and 100%) of the longitudinal distance from the home position to the target, as well as the direction of the resultant velocity vector at the 100 ms time point after movement onset.

Results

A major premise of the current protocol was that the participants would not perceive the visuomotor discrepancy. None reported knowledge of the bias when asked by the experimenter after testing. We were thus confident that the reliance on vision was reflective of normal conditions, as well as precluding any conscious strategies such as “side pointing” (Redding and Wallace, 2002).

Adaptation analysis

The average course of adaptation to the bias is shown in figure 1 for the NV group (a) and the FV group (b). The data are expressed in absolute terms and represent the extent to which the participant’s hand deviated to the right of the target at movement endpoint. Because pre- and post-test only involved the central target, adaptation data is only reported for the central target. Note that the rate and magnitude of adaptation were similar for all three targets. The FV group adapted more quickly than the NV group, as expressed by the greater slope of a logarithmic curve fitted through the first 10 trials of the adaptation phase (0.93 for FV group vs. 0.70 for NV group).

In order to assess adaptation as well the presence of aftereffects, we compared the endpoint locations of the last 5 trials in the pre-test, the last 5 trials in the acquisition phase (late adaptation), the first 5 trials in the post-test (early post-test), and the last 5 trials in the post-test (late post-test). A 2 (group) X 4 (phase) repeated-measures ANOVA produced a significant interaction ($F_{(3,36)}=5.6, P<0.01$). Post-hoc analysis (Tukey’s HSD $P<0.05$) revealed that the endpoints of both groups were significantly more biased in late adaptation than in the pre-test, suggesting that adaptation had taken place. More importantly, the NV group showed strong aftereffects, as movement endpoints from early

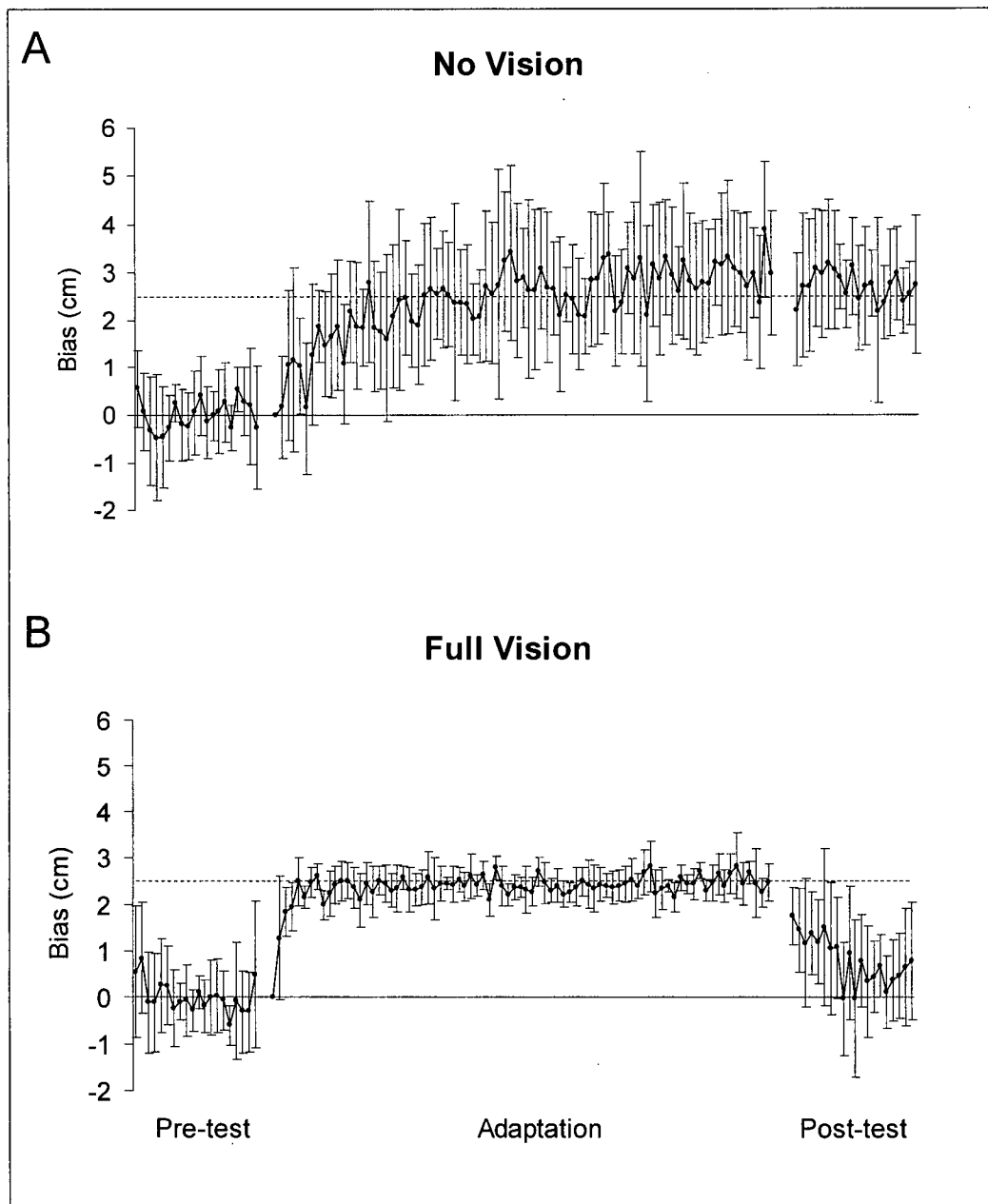


Figure 1. Trial by trial magnitude of the deviation of the hand to the right of the target at movement endpoint, expressed in absolute terms, for the NV group (a) and the FV group (b). Since the magnitude of the induced bias was 2.5 cm, a value close to the 2.5 cm dotted line represents complete adaptation to the bias. Note the presence of aftereffects for the NV group and the gradual decay of the aftereffects for the FV group.

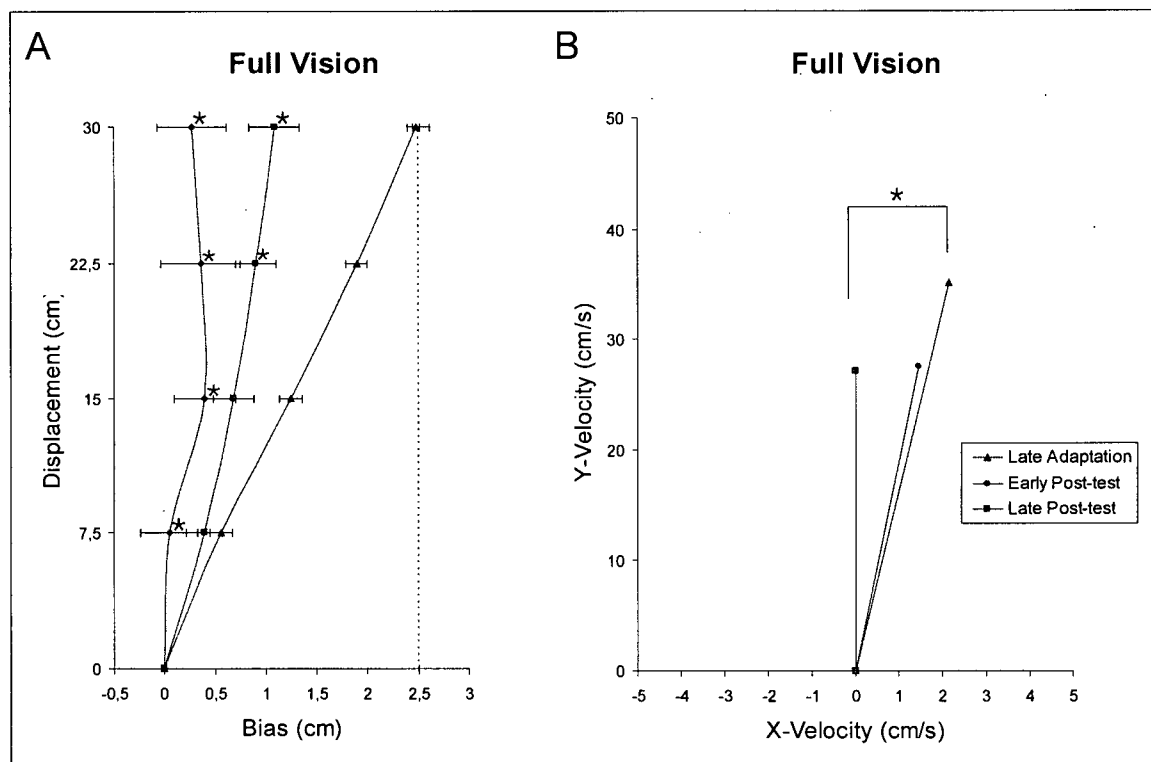


Figure 2. Mean trajectories of the hand (a), and mean resultant velocity vectors at the 100 ms time point after movement onset (b) for the FV group. In a), the asterisk (*) represents a significant difference ($P < 0.05$) in the x-direction of a landmark in the Post-test compared to its value in Late Adaptation. Since the magnitude of the induced bias was 2.5 cm, an endpoint close to the 2.5 cm dotted line represents complete adaptation to the bias. In b), the direction of the vector in Late Post-test was significantly different than in Late Adaptation. (* Significant at $P < 0.05$)

and late post-test were significantly more biased than those in the pre-test. For the FV group, aftereffects were present early, as reflected by the significantly more biased endpoints in early post-test compared to pre-test. However, those aftereffects decayed rapidly. In fact, endpoints in late post-test were significantly less biased than in early post-test, and were actually no different than in the pre-test.

In order to better capture the decay in aftereffects for the FV group, we compared the kinematics of trials from late adaptation to those from early as well as late post-test (Fig. 2a). A 3 (phase) X 4 (landmark) repeated-measures ANOVA revealed a significant interaction ($F_{(6,54)}=13.2$, $P<0.001$). Post-hoc analysis ($P<0.05$) showed that the hand position at 75% and 100% of the movement differed significantly between early post-test and late adaptation, whereas all four landmarks differed significantly between late post-test and late adaptation.

Finally, the direction of the resultant velocity vector at the 100 ms time point was compared between late adaptation, early post-test and late post-test (Fig. 2b). A 3 (phase) repeated-measures ANOVA revealed that the vector direction late in the post-test was significantly less biased than late in the adaptation phase ($F_{(2,12)}= 4.41$, $P<0.05$).

Discussion

This study sought to determine whether proprioception is calibrated during visually guided movements. The fact that the NV group presented strong aftereffects while the FV group only showed modest aftereffects early in the post-test suggests that proprioception was not calibrated when vision was concurrently available. Although the presence of early aftereffects for the FV group could be taken as evidence of calibration, an analysis of the kinematics reveals that their presence was more likely due to offline effects of vision on movement planning. This finding is consistent with those of Baraduc and Wolpert (2002), who suggested that a major part of the aftereffects must be attributed to a change in the motor commands issued.

In fact, hand positions at 75% and 100% of the movement were significantly less biased for the first 5 trials in the post-test than in late adaptation (Fig. 2a). This precludes that movements were made exclusively in a feedforward fashion, but rather suggests that vision was used extensively to guide the limb when it was available. However, the trajectories were not significantly different after 25% and 50% of the movement, strongly suggesting that the planning was similar. To further analyze movement planning, we compared the direction of the resultant velocity vectors at the 100 ms time point after movement onset (Fig. 2b), assuming that the direction of these vectors at this time reflects only response planning processes. We found that their direction regressed towards the actual location of the target during the post-test. This is consistent with the reduction in aftereffects shown in figure 2a. Therefore we suggest that in the adaptation phase, participants became reliant on vision as an online source of feedback, as well as using it to plan subsequent movements. Its removal in the post-test then prevented

participants from accurately planning their movements, which forced them to use the only source of information available, namely proprioception. The observation that the latter portion of the movements, mediated by proprioception, tended to drift in a direction away from that of the bias, strongly suggests that proprioception was not calibrated.

Interestingly, our finding that the FV group presented small aftereffects is at odds with prism adaptation (Redding & Wallace, 2002) and visuomotor adaptation (Krakauer et al., 1999) studies, which show that practicing with full vision leads to robust aftereffects. It is generally agreed that adaptation is achieved by gradually modifying an internal reference frame, or internal model (Krakauer et al., 1999). Importantly, this remapping between vision and proprioception *requires* detection of the sensory misalignment to occur (Redding and Wallace, 2002). This is supported by the finding that deafferented patients do not show aftereffects following a period of exposure to displacing prisms. In this case, the realignment mechanisms would not operate because of the lack of conflict between vision and proprioception (Guédon et al., 1998). A major factor that could account for our differential findings is that none of the participants in our study detected the induced bias. This lack of conflict detection might have prevented participants from calibrating proprioception (i.e. updating an internal model), as the task could be successfully achieved on the sole basis of online visual processes. This raises an interesting question regarding sensorimotor integration. If the processing of vision masks the processing of proprioception, how can the conflict between both modalities, necessary for adaptation to occur, be detected? Our results would suggest that as long as no discordance is perceived, one would not attend to proprioception, and no realignment process would take place. Conversely, the detection of a conflict would prompt one to

process both modalities, and lead to an updating of the internal model. This view is supported by a recent fMRI study (Balslev et al., 2005), which compared brain activity across two conditions with similar visual and proprioceptive stimulation but with different levels of congruence between both modalities. Interestingly, cortical areas generally involved in shifts of visual attention (i.e. right temporoparietal junction, premotor cortices) were found to be more highly activated in the incongruent condition compared to the congruent condition. In line with our findings, this would suggest that the detection of a sensory conflict mediates the processing of those modalities.

Experiment 2

Sensory recalibration in response to proprioceptive bias

Our ability to execute accurate movements towards visible targets depends on a complex set of sensorimotor transformations. It has been suggested that the location of the target, initially coded in retinocentric coordinates, would first be transformed into hand-based coordinates, in which movement is thought to be coded (Vindras and Viviani, 1998). Then the CNS specifies the motor commands necessary to accomplish the planned displacement, likely represented as a vector joining the initial hand position and the target. This capacity to estimate the motor commands necessary to achieve desired outcomes is referred to as an internal model (Shadmehr and Mussa-Ivaldi, 1994; Wolpert et al., 1995).

Several authors have investigated the flexible nature of these sensorimotor transformations by exposing participants to novel visuo-motor environments. This was done using displacing prisms (Redding and Wallace, 2002), or rotating virtual displays of limb position (Krakauer et al., 1999). Performance is generally poor early in the exposure period. Over repeated trials, however, participants are able to adapt to the novel visuo-motor mapping and often reach levels of performance similar to those of pre-exposure. This rapid error reduction that occurs during the transient phase of exposure can result from strategic modifications of the initial direction of the pointing movement (Rossetti et al., 1993) as well as online visual guidance (Pisella et al., 2004). When brought back to a normal environment following the exposure period, participants generally display patterns of error similar but opposite to those observed during the exposure phase. These

“aftereffects” are thought to represent real adaptation to the novel environment, and would result from a coordinative remapping between sensory representations.

Conceptually, this perceptual recalibration suggests that an internal model that captures the mapping between motor commands and sensory consequences has been updated. This would explain the plastic changes in movement kinematics that take place following a period of exposure to a novel visuo-motor environment.

Although authors are not unanimous with regards to the actual mechanism that leads to perceptual recalibration, most emphasize the importance of the detection of a sensory misalignment. For example, Guédon et al. (1998) suggested that it is the detection of a conflict between visual and proprioceptive cues resulting from the induced distortion that leads to the adaptive state. They supported this hypothesis by investigating the adaptive capacities of a deafferented patient. Consistent with previous studies, they found that aftereffects were almost nonexistent for the patient. This absence of plastic changes would result from the fact that no discrepancy between visual and proprioceptive modalities can be detected by deafferented patients. Similarly, Redding and Wallace (2002) suggested 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 the two signals are not different.

Recently, authors have investigated whether specific central (Balslev et al., 2005) or peripheral (Jones et al., 2001) responses take place when one interacts within a discrepant visuo-proprioceptive environment. By manipulating visual feedback of the hand, Balslev and colleagues compared cortical activity between congruent and non-congruent visuo-proprioceptive conditions. They found a higher level of activity in the

right temporoparietal junction and the premotor cortices when there was spatial disagreement between the sensory modalities. Because these brain areas have been associated with shifts of visual attention (Corbetta et al., 1998), these results led the authors to suggest that an attentional link may exist between proprioceptive hand space and visual space. Furthermore, Jones et al. (2001) demonstrated that the integration of visual and proprioceptive information is affected by the introduction of a discrepancy between the modalities. They recorded muscle spindle activity in forearm muscles during the early period of exposure to a rotated visual feedback of hand position. Surprisingly, they found that the firing rates of spindles were transiently reduced during that period. It was suggested that this decrease would be a strategy for resolving the conflict between visual and proprioceptive input caused by the manipulation of the visual feedback.

A common feature in studies investigating visuo-motor adaptation is that the discrepancy between sensory modalities has always been introduced by manipulating visual information. Hence it is unclear whether similar adaptation would be observed 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 exposing participants to a proprioceptive bias, using the technique of tendon vibration, which produces a powerful stimulus of activity in primary afferents by entraining their discharge rate (Roll and Vedel, 1982). This artificial increase in primary input creates the illusion that the vibrated muscle is being stretched, resulting in a directional shift in one's perception of limb position. Consequently, at high frequencies (> 40 Hz), vibration of the antagonist typically leads to undershoot errors during active movement (Inglis and Frank, 1990).

The coordinated movement task that was used required participants to open thumb and index finger at a specific elbow angle during passive elbow extension. Using a similar task, Cordo et al. (1994) showed that in the absence of vision, the CNS uses proprioceptive information related to the velocity and position of the elbow to trigger the hand opening. In the present study, however, visual feedback of a cursor representing the limb was provided to participants. In addition, tendon vibration was applied during the movement to the extending right biceps brachii muscle. The vibration created a discrepancy between the proprioceptively perceived and visually perceived location of the effector. Of interest was whether this visuo-proprioceptive conflict would lead to a recalibration of the sensory modalities. Any coordinative remapping would be assessed by the presence of significant overshooting following the removal of visual feedback and vibration in a post-test phase (i.e. aftereffects). Finally, it has been shown that adaptation is mediated by the availability of concurrent visual feedback during movement (see Experiment 1). Therefore, a group performing with visual feedback was compared to a group performing without visual feedback but provided with terminal knowledge of results.

Methods

Participants

A total of sixteen right-handed (24 years \pm 2.1) participants took part in the study. All were naïve to the hypothesis being tested and 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 opening was measured using a finger-tip switch made from two pieces of thin copper sheet metal attached to the participant's index finger and thumb with double-sided tape.

Vibration

A custom tendon vibrator, consisting of a low voltage DC motor with a rotating counterweight in a cylindrical plastic case, was positioned over the biceps brachii tendon. The muscle vibrator was controlled through an adjustable power supply to provide a 90 Hz pulse with peak-to-peak amplitude of 2 mm. This vibrating frequency has previously been shown to evoke strong muscle lengthening illusions in antagonist muscles (Inglis and Frank, 1990).

Procedure

While seated at a table, participants faced a video monitor, and an opaque screen covered the right arm (see Fig. 3). This setup allowed participants to see a cursor representing their movement path on the monitor but prevented them from seeing their arm. The monitor was positioned 1 m in front of the subjects. Motion of the forearm was represented by a white line (2 mm in width and 25 cm long) moving perpendicularly along a curved path representing circular movement trajectory. Stationary red lines perpendicular to the curved path indicated the target angle. 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 movements mainly around the elbow joint. The elbow was rotated at a constant velocity of $22^\circ/\text{s}$. This relatively low velocity was selected because Cordo et al. (1995) have shown that the effects of vibration increase with slower velocities of elbow rotation.

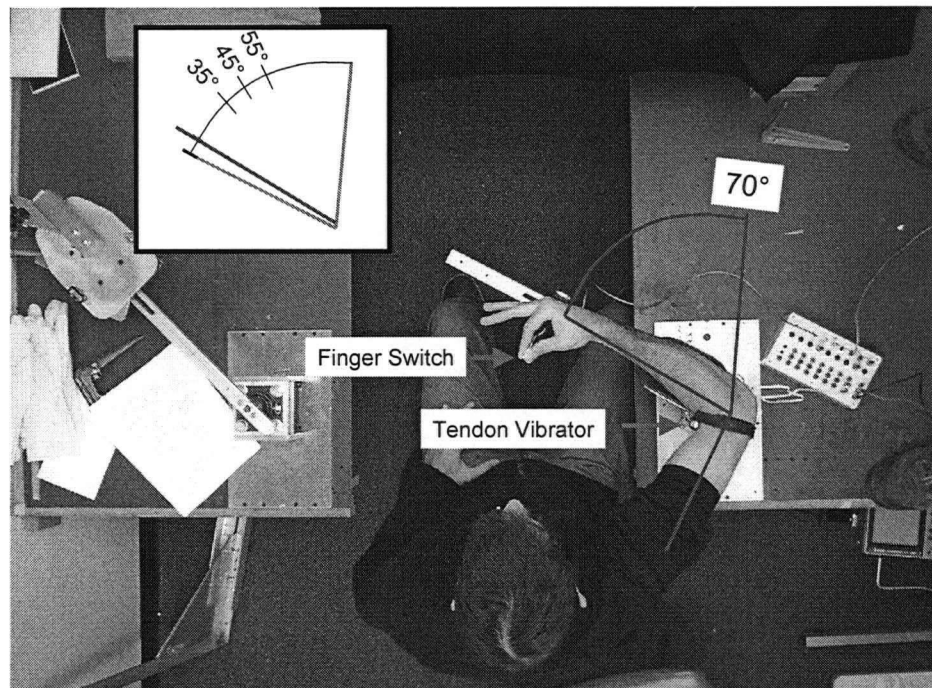


Figure 3. Overhead view of the setup. Note that an opaque screen covered the arm. Inset: Visual feedback shown on monitor (not to scale).

Participants were randomly assigned to one of two groups (8 per group). A first group executed the task with full vision of the cursor during movement (FV group). Immediately on opening of the hand, the cursor stopped moving and turned from white to red. A second group performed the task without vision of the cursor during movement (NV group). Immediately on opening of the hand, a red line representing the triggering angle appeared on the screen, which served as a source of knowledge of results (KR). All participants took part in three experimental phases: a pre-test, an adaptation phase and a post-test. Prior to data collection, participants did a practice session to get comfortable with the setup. During this practice session, their arm was passively moved out and back ten times, with vision of the cursor. Following this, all participants took part in a pre-test, which consisted of 10 trials performed without vibration (pre-test 1), immediately followed by 10 trials with vibration (pre-test 2). Only the 45° target was used, and all movements were executed without vision and knowledge of results. This allowed us to establish each participant's perception of middle target position and provided a measure of the magnitude of the proprioceptive shift induced by vibration. In the adaptation phase, participants performed 45 trials (15 towards each of the three targets) in one of the two visual conditions (FV or NV). Vibration was applied on every movement during this phase. Finally, all participants took part in a post-test, which was identical to the pre-test. That is, participants performed 10 trials without vibration (post-test 1), immediately followed by 10 trials with vibration (post-test 2). Again, only the 45° target was used, and all movements were executed without vision or knowledge of results.

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 the release of the fingers at the required target angle. Vibration was applied on initiation of movement and continued for 1 s after finger release. Following a trial, the participant's arm was brought back to the starting position at a velocity of $10^{\circ}/\text{s}$. Therefore, consecutive trials were always separated by a minimum of 14 s. Such a delay was implemented to prevent postvibratory effects. As such, Ribot-Ciscar et al. (1998) showed that the static stretch sensitivity of muscle spindles was decreased for 3 s following vibration exposure.

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, absolute errors as well as variable errors were calculated for each subject and each experimental phase. Moreover, as changes were expected both in terms of accuracy and variability during the acquisition phase, these trials were separated into 3 blocks of fifteen trials for analysis.

Results

We first assessed the magnitude of the shift in perceived arm position induced by vibration for each participant. 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) (Table 1). Although the NV group had a greater overall tendency to undershoot the target in the pre-tests than the FV group, the magnitude of the vibratory-induced shift was very similar for both groups. On average, the FV group released the fingers $7.2 \pm 3.8^\circ$ earlier in pre-test 2 than in pre-test 1. Similarly, the NV group released the fingers $7.0 \pm 2.3^\circ$ earlier in pre-test 2 than in pre-test 1. The effect of vibration was also observable in the post-tests, as the FV and NV group values were $7.6 \pm 5.0^\circ$ and $8.1 \pm 2.9^\circ$ respectively.

The average course of adaptation to the bias is shown in figure 4 for the FV group (a) and the NV group (b). The data represent the angular constant error at finger release. Participants in the FV group adapted immediately to the bias, as expressed by their ability to perform accurately on the first trial of the adaptation phase. Conversely, the NV group presented large undershoots early in the adaptation phase, which gradually decreased with practice.

Initially, we wanted to confirm that vibration was not causing a loss of proprioceptive sense, but was simply shifting participants' perception of limb position. Therefore, we introduced two further control groups ($N = 8$ per group) which performed the same experimental protocol as the FV and NV groups, with the only exception that they were not vibrated during the adaptation phase. We then compared the control groups' absolute errors (Fig. 5) and intra-individual variability (Table 2) at finger release to those of the NV and FV vibration groups during that phase. Separate 4 (group) x 3

Table 1

Mean constant error (and mean intra-individual standard deviation) in elbow angle at finger release for the Full Vision group and the No Vision group during the pre-tests and post-tests (degrees)

	Pre-test 1	Pre-test 2	Post-test 1	Post-test 2
Full Vision group	1.0 (4.5)	-6.2 (3.6)	-0.4 (3.8)	-8.1 (3.0)
No Vision group	-5.0 (4.1)	-12.0 (3.3)	0.3 (4.6)	-7.9 (4.6)

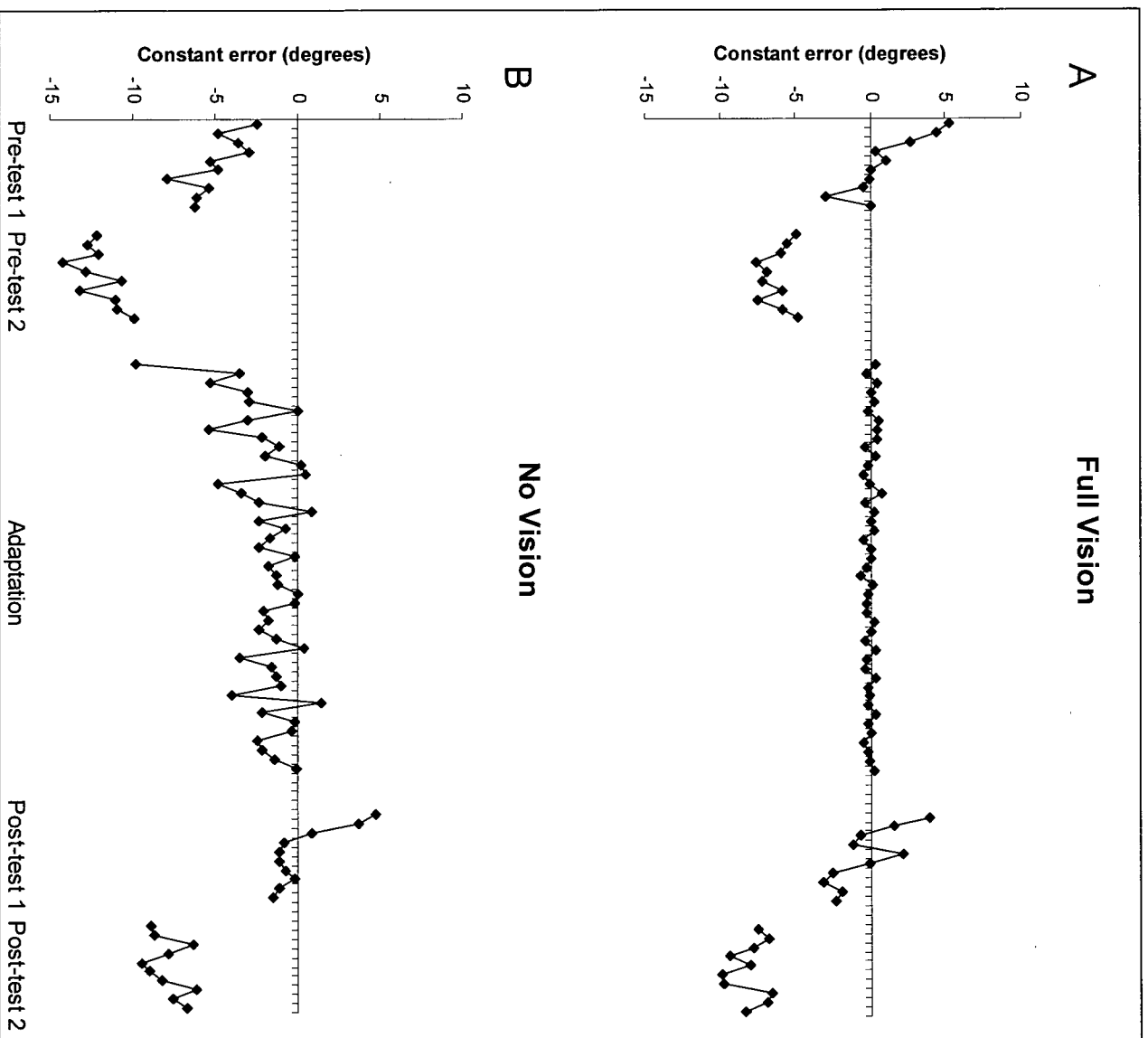


Figure 4. Constant error in elbow angle at finger release for the FV group (a) and the NV group (b) during the pre-tests, the adaptation phase, and the post-tests

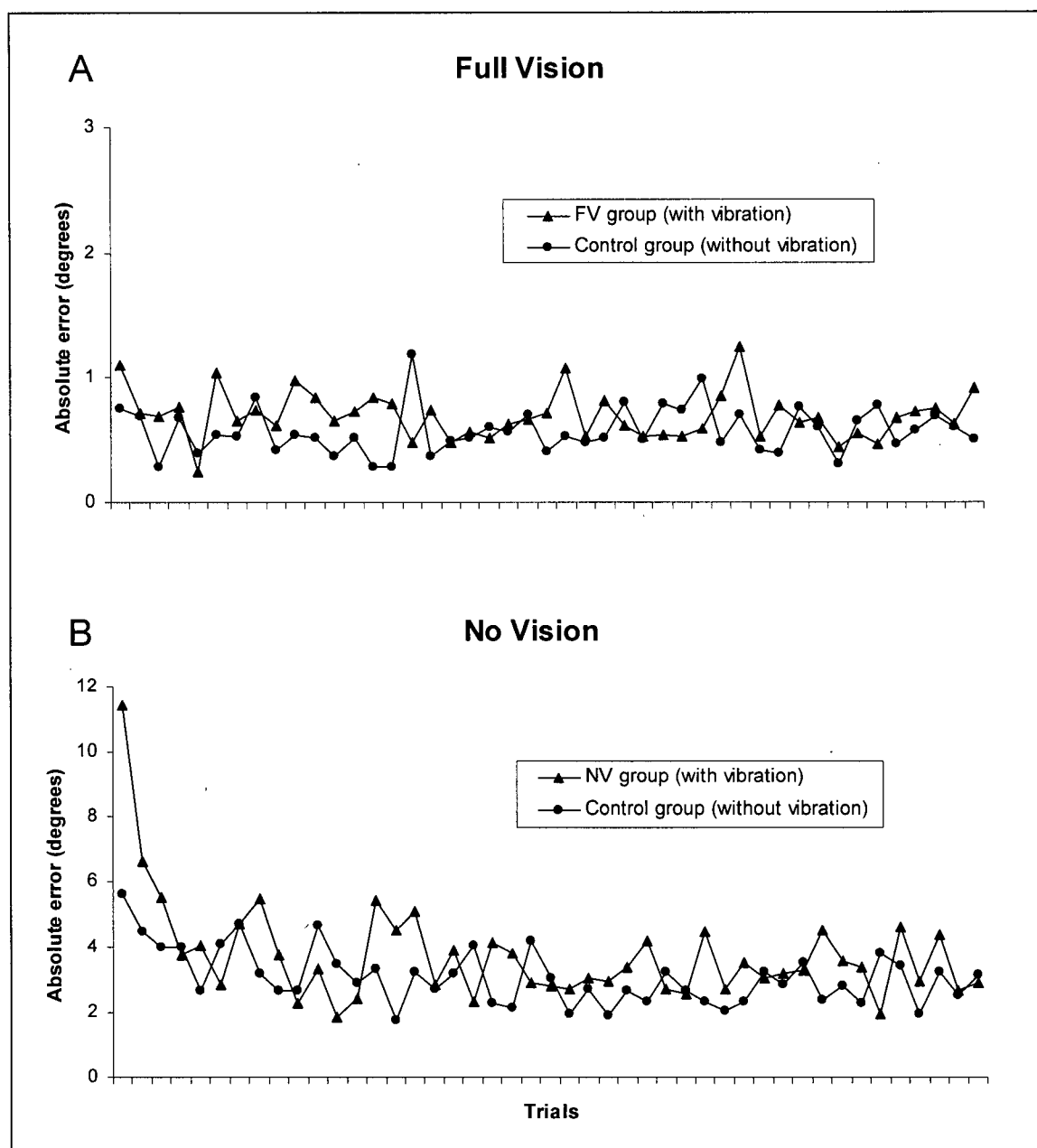


Figure 5. Absolute error in elbow angle at finger release for the FV group (a) and the NV group (b) during the adaptation phase

Table 2

Intra-individual variability in elbow angle at finger release for the Full Vision group, the No Vision group and the two Control groups during the adaptation phase (degrees)

	Block 1	Block 2	Block 3
Full Vision group	0.9	0.8	0.9
Control group (full vision)	0.6	0.8	0.6
No Vision group	5.0	4.0	4.0
Control group (no vision)	4.5	3.6	3.5

(block) repeated measures ANOVAs contrasting these variables over the three blocks of the adaptation phase were performed. The analysis of absolute errors revealed a significant interaction [$F(6,56) = 3.3, P < 0.01$]. Post-hoc analysis (Newman-Keuls, $P < 0.05$) indicated that the two groups performing in full vision were significantly more accurate than the no vision groups during all three blocks. More importantly, however, no difference in accuracy was found between the control group performing in full vision (without vibration) and the FV group (with vibration). For the no vision groups, we found that the control group (without vibration) significantly outperformed the NV group (with vibration) only during the first block, while no difference in accuracy was noted for the second and third blocks between these groups. In terms of intra-individual variability, a main effect for group [$F(3,28) = 121.7, P < 0.001$] and a main effect for block [$F(2,56) = 5.1, P < 0.01$] were found. Precisely, both groups performing in full vision were significantly less variable than the groups performing in no vision. In addition, participants presented significantly greater variability in the first block than in the second and third, which did not differ from each other.

In order to assess the presence of aftereffects, we compared the constant errors at finger release in the pre-tests to those in the post-tests. For the analysis, we separated every pre- and post-test into two 5 five trial segments, and also included the last five trials from the adaptation phase. Importantly, we only selected the last five trials from the adaptation phase that were directed towards the 45° target (from herein called “Late Adaptation”). This caution was taken to be consistent with the fact that the pre- and post-tests were all directed towards that target. The data for both groups were submitted to separate 9 (segment) repeated-measures ANOVAs. For the FV group, a main effect was

found [$F(8,32) = 46.9, P < 0.001$; (Huynh-Feldt adjustment)]. Post-hoc analysis revealed that vibration caused this 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, the elbow angles at finger release were not significantly different between pre- and post-tests, suggesting an absence of aftereffects. For the NV group, a main effect was also found [$F(8,32) = 69.6, P < 0.001$; (Huynh-Feldt adjustment)]. Similar to the FV group, post-hoc analysis revealed that vibration led to significant undershooting in pre-test 2 and post-test 2 (with vibration) compared to pre-test 1 and post-test 1 (without vibration) respectively. In addition, the triggering angles in the post-tests proved to be significantly greater than in the pre-tests, revealing that aftereffects were present. However, caution should be exercised when interpreting these results, as visual inspection of figure 4 would suggest otherwise. More precisely, because the magnitude of the vibratory illusion was approximately 7.0° , “true” aftereffects should have resulted in participants releasing the fingers with an overshoot error of about 7.0° in post-test 1, while showing error levels near 0° in post-test 2. Clearly this was not the case, as aftereffects of such magnitude were only present for the first few trials of post-test 1, and rapidly decayed thereafter. In fact, the FV group released the fingers 4° further on the first trial of post-test 1 than in Late Adaptation. Similarly, the NV group released the fingers respectively 7° and 6° further on the first two trials of post-test 1 than in Late Adaptation. To assess whether these early overshoots were true aftereffects, we compared every participant’s constant error in Late Adaptation to these trials individually. For the FV group, the ANOVA revealed a main effect [$F(1,7) = 8.5, P < 0.05$], confirming that the triggering angle of the first trial in post-test 1 was significantly greater than in Late

Adaptation. Similar results were obtained for the NV group, for which the first two trials of post-test 1 were found to be significantly different than in Late Adaptation ($P < 0.05$).

Finally, we compared each participant's variable error (i.e. intra-individual standard deviation) during the pre-tests and post-tests. The variable error data were submitted to a 2 (group) x 4 (phase) repeated-measures ANOVA. As seen in table 1, participants in the FV group were slightly less variable in the post-tests than in the pre-tests, while those in the NV group proved to be slightly more variable in the post-tests than in the pre-tests. However no significant interaction was found between the groups ($P = 0.09$). Furthermore, no main effect for phase was found ($P = 0.27$), suggesting that variability was similar whether vibration was present or not.

Discussion

In the present study, we wanted to determine whether a sensory conflict induced through proprioceptive distortion would lead to a recalibration similar to that observed when visual feedback is manipulated. Proprioceptive distortion was achieved by means of tendon vibration, which creates a directional bias in one's perception of limb position. During an adaptation phase, participants were provided with online visual feedback of their movement (FV group), or only terminal KR (NV group) while being vibrated on every trial. Vibration created the illusion that the elbow was extended approximately 7° further than its visually perceived position. Evidently, both groups proved to be able to accommodate to the shift in perceived arm position by significantly reducing constant error during the adaptation phase (Fig. 4). In fact, the FV group had already settled to its final level of performance by the first trial of adaptation. As suggested elsewhere (Pisella et al., 2004), much of this rapid error reduction was likely due to online visual guidance (see Experiment 1). In contrast, the NV group could only rely on proprioceptive feedback to trigger the finger opening during that phase. Therefore the gradual increase in accuracy showed by that group suggests that participants were able to correctly associate the visually perceived target angle to the appropriate proprioceptively derived elbow angle. Had this visuo-proprioceptive conflict led to a perceptual recalibration, we would have expected participants to systematically overshoot the target following the removal of visual feedback and vibration (i.e. aftereffects). Somehow, none of the groups showed persistent aftereffects following the exposure period. In fact, the NV group only presented overshoots consistent with the magnitude of the proprioceptive shift for the first two trials of post-test 1, while such overshooting only occurred on the first trial of

post-test 1 for the FV group. Following these initial trials, both groups showed a strong tendency to revert to their pre-exposure levels.

It is thought that for adaptation to occur, one needs to detect a conflict between visual and proprioceptive cues (Guédon et al., 1998). In this light, it could be argued that the absence of persistent aftereffects in the present study stems from the distorting effect of the vibratory stimulus. Specifically, vibration might have rendered proprioceptive input unreliable, rather than inducing a consistent directional shift in the participant's perception of limb position. This would have prevented participants from clearly perceiving the sensory misalignment, hence making adaptation impossible. However, we do not favor this hypothesis for several reasons. Firstly, we introduced two control groups that performed in visual conditions identical to our FV and NV groups, with the only difference that they were not vibrated during the adaptation phase. We found that the control groups were no less variable than the FV and NV groups during that phase (Table 2). Moreover, in terms of accuracy, the control group performing in no vision proved to be more accurate than the NV group only during the first block of the adaptation phase (Fig. 5). This difference stemmed from the strong tendency of the NV group to undershoot the targets early in the adaptation phase due to vibration. Once performance of the NV group stabilized in the second and third blocks, both groups showed equivalent absolute error values. Similarly, despite being vibrated, the FV group proved to be as accurate as the control group performing in full vision during the entire adaptation phase. Taken together, these results strongly suggests that vibration was not causing a loss of proprioceptive sense, but rather that participants still relied on this source of information to estimate elbow angle. Furthermore, we calculated the intra-individual variability in

elbow angle at finger release during the pre-tests and post-tests (Table 1). If vibration did render proprioceptive information unreliable, one would expect the intra-individual variability to be greater during pre- and post-test 2 (with vibration) than during pre- and post-test 1 (without vibration). This was not the case, as no significant differences were found between these phases. This view is also supported by findings from Inglis et al. (1990), who 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.

A more likely explanation for the transient aftereffects might reside in the nature of the task we used. Specifically, because the elbow was passively extended by a torque motor, participants did not have to generate motor commands to initiate and perform the movement. We chose to use a passive movement sequence to preclude the hand opening from being influenced by motor commands subserving elbow extension. This precaution stemmed from grasping studies which suggested that coordination between reaching and grasping would be assumed centrally by a feedforward command (Simoneau et al., 1999). The passive nature of the task prevented any discordance to be detected between the feedforward-expected position and the feedback-achieved position (Redding and Wallace, 2002), precluding any adaptation to occur at the level of the motor output. Rather, our task involved the detection of a misalignment between visual and limb-centered frames of reference, and therefore adaptation could only result from a proprioceptive recalibration. In theory, this remapping could be achieved simply by specifying a new final limb configuration in motor space corresponding to a particular input in visual space. However, it was recently put forth by Wang and Sainburg (2005)

that one's ability to interact in a perturbed visuo-motor environment was not due to a remapping of the final position of the limb in the workspace, but rather to a remapping of the representation of the movement vector. Specifically, they measured generalization of adaptation to a visuo-motor rotation by having participants aim towards different targets and from different initial locations than those used during the exposure period. They showed that generalization was greatest for movements made in similar directions, regardless of changes in spatial location. This implies that adaptation occurred through adjustments of the motor commands defining the movement trajectory. This view is also supported by studies showing that prism adaptation is specific to the movement velocity experienced during the exposure phase (Kitazawa et al., 1997), suggesting that a major part of the aftereffects are due to adjustments to the planning process (Baraduc and Wolpert, 2002). In this light, we suggest that participants detected the sensory conflict, but that the passive task did not allow them to update the motor commands, hence preventing persistent aftereffects from occurring.

In experiment 1, in which a visuo-motor bias was induced through visual manipulation, we showed that a rapid decay in aftereffects occurred when vision and KR were removed following a period of exposure. In contrast to the present study, we had participants perform *active* pointing movements towards targets. Interestingly, we found that the reduction in aftereffects was closely paralleled by a shift in the direction of the movement vector at peak velocity. Therefore it was concluded that the reduction in aftereffects resulted from a decay in the specification of the motor commands necessary to achieve the task within the altered visuo-motor environment. The results of the present study extend these findings by providing evidence that proprioceptive control of a

coordinative sequence task also decays if not “refreshed” by vision or KR. Part of this decay might be attributable to the distorting nature of 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 regards, 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 subjects, 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.

In summary, the present study provides evidence that participants are able to perform accurately during a period of exposure to a proprioceptive shift, even when concurrent visual feedback is not available. This is consistent with studies introducing sensory conflicts through visual manipulation, and further reflects the flexible character of the motor system. However, the fact that aftereffects were solely present early in post-test 1 suggests that exposure to the visuo-proprioceptive conflict only led to a weak and transient perceptual recalibration. We propose that our use of a passive task prevented participants from updating an internal model. In fact, the definition of an internal model, understood as the capacity to estimate the motor commands required to achieve a desired outcome (Tong and Flanagan, 2003), implies that adaptation occurs primarily through a change in the translation between sensory input and motor output. In this light, future studies should directly manipulate the extent to which the outcome of experimental tasks

reflects preplanning processes, in order to confirm whether recalibration is only expressed through altered motor commands.

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