Prediction in the Vestibular Control of Arm Movements

Jean Blouin [1,*], **Jean-Pierre Bresciani** [2,3], **Etienne Guillaud** [4] **and Martin Simoneau** [5]

[1] Laboratory of Cognitive Neuroscience, CNRS, Aix-Marseille University, FR 3C 3512, Marseille, France

[2] University of Fribourg, Department of Medicine, Fribourg, Switzerland

[3] LPNC, University Grenoble Alpes and CNRS, F-38000 Grenoble, France

[4] CNRS and University of Bordeaux, UMR 5287 INCIA, Bordeaux, France

[5] Faculté de Médecine — Département de Kinésiologie, Université Laval and Centre de recherche du CHU de Québec, Québec, QC, Canada

Abstract

The contribution of vestibular signals to motor control has been evidenced in postural, locomotor, and oculomotor studies. Here, we review studies showing that vestibular information also contributes to the control of arm movements during whole-body motion. The data reviewed suggest that vestibular information is used by the arm motor system to maintain the initial hand position or the planned hand trajectory unaltered during body motion. This requires integration of vestibular and cervical inputs to determine the trunk motion dynamics. These studies further suggest that the vestibular control of arm movement relies on rapid and efficient vestibulomotor transformations that cannot be considered automatic. We also reviewed evidence suggesting that the vestibular afferents can be used by the brain to predict and counteract body-rotation-induced torques (e.g., Coriolis) acting on the arm when reaching for a target while turning the trunk.

1. Introduction

Our sensory systems underlie our perception of our own body and of its interaction with the external word. Yet, the role played by afferent signals, arising

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[*] To whom correspondence should be addressed. E-mail: jean.blouin@univ-amu.fr

for instance from visual, somatosensory and vestibular receptors, goes far beyond perceptual-related processes. In particular, sensory signals provide rich and reliable information for the motor system to plan and control goal-directed movements, such as those that we frequently perform with the hand. In their simplest description, these movements consist in transforming information related to the spatiotemporal goal of the movement into appropriate motor commands.

Because many of our daily arm movements are directed towards visual objects or specific regions of our body, a substantial amount of research has focused on the neural processes responsible for converting visual (Beurze *et al.*, 2007; Blouin *et al.*, 2014; Burnod *et al.*, 1999; Reichenbach *et al.*, 2009, 2011) or proprioceptive (Bernier *et al.*, 2007, 2009; Reichenbach *et al.*, 2014; Van Beers *et al.*, 2002) signals into motor commands. However, there are several situations in which sensory inputs related to body motion in space are important to control arm movements. This is the case for instance when filling a glass at the tap while rotating the trunk or when trying to balance a serving tray of filled glasses while turning the trunk. In these examples, in order to achieve the intended motor task (i.e., fill the glass or keep the glass upright), the brain must generate compensatory hand movements with the same velocity but in the direction opposite to body, and these compensatory movements must occur quickly.

Here we review work performed by our group as well as by others showing that the control of arm movements during body motion involves, especially during passive displacements, the processing of vestibular signals. Several of the reviewed studies were specifically designed to provide insight into the nature of this vestibular control of arm movement. Other aspects of the control of arm movements have already been reviewed in the literature and will not be considered here (see for instance, Avella and Lacquaniti, 2013; Desmurget and Grafton, 2000; Desmurget *et al.* 1998; Khan *et al.*, 2006; Shadmehr *et al.*, 2010).

Together, the studies reviewed here suggest that the compensatory arm movements produced during body motion rely on rapid and efficient vestibulomotor transformations but cannot be considered as being automatic in nature. These sensorimotor transformations appear to be under the influence of vestibular-based predictive mechanisms which would allow the central nervous system to counteract the detrimental effect of motion-induced torques (e.g., Coriolis) on the hand position and trajectory during body motion.

2. Integration of Vestibular and Cervical Information to Code Trunk Motion

The vestibular system is a good candidate for providing body motion information to the arm motor system during self-motion. This is because signals from the semicircular canals and otoliths convey information about angular and linear head velocity with respect to the external environment (after integration of the acceleration stimulus due to the mechanics of the vestibular system — Goldberg and Fernandez, 1975). However, in order to generate appropriate compensatory arm movements during whole body motion, the brain needs to be informed about trunk motion rather than head motion. Indeed, rotating the head while the trunk remains stationary would have no effect on the position or motion of the arm. Thus, vestibular information alone would be insufficient to control arm movements.

One mechanism by which the brain could be informed about trunk motion in space is through the combination of vestibular and neck proprioceptive signals (Ali et al., 2003; Blouin et al., 2007; Cohen, 1961; Ivanenko et al., 1999; Mergner et al., 1983). The importance of cervical afferents for coding trunk displacements has been notably evidenced in studies with deafferented patients. In previous experiments, we tested a rare patient (GL) with a large-fiber sensory neuropathy that resulted in a severe loss of position sense from the nose down to the feet, thus including the cervical region (see Forget and Lamarre, 1995 for a detailed clinical description of this patient). Despite a normal vestibular system (as attested by vestibulo-ocular reflex assessment), the accuracy with which this patient determined the magnitude of passive body rotations in the dark was largely deteriorated when compared to healthy control participants (Blouin et al., 1995). More specifically, the patient showed large overestimation of body rotations that might suggest improper calibration at the perceptual level of the vestibular inputs. In healthy subjects, this calibration could involve neck proprioception because it provides reliable information about changes in head-to-trunk positon during and after head rotations (Blouin et al., 1998a, b; Mergner et al., 1991; Nakamura and Bronstein, 1995). But, the most compelling demonstration of the critical role of neck proprioceptive input to code trunk motion stemmed from the patient's large increase of body oscillations when her head was rotated ~50° about the yaw axis while she was seated (without seat back) with her eyes closed (Blouin et al., 2007, see Fig. 1). In this experiment, in order to weaken head motion perception through vestibular inputs, the patient's head was slowly rotated (50° in ~15 s, rotation mostly sub perceptual threshold). With the head subliminally turned towards her shoulder, and with the lack of neck proprioception, the vestibular signals elicited during body oscillations did not provide veridical information about her trunk displacements in space (note that with the eyes closed, body oscil-
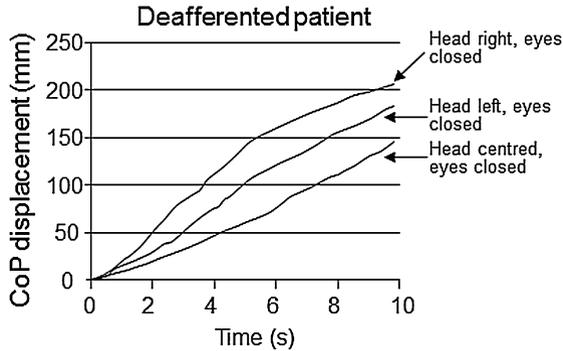
Figure 1. Mean center of pressure (CoP) displacement over time exerted on the platform on which the deafferented subject was seated in the different experimental conditions. The patient's stability was considerably deteriorated when she had the head unconsciously turned towards her shoulder. Figure adapted from Blouin *et al.* (2007).

lations were much larger in the patient than in the control healthy subjects). The fact that the postural responses were based on head motion rather than on trunk motion likely led to a series of inappropriate postural adjustments with respect to the actual patient's body oscillations resulting in the observed increase of body sway.

3. Vestibular Information: an Important Input Signal to Control Arm Movement

Direct evidence that goal-directed arm movements are under the online guidance of vestibular information was obtained in studies that stimulated the participants' labyrinths at the onset of reaching movements towards earth-fixed memorized visual targets (Bresciani *et al.*, 2002a; Mars *et al.*, 2003). In these studies, the stimulations were produced using bipolar galvanic vestibular stimulations (GVS, see Fitzpatrick and Day, 2004) and, depending on the paradigm used, participants' trunk remained either stationary (Bresciani *et al.*, 2002a) or moved forward to accompany the manual reaching (Mars *et al.*, 2003). When GVS simulated leftward body motion (i.e., cathode left), the hand trajectory deviated to the right (Fig. 2). In contrast, left hand deviation was observed when the cathode was located on the right side. The direction of hand deviations provided strong indications that the change in hand trajectory, which occurred ∼250 ms after GVS onset in Bresciani *et al.* (2002a), constituted a response delivered by the arm motor system to compensate for a vestibular-evoked illusory displacement of the body. More specifically, the hand deviation observed during the illusory displacement likely aimed at preserving the planned hand-in-space trajectory unaltered. Remarkably, in the study of Bresciani and colleagues (Bresciani *et al.*, 2002a), all sensory af-
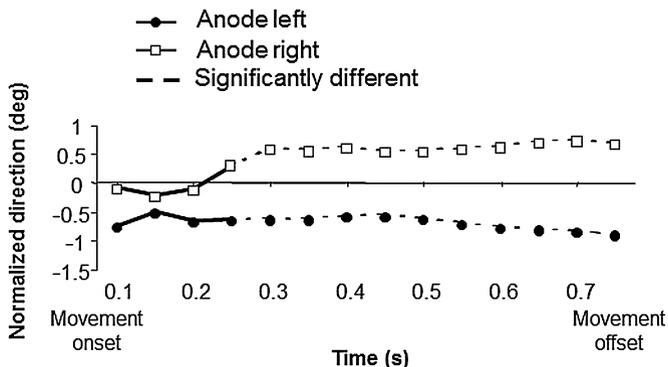
Figure 2. Mean hand directions measured every 50 ms when subjects reached for a memorized visual target located straight-ahead in darkness (0° in the graph). At the onset of the movement, a 3 mA rectangular, unipolar binaural direct electric current stimulated the vestibular system (using electrodes on the mastoid processes). The anode could be either located on the left or the right side (stimulating the right and left labyrinth, respectively). Dashed lines indicate the time at which hand directions recorded in both conditions became significantly different. The data were normalized with respect to those recorded in a control condition without GVS. Negative and positive normalized directions, respectively represent left and right deviations from mean control trajectories. Figure from Bresciani *et al.* (2002a) with kind permission of Elsevier.

ferents but the GVS-induced vestibular input informed the brain about body stability (a bite-board prevented head and body motion). This irrefutably confirmed the powerful influence of vestibular information to the control of spatially-oriented arm movements. More recently, Moreau-Debord and colleagues (2014) showed that this GVS effect on hand trajectory was modulated by head orientation, consistent with a transformation of the vestibular cues from head-centered to body centered reference frame.

The fact remains, however, that the deviations of hand path observed in previous studies after GVS do not provide definitive information about subjects' ability to process vestibular information to preserve reaching accuracy. A method that can be used to challenge the capacity of the brain to process vestibular information to accurately control arm movement consists in asking individuals submitted to passive whole-body displacements in darkness to continuously point at a remote memorized target or to stabilize the hand in space during these displacements. The advantage of this procedure is twofold. Because passive body displacement can be easily measured and quantified in terms of direction, speed, and amplitude, it allows for establishing whether the arm motor response accurately compensates for body displacements. The other important advantage is that, in the absence of visual feedback, the vestibular information obtained during passive body motions appears as the only sensory cue that can be used to generate appropriate compensatory arm movements. Indeed, although passive body motion stimulates a panoply of

sensory receptors (e.g., cutaneous mecanoreceptors and graviceptors embedded in the abdominal viscera (Mittelstaedt, 1992, 1995), somatosensory input resulting from motion of the arm due to inertial forces), it is unlikely that inputs from non-vestibular receptors can provide precise information about spatiotemporal characteristics of body motion.

All previous studies that used passive body motion highlighted the capacity of individuals to stabilize their hand (or pointer) in space during body motion in darkness (Blouin *et al*., 2010; Bresciani *et al*., 2005; Frissen *et al*., 2011; Guillaud *et al*., 2006a; Ivanenko and Grasso, 1997; Ivanenko *et al*., 1997a, b; Philbeck *et al*., 2001; Schomaker *et al*., 2011). Even more remarkably perhaps, individuals who undergo whole-body rotations while reaching for an earth-fixed memorized target can modulate online the hand trajectory to preserve reaching accuracy. This is illustrated in Fig. 3, taken from Bresciani *et al*. (2002b), showing the mean hand trajectories produced by one participant submitted to 40° counterclockwise (CCW) or 40° clockwise (CW) rotations at the onset of reaching movement towards a memorized target located at 20°. The reaching trajectories are compared to the trajectory observed in a control condition where the participant was not rotated during reaching. The body rotations, which were produced by a motorized chair, had Gaussian velocity profile to simulate natural self-generated head rotations (Blouin *et al*., 1998a; Guitton and Volle, 1987). The figure shows the 2D hand trajectories in space (i.e., top view, left graph) and with respect to body midline (egocentric view, right graph). It can be seen that hand trajectories in space remained similar in conditions with or without body rotations (trajectories from all conditions are superimposed in space). The preserved spatial constancy resulted from egocentric hand paths (i.e., with respect to body midline) that were markedly different depending on rotation direction (Fig. 3B).

4. Vestibulo-Manual Control: a Sensorimotor Process Largely Independent of Cognitive Factors

Vestibular information is known to be involved in spatial updating (cognitive process) and in the control of movement (sensorimotor process). Two distinct mechanisms could then underlie the vestibular control of arm-reaching movements during body rotation. First, the compensatory arm movements could result from a continuous updating of the internal representation of the body-target relative position during self-motion. Alternatively the arm movement could stem from a more direct sensorimotor transformation between vestibular input and arm motor commands. We conducted a series of experiments to determine which of these two alternatives was more likely to explain the reaching adjustments observed during body rotations.
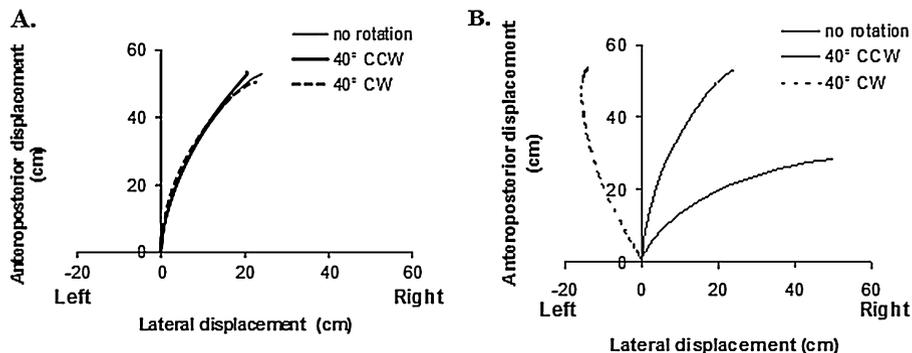
Figure 3. Mean hand trajectories produced by a subject when reaching for a 20° memorized visual target in a condition without body rotation, and in conditions with body rotations during the reaching movements (40° CW and CCW rotations). The same trajectories are represented in an earth-fixed reference frame (A) and in the subject's reference frame (B). Figure taken from Bresciani *et al.* (2002b) with kind permission of Wolters Kluwer Health.

In one of these studies, we used an original procedure in which we separately and specifically adapted (i) the vestibular-based spatial updating and (ii) sensorimotor processes (Bresciani *et al.*, 2005). We then tested whether these modifications transferred to (i.e., impacted) the compensatory arm movements observed during body motion. Our rationale was that if a given process underlies a given behavior, any adaptive modification of this process (here either the cognitive or sensorimotor process) should give rise to observable modification of the behavior (here, the compensatory arm movements during body rotation). The specific methods used to produce these adaptive modifications are too lengthy to be detailed here. Full details of each adaptive procedure can be found in the original paper (Bresciani *et al.*, 2005). Briefly, adaptation of the vestibular-based updating process aimed at modifying the matching between vestibular input and the perceived amplitude of body rotation in space. More specifically, the purpose of the procedure was to make the subjects underestimate the amplitude of body rotation. Adaptation of the vestibular-based sensorimotor process (referred here as the vestibulomotor process) aimed at modifying the matching between vestibular input and the arm motor commands that allow keeping the hand stable in space during body rotation. More specifically, the goal of the vestibulomotor adaptation was to reduce the gain of the transfer function between vestibular input and arm motor output. Importantly, both adaptive procedures proved to be efficient in bringing adaptive modifications to their targeted process. In other words, after the adaptation of the vestibular-based spatial updating, participants underestimated body rotation amplitude. After the adaptation of the vestibulomotor process, the amplitude of the arm movements produced during body rotation was insufficient to stabilize the hand-in-space during body rotations. After each adaptive proce-
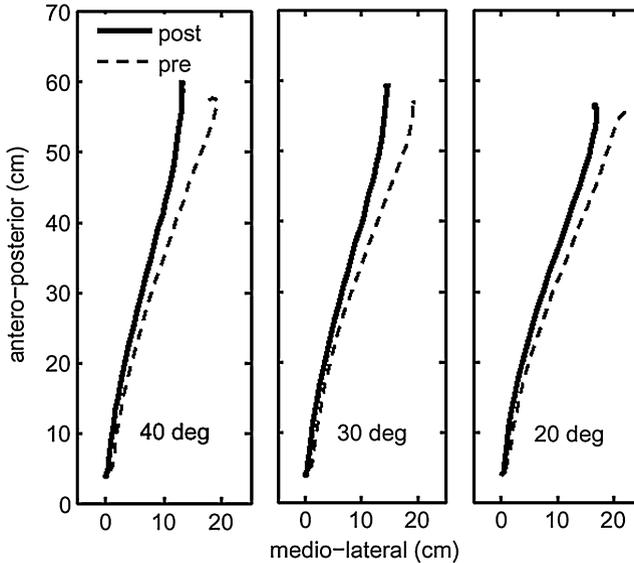
Figure 4. Mean hand trajectories produced by a subject during 20°, 30° and 40° body rotations in the pre and post blocks of the sensorimotor adaptation condition. The adaptation of the vestibulomotor transformation markedly impacted the trajectories of reaching movements performed during passive body rotations. Figure taken from Bresciani *et al.* (2005) with kind permission of Springer Science+Business Media.

dure, the subjects had to reach for a memorized earth-fixed target during passive CCW body rotations in darkness. The adaptation of the vestibular-based spatial updating process had no effect on the compensatory arm movements (i.e., hand trajectories and reaching endpoints were both similar before and after the adaptation). However, adaptation of the vestibulomotor process brought significant changes in the compensatory arm movements during the rotations. This can be seen in Fig. 4 that shows the mean hand paths recorded in a subject when reaching for a 10° target during 20°, 30° and 40° counterclockwise rotations, both before and after adaptation of the vestibulomotor processes. The hand paths produced during body rotations were markedly deviated to the left after adaptation (solid lines, indicating undercompensation for the CCW body rotation) compared to those produced before adaptation (broken lines). Together, these results are in line with the suggestion that during passive self-motion, the vestibular control of arm-reaching movements essentially derives from a sensorimotor process by which arm motor output is modified on-line to preserve hand trajectory in space despite body displacement. These results also suggest that, in contrast, the updating process which maintains up-to-date the egocentric representation of the visual space during body motion contributes little to the arm motor compensation during body rotations.
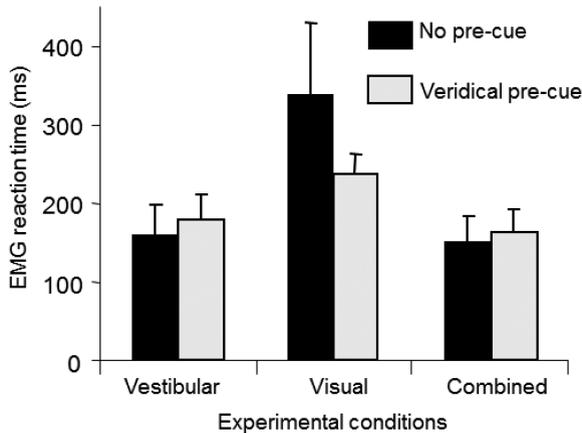
Figure 5. EMG response times (pectoralis major and posterior deltoid muscles) with and without prior information about arm movement direction when the goal of the movement was to stabilize the hand during body rotation ('Vestibular' and 'Combined' conditions) or to track the moving target with the finger ('Visual' condition). Providing advance information had no effect on the latency of the muscular activities responsible to keep the hand stationary during body rotations but largely reduced electromyographic (EMG) response times during visually-tracking arm movements. Figure taken from Blouin *et al.* (2010) with kind permission of Wolters Kluwer Health.

The limited contribution of cognitive processes in the vestibular control of arm movements was further evidenced in a study in which we provided advance information to the subjects about the direction of the required arm movement to keep the (unseen) hand stationary in space during passive whole-body rotation (Blouin *et al.*, 2010). Providing either true or false information about the required movement direction had no effect on the latency of the arm motor response [the first burst of electromyographic (EMG) activity was observed ∼160 ms after body rotation onset]. This was the case regardless of whether an earth-fixed visual anchor for the finger was displayed or not during body rotation (conditions '*Combined*' and '*Vestibular*', respectively in Fig. 5). This contrasted with the marked effect of providing advance information about the future direction of a moving visual target that the subjects had to track with the unseen finger (a task that is considered to depend largely on cognitive processes (Masson *et al.*, 1995; Mrotek *et al.*, 2006; Poulton, 1981)). In this visuo-manual tracking task, the pre-cue on movement direction reduced EMG response time by ∼120 ms (condition '*Visual*' in Fig. 5). It is worth noting that the required horizontal arm movement with respect to the trunk was the same (i.e., amplitude and speed) in this manual tracking task and in the body rotation condition during which participants had to maintain the hand stationary in space.

Even more surprisingly, in 86% of the trials of the visuo-manual tracking task in which the subjects received false pre-cues about the future movement direction, a burst of EMG activity appeared first in the antagonist muscle, i.e., the muscle moving the arm in the direction congruent with the false pre-cues, but opposite of the direction of the target that the subjects had to track. This effect of the false pre-cues was seldom observed when the subjects had to keep the hand stationary in space during body rotation. It is worth noting that the EMG response time recorded in the visuo-manual tracking task with no pre-cueing (i.e., $\sim$350 ms) was more than twice as long as those observed when subjects had to stabilize the hand in space during body rotation (i.e., $\sim$165 ms). Importantly, tested in the same paradigm, the deafferented patient GL showed EMG response times that closely matched those recorded in healthy subjects (see Fig. 6). This result strongly hints at a vestibular origin (rather than at a proprioceptive) to the compensatory arm movements observed during body rotations. Taken together, these results suggest that the vestibular control of arm movements is more immune to cognitive processes than visually driven tracking arm movements. This distinction between vestibular and visual control of movements was also evidenced by Barnes and Paige (2004) for the control of eye movements and by Guerraz and Day (2005) for the control of balance.

Performing a motor task that is largely controlled by automatic processes is known to have little or no effect on the performance of a simultaneously performed task which involves other effectors (Ehrenfried *et al.*, 2003; Fleury *et al.*, 1994; Lajoie *et al.*, 1993; Teasdale and Simoneau; 2001; Yardley *et al.*, 1999, 2002). We exploited this well-known phenomenon to assess the automatic nature of the vestibular control of arm movement by comparing the amount of interference of reaching movements performed with or without whole-body rotations on a concurrent cognitive task (Guillaud *et al.*, 2006b). This cognitive task consisted of responding verbally as fast as possible to an auditory stimulus (50 ms beep). We found that the reaction times to the auditory stimulus was $\sim$120 ms longer when participants were rotated during reaching movements than when they remained stationary. Note that we also observed that the reaction times to the stimulus were $\sim$40 ms longer when subjects were submitted to passive body rotations without concurrent reaching movement compared to the condition without the rotation and reaching movement. This reaction time increase may be due to the massive flow of whole-body motion-related information reaching the brain (e.g., from labyrinths, skin, body graviceptors) while subjects were processing and responding to the auditory stimulus. More importantly, the larger reaction time increase observed when subjects were reaching for a target during whole-body rotation suggests that the control of arm movement during body motion cannot be considered as being an automatic motor task.
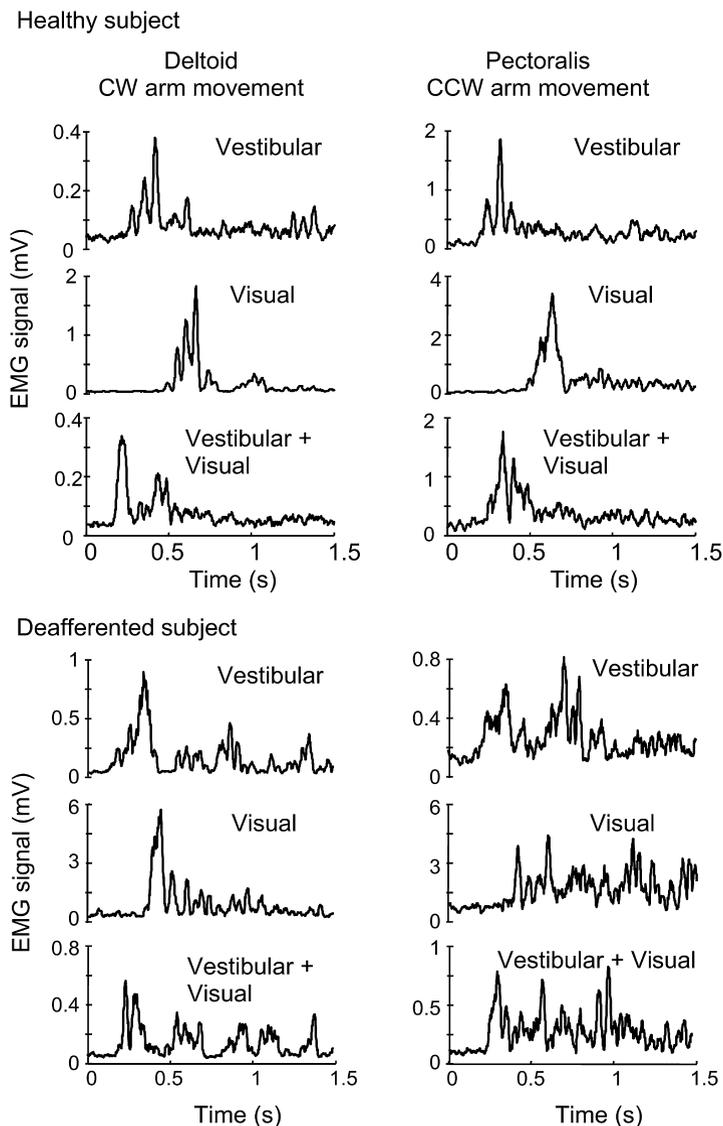
Figure 6. EMG recordings of the arm muscles from representative trials by a healthy subject (upper panel) and by a deafferented subject (lower panel) when the goal of the arm movement was to stabilize the hand during body rotation ('Vestibular' and 'Vestibular+Visual' conditions) or to track a moving target with the finger when the body remained stationary ('Visual' condition). Irrespective of the goal of the movements, clear EMG bursts occurred in the posterior deltoid muscle during CW arm movements and in the pectoralis major muscle during CCW arm movements. The latency of the EMG response was considerably shorter for movements that compensate for body rotation (thereby keeping the hand stationary in space) than for visually-guided manual tracking (in the graphs, the onset of chair rotation or visual target motion occurred at 0 s). Figure taken from Blouin *et al.* (2010) with kind permission of Elsevier.

5. Body Rotation Induces Perturbing Torques on the Arm during Reaching Movements

Rotating the trunk when reaching for a target induces centrifugal and Coriolis torques that deviate the hand away from the planned trajectory in the opposite direction to the rotation (Bortolami *et al.*, 2008a, b; Guillaud *et al.*, 2006b; Pigeon *et al.*, 2003). The impact of these forces on the arm is particularly noticeable when subjects reach for a target during sustained passive body rotation at constant velocity. Because the vestibular receptors are sensitive to acceleration, sensation of body motion rapidly vanishes when angular velocity reaches a constant value (Dodge, 1923; Goldberg and Fernandez, 1971; Laurens and Angelaki; 2011). When reaching for a body-fixed target in such conditions, the hand trajectory and the endpoint of the reaching movement largely deviate in the direction of the Coriolis force applied on the arm (Bortolami *et al.*, 2008b; Bourdin *et al.*, 2001; Coello *et al.*, 1996; Lackner and DiZio, 1992, 1994; Sarlegna *et al.*, 2010).

As the magnitudes of centrifugal and Coriolis torques depend on trunk angular kinematics, errors in coding trunk kinematics may therefore have detrimental effects on reaching accuracy. We have adapted the biomechanical model of Pigeon *et al.* (2003) to assess the consequences of such errors on reaching accuracy (Simoneau *et al.*, 2013). Our feedforward model simulated underestimation of torso acceleration occurring during the planning stage of reaching, and excluded any online correction of hand deviation based on sensory feedback (e.g., proprioceptive, vestibular or visual information). Results of the model demonstrate that even small errors in perceiving or predicting the kinematics of torso rotation may impair the accuracy of reaching movements. For instance, underestimating by only 10% CCW torso rotation having a sinusoidal velocity profile peaking at 3 rad/s induced a final hand deviation as large as 11 cm when reaching for a straight-ahead target. Therefore, the high accuracy with which subjects reach for targets during self-initiated or imposed discrete torso rotation (Bortolami *et al.*, 2008b; Bresciani *et al.*, 2002b, 2005; Pigeon *et al.*, 2003) or continuously point at a remote target during body displacement without visual feedback (Blouin *et al.*, 2010; Bresciani *et al.*, 2005; Frissen *et al.*, 2011; Guillaud *et al.*, 2006a; Ivanenko and Grasso, 1997; Ivanenko *et al.*, 1997a; Loomis *et al.*, 1992; Philbeck *et al.*, 2001) suggests that the brain precisely estimates trunk kinematics and takes into account the additional torques generated by the torso rotation.

6. Vestibular-Based Prediction of Body Rotation Induced Torques on the Arm During Reaching Movements

Torso rotation usually accompanies the arm movement when reaching for an eccentric object. During such voluntary torso rotation, the self-induced

Coriolis force applied on the arm could be compensated for by anticipatory pre-programmed processes (Bortolami *et al.*, 2008b; Pigeon *et al.*, 2003). However, anticipatory pre-programmed processes cannot intervene when subjects are submitted to passive rotations during reaching movements. The high accuracy with which subjects reach for a target in such conditions (as discussed above), even when visual feedback is not available, suggests that other mechanisms might be involved for compensating for the perturbing forces acting on the arm.

The amplitude and direction of the rotation-induced torques depend on the velocity and direction of trunk rotation. Given the high computational capabilities of the brain (Angelaki *et al.*, 2004; Merfeld *et al.*, 1999; Sarway *et al.*, 2013), the vestibular signal generated during body rotation could provide valuable information for estimating the rotation-induced torques on the arm. The results of an elegant study by Bockisch and Haslwanter (2007) have provided convincing support for this hypothesis. In their study, the authors exploited the velocity-storage mechanisms which allow prolonging vestibular signals (Raphan *et al.*, 1979; Shaikh *et al.*, 2013; Sinha *et al.*, 2008) and therefore sensation of rotation when body rotation rapidly decelerates to a stop. As classically observed in such conditions (e.g., St George *et al.*, 2011), when the strong deceleration occurred after sustained rotation at constant velocity, participants perceived that they were rotated in the opposite direction. This is because the response of the vestibular receptors during motion deceleration in a given direction is similar to the response evoked when accelerating in the opposite direction. The authors found that the hand trajectories produced immediately after the rotation were deviated in the same direction as the illusory body rotations. The direction of the hand deviation suggested that the immobile subjects anticipated the (nonexistent) perturbing torques based on the vestibular signals and attempted to compensate for them. Note that similar hand deviation was observed by Cohn *et al.* (2000) when illusory body rotation was induced using a rotating visual field.

Bockisch and Haslwanter's (2007) findings provided a nice demonstration that vestibular information can be processed by the brain to predict rotation-induced torques applied on the arm. However, they do not provide clear indication as to the accuracy of the prediction. This is due, first, to the difficulty to precisely quantify either the actual vestibular stimulation during the reaching movements or the perturbing torques that are normally associated with it during real body rotations. For instance, in Bockisch and Haslwanter's (2007) study, the vestibular stimulation during the reaching could only be estimated with the assumption that the cupula returned to the resting position with a time constant of 6 s. Moreover, and perhaps most importantly, because the processing of arm somatosensory inputs may have resulted in trajectory corrections (their subjects had to reach for a target positioned straight-ahead), neither the

hand path curvature nor the reached endpoint could provide clear images of the vestibular based prediction of the perturbing torques.

To gain insight into the accuracy of the vestibular-based prediction of the torques induced by body rotations, we asked the deafferented patient GL to reach for a memorized visual target located straight-ahead while her torso was rotated in complete darkness thus without visual feedback of the hand (Guillaud *et al.*, 2011). In one condition, a headrest attached to the motorized chair prevented head-on-trunk displacement. Therefore the trunk motion induced by the chair rotation stimulated the patient's vestibular system. In another condition, an experimenter held the patient's head stationary in space during chair rotations. With this manipulation, the patient's perception of the torso rotations under the stationary head was greatly degraded by the absence of rotation induced vestibular signals and by her loss of somatosensory information of the cervical region. Importantly, as the torso rotations (triggered at reaching onset) were identical in both conditions (i.e., amplitudes of $\pm25°$ and $\pm40°$), the rotation-induced torques applied on the arm were also similar. In both conditions (i.e., head fixed and head rotation), the deafferented patient's hand similarly and considerably deviated from body midline in the direction opposite to the body rotation (see Fig. 7). When the patient's head was prevented from rotating (i.e., in absence of vestibular stimulation), the hand deviation remained uncorrected at the end of the reaching movement. Strikingly, the hand path deviations evoked by the torso rotation were corrected when the patient's head rotated with the trunk, that is, when vestibular inputs provided infor-
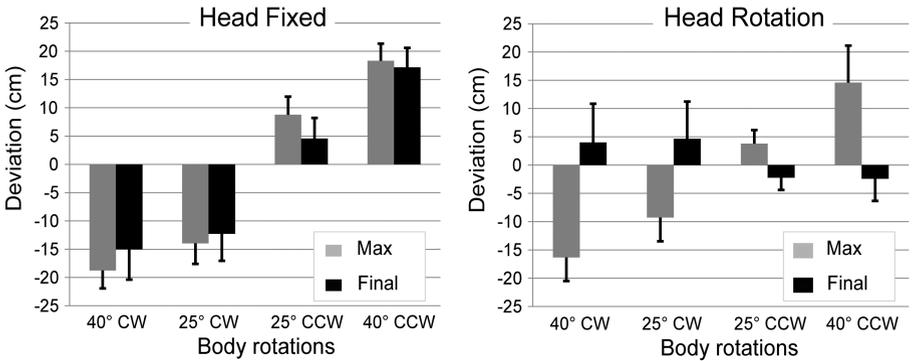

Figure 7. Mean maximal lateral hand deviations (gray bars) and mean final hand deviations (black bars) measured when a deafferented patient was rotated at the onset of her reaching movement towards a memorized visual target located straight-ahead. In the Head Fixed condition (left panel), the patient's head was maintained stationary in space during the body rotation. In the Head Rotation condition (right panel), the patient's head rotated with her trunk allowing the vestibular system to be stimulated by the rotation. The data were normalized with respect to the data recorded in a condition without trunk rotation. Error bars indicate between trials standard deviations. Figure taken from Guillaud *et al.* (2011) with kind permission of Elsevier.

mation about the rotations. These path corrections occurred despite the fact that the patient had no sensation of hand trajectory deviation (and correction). These findings therefore provide compelling evidence that vestibular information can be processed for predicting the consequence of the rotation dynamics on the reaching arm movements.

Acknowledgements

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