

Prediction of the body rotation-induced torques on the arm during reaching movements: Evidence from a proprioceptively deafferented subject

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ARTICLE INFO

Article history:

Received 25 October 2010

Received in revised form 14 March 2011

Accepted 24 March 2011

Available online 31 March 2011

Keywords:

Reaching

Body rotation

Vestibular

Prediction

Deafferentation

ABSTRACT

Reaching for a target while rotating the trunk generates substantial Coriolis and centrifugal torques that push the arm in the opposite direction of the rotations. These torques rarely perturb movement accuracy, suggesting that they are compensated for during the movement. Here we tested whether signals generated during body motion (e.g., vestibular) can be used to predict the torques induced by the body rotation and to modify the motor commands accordingly. We asked a deafferented subject to reach for a memorized visual target in darkness. At the onset of the reaching, the patient was rotated 25° or 40° in the clockwise or the counterclockwise directions. During the rotation, the patient's head remained either fixed in space (Head-Fixed condition) or fixed on the trunk (Head Rotation condition). At the rotation onset, the deafferented patient's hand largely deviated from the mid-sagittal plane in both conditions. The hand deviations were compensated for in the Head Rotation condition only. These results highlight the computational faculty of the brain and show that body rotation-related information can be processed for predicting the consequence of the rotation dynamics on the reaching arm movements.

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1. Introduction

Rotating the trunk while reaching for an object adds stress on the control of the arm movement. Indeed, in such circumstance, the arm will deviate in the opposite direction to the rotation if its motor commands are not adjusted according to the direction and velocity of the rotation. This is because trunk rotations induce torques (e.g., centrifugal and Coriolis torques) that deviate the hand away from the planned trajectory while the arm's inertia tends to keep the arm still in space during body motion (Pigeon, Bortolami, DiZio, & Lackner, 2003). Remarkably, hand trajectories during self-initiated or imposed torso rotation remain highly accurate even if visual feedback of the arm and target is not available (Bresciani et al., 2002; Bresciani, Gauthier, Vercher, & Blouin, 2005; Pigeon et al., 2003). This suggests that the brain takes into account the torques generated by the torso rotation (hereafter called perturbing torques) during movement planning or execution.

The amplitude and direction of the perturbing torques depend on the velocities and directions of trunk rotation. Given the high computational capabilities of the brain (see for instance, Angelaki, Shaikh, Green, & Dickman, 2004; Merfeld, Zupan, &

Peterka, 1999), rotation-induced sensory signals (e.g., vestibular) could provide valuable information for predicting and compensating the effect of the perturbing torques. Bockisch and Haslwanter (2007) found convincing support for this possibility. These authors prompted subjects to reach for a memorized straight-ahead target immediately after a sudden stop of sustained passive whole-body rotations in darkness. After the rotations, due to the endolymph and hair cells mechanics of the semi-circular canals, the stationary subjects had the illusion of self-rotation in the opposite direction to the rotation. Surprisingly, subjects produced hand trajectories that were slightly (~3 cm) but significantly deviated in the same direction as the illusory body rotations. The direction of the hand path curvatures suggested that the subjects anticipated the (nonexistent) perturbing torques based on the vestibular signals and attempted to compensate for them.

While these findings show that prediction of rotation-evoked torques applied on the arm can be based on the sole basis of vestibular information, they do not provide information on the accuracy of the prediction. Indeed, as no actual body rotation occurred during the arm movements in Bockisch and Haslwanter's (2007) study, it proves difficult to quantify the actual subjects' vestibular stimulation while reaching straight-ahead (and the perturbing torques that are normally associated with this vestibular stimulation). More importantly, because muscle proprioception provides continuous

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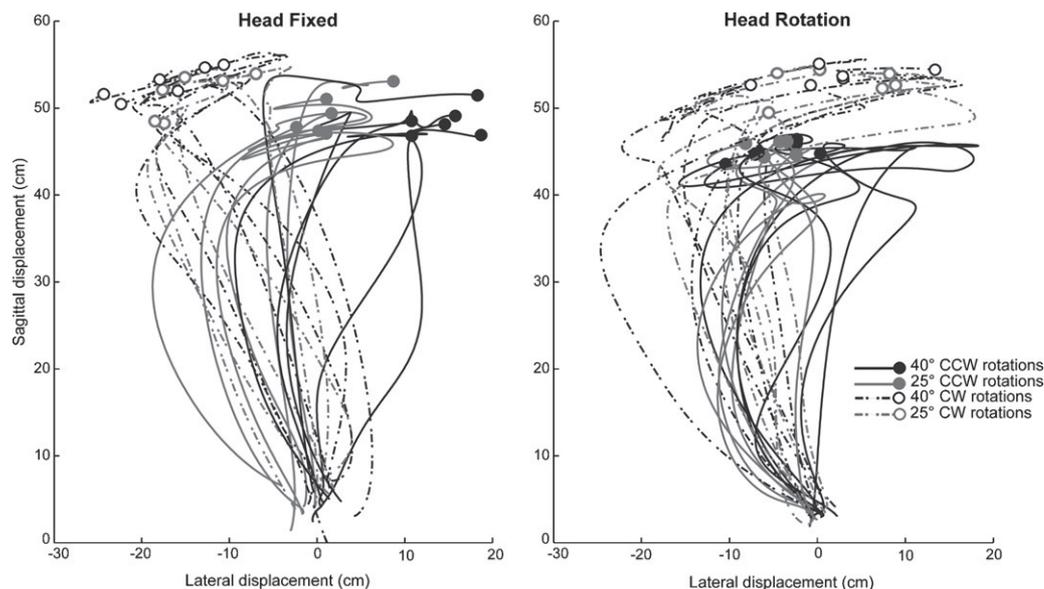


Fig. 1. Top view of the hand reaching trajectories recorded for both amplitude of rotations (25° and 40°) during clockwise (CW) and counterclockwise (CCW) body rotations, represented in trunk-fixed space.

feedback on hand position, neither the hand curvature nor the reached endpoint provides clear images of the vestibular-based prediction of the perturbing torques.

Here, we designed a protocol that enabled us to assess the accuracy that rotation-induced information can be used for predicting and compensating the effect of the perturbing torques on reaching arm movements. Toward that aim, we tested the capacity of a woman having a normal vestibular system but who is suffering from an extremely rare somatosensory loss (from the nose to the feet) to reach straight-ahead while her torso was being simultaneously rotated. During the rotations performed in the dark, the patient's head remained either fixed in space or fixed on her trunk. We reasoned that the hand trajectory recorded in the former condition wherein the patient had presumably no sensory information related to torso rotation should provide direct assessments of the impact of the perturbing torques on the hand trajectories if not compensated. Indeed, in such condition, the selected motor commands should be similar to those used in the absence of body rotation and should not allow compensation for the torques caused by the rotations. On the other hand, allowing the patient's head to rotate with the trunk in the latter condition gave the unique opportunity to establish the capacity of the brain to use inertial rotation-induced signals from the inner ears for predicting and compensating for these torques.

2. Methods

2.1. Deafferented patient

At the age of 31, after a severe sensory polyneuropathy, the deafferented subject (right-handed female, 55 years) incurred the loss of the large myelinated fibers. At this time, and since then, she has an acute loss of all somatosensory modalities (kinaesthesia, tendon reflexes, touch, vibration, pressure) from her nose to her feet (Forget & Lamarre, 1995). The percentage of myelinated fibers larger than 9 μm in diameter is very small (0.31% compared to 18% for healthy subjects). The patient's vestibular nerves remained intact as confirmed by assessment of her vestibulo-ocular reflex (Blouin et al., 1995). Deafferentation of the cervical muscles is evidenced by the patient's failure to detect passive slow head-on-trunk rotations (i.e., below vestibular threshold) as large as 50° in the dark (Blouin, Teasdale, & Mouchino, 2007). Prior to the experiment, the patient gave a signed consent to participate in this experiment in accordance with the ethical standards set out in the 1964 Declaration of Helsinki.

2.2. Apparatus and procedures

The deafferented subject was securely seated in the dark on a chair positioned above the axis of a revolving platform. She wore audio earphones diffusing a white noise to mask possible auditory spatial reference cues. The platform was rotated by a servomotor whose speed was controlled by a Smart Motor Control Card (Baldor SMCC, Arkansas, USA). The platform's angular position was returned to the computer by the axis control card. It provided measurement of the patient's trunk orientation. A light emitting diode (LED) fixed on the right index finger could provide visual feedback of the finger. The positions of the patient's finger and head were measured by electromagnetic sensors (Polhemus, Fastrak, Vermont, USA). Because magnetic fields are sensitive to metallic environments, all the elements positioned inside the working volume were made of wood or plastic. The absolute position of the finger could be measured with an accuracy of 1 mm and with a sampling rate of 60 Hz.

A large micro-switch, fixed on the patient's chin, was used as the starting finger position. A target (LED) was located in her mid-sagittal plane, at chin level. Its distance was adjusted in order to be slightly out of reach. At the start of each trial, the finger LED was switched on, prompting the patient to bring her finger onto her chin. Pressing on the switch turned on the target. Whenever she felt ready, the patient extended the arm to reach the target at her preferred speed. The release of the switch extinguished both the finger LED and the target, the onset of the chair rotation occurred 300 ms later. The pseudo-randomly selected magnitudes of the rotation were 25° or 40° in the clockwise (CW) or the counterclockwise (CCW) directions. All rotations lasted 1 s and had bell shaped velocity profiles peaking at 58°/s and 93°/s for the 25° and 40° rotations, respectively.

In the condition Head Rotation (hereafter called HR, first tested), a headrest attached to the seat prevented head-on-trunk displacement. Because of the patient's massive loss of somatosensory information, the rotation activated mainly the horizontal semi-circular canals of the vestibular system. No instructions were given regarding eye movements but ocular movements most likely occurred during the vestibular stimulation. In the Head-Fixed condition (hereafter called HF), an experimenter, standing on a fixed stand behind the patient, held her head stationary in space during the rotations. Deprived of somatosensory information at the cervical region, the patient's perception of the torso rotation should be severely impaired in this condition. For each condition, 6 trials were performed per direction (i.e., CCW and CW) and per amplitude of rotation (i.e., 25° and 40°) and 6 trials were performed without body rotation (control condition).

The performance of healthy subjects while aiming at a straight-ahead target during passive torso rotation has already been reported (Guillaud, Simoneau, Gauthier, & Blouin, 2006). Because arm proprioception provides information about hand position relative to the trunk, their performance does not inform on the faculty of the brain to use rotation-induced signals for predicting perturbing torques acting on the arm. For these reasons, healthy subjects were not considered in this study. Because the perturbation torques acted principally perpendicularly to the direction of the reaching movement, we computed the patient's mean finger position relative to the mid-sagittal plane. Using the measured trunk rotations, we converted the hand kinematic data recorded in the environment frame of reference into a torso frame of reference. Both the maximal deviation of the hand from straight-ahead and the final hand position were computed. Maximal hand deviation was the maximal perpendicular distance between the hand trajectory and the mid-sagittal plane. Final

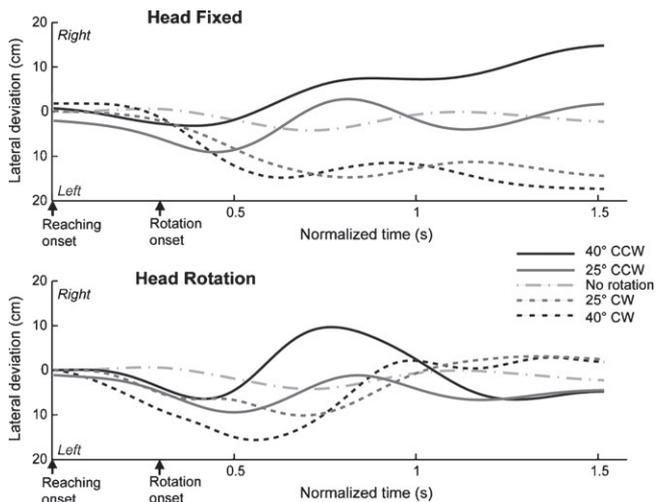


Fig. 2. Deafferented patient's mean finger position relative to the mid-sagittal plane during the 25° and 40° body rotations in the Head Rotation (lower panel) and Head-Fixed (upper panel) conditions. As the maximal deviations relative to the midsagittal plane did not occur at the same time for all trials of a given condition, the mean trajectories had smaller maximal hand deviations than the computed mean maximal deviations illustrated in the histograms of Fig. 3.

hand position was the distance between the hand and the mid-sagittal plane when reaching movement offset was detected. After movement onset, the hand of the patient never completely stabilized. Movement offset was operationally defined as when hand velocity dropped below 1 cm/s for 0.5 s. A negative sign represents hand deviation to the left side of mid-sagittal plane whereas a positive sign represents hand deviation to the right side. The mean final hand position obtained for each rotation amplitude and each condition, was subtracted from the mean final hand position calculated in the trials without body rotation. The same procedure was applied for the maximal path deviations. This data normalization allowed better comparison of the effect of the rotational-induced torques on the hand trajectories across conditions.

The perturbing torques evoked by body rotations are proportional to both the trunk angular velocity and the velocity of the reaching movement. To verify whether the perturbing torques differed between the conditions with torso rotations, we compared the peak velocity of the movements produced by the patient the HR and HF conditions.

We used two-tailed *t*-tests for related samples to compare the effect of the experimental conditions ($p < 0.05$).

3. Results

The deafferented patient's initial hand trajectories tended to be deviated to the left (Figs. 1 and 2) as often observed with right handed subjects performing 3-dimensional unconstrained movements (Desmurget, Jordan, Prablanc, & Jeannerod, 1997; Scott, Gribble, Graham, & Cabel, 2001). Following the rotation onset, the hand largely deviated in the opposite direction of the rotations in both the HF and HR conditions. As expected, the deviation increased with the magnitude (and velocity) of the rotation (Fig. 2). The maximal deviations did not significantly differ between HF and HR conditions for the 25° CW rotations (mean = -11.65 cm, $t(10) = -2.08$, $p > 0.05$), the 40° CW rotations (mean = -17.55 cm, $t(10) = -1.15$, $p > 0.05$) and the 40° CCW rotations (mean = 16.45 cm, $t(10) = 1.27$, $p > 0.05$) (Fig. 3). Only for 25° CCW rotations, the maximal hand deviations were significantly larger when the head was fixed in space than when it rotated with the trunk (8.8 cm and 3.8 cm, respectively; $t(10) = 3.05$, $p = 0.01$).

Compared to the HR condition, in the HF condition, the patient's hand remained largely deviated from the mid-sagittal plane at the end of the reaching (Fig. 2 – lower panel versus upper panel), with final hand deviations of -12.3 cm and -15 cm for the 25° and 40° CW rotations respectively, and 4.6 cm and 17.2 cm for the 25° and 40° CCW rotations respectively (Fig. 3 – left panel). This was con-

firmed by the *t*-tests revealing that the maximal and final hand deviations were not significantly different in all rotation conditions ($t(10) = -0.69$ for 25° CW; $t(10) = -1.47$ for 40° CW; $t(10) = 2.12$ for 25° CCW; and $t(10) = 0.62$ for 40° CCW, all $p > 0.05$). Deprived of sensory information at the cervical region, the patient could only report vague sensation of self-motion but she was unable to determine whether it was her head or her trunk that had slightly rotated. This sensation might have arisen from the pressure applied by the experimenter's hands on her head, where somatosensory information is preserved.

Remarkably, in the HR condition, the deafferented patient largely compensated for the large shift in hand trajectory (Fig. 3 – right panel). In this condition, the patient even over-compensated the perturbing torques as her mean final hand positions were in the opposite direction of the maximal deviation (4.7 cm and 4 cm for the 25° and 40° CW rotations respectively, and -2.4 cm and -2.2 cm for the 25° and 40° CCW rotations, respectively). Irrespective of the amplitude and direction of the rotations, the *t*-tests revealed that the hand deviations at movement offset were significantly smaller than the maximal hand deviations ($t(10) = -4.38$ for 25° CW; $t(10) = -6.21$ for 40° CW; $t(10) = 4.58$ for 25° CCW; $t(10) = 5.45$ for 40° CCW, all $p < 0.05$). We estimated the time required to initiate the correction of the hand trajectories by subtracting 300 ms (i.e., rotation onset) from the time to peak hand deviation. This time did not significantly differ between the different directions ($t(22) = 0.27$, $p = 0.79$) and amplitudes ($t(22) = -1.05$, $p = 0.3$) and was on average 571 ms (± 134 ms).

As shown in Fig. 1, the trajectories produced by the patient were characterized by a large variability. This is typical of 3-dimensional unconstrained multijoint movements performed by deafferented patients (e.g., Sainburg, Poizner, & Ghez, 1993; Sarlegna, Gauthier, Bourdin, Vercher, & Blouin, 2006). The reaching peak velocity was significantly smaller in HR condition than in HF condition indicating slower movements in the former condition (HR = 120.7 ± 22.8 cm s⁻¹, HF = 142.9 ± 29.8 cm s⁻¹; $t(46) = -2.90$, $p = 0.01$). The time of occurrence of the peak velocity did not significantly differ between the HR and HF conditions [HR = 0.48 ± 0.12 s, HF = 0.47 ± 0.21 s, $t(46) = 0.17$, $p = 0.87$]. Finally, the movements produced by the patient had a longer duration in the HR condition than in the HF condition (HR = 1.64 ± 0.27 s, HF = 1.43 ± 0.26 s, $t(46) = 2.65$, $p = 0.01$).

4. Discussion

Submitting the deafferented patient to passive whole-body rotations while she extended her arm to point straight-ahead considerably deviated her hand from body midline. Such deviations, which were in the opposite direction of the body rotations, have also been reported in healthy subjects, but with much smaller amplitude (Dizio & Lackner, 1995; Guillaud et al., 2006). These hand deviations most certainly resulted from a combined effect of the arm's inertia that tends to keep the arm still in space and the rotations induced torques that acted on the arm (e.g., centrifugal and Coriolis torques).

However, the most striking finding was that in the absence of arm position sense and visual feedback, the deafferented patient corrected for these hand deviations when her head rotated with her trunk. In this condition, the patient reported clear perception of trunk rotation but no sensation of hand trajectory deviation and correction. Perception of rotation most likely arose from the activation of the vestibular system and perhaps from the resulting putative eye movements. Together, the rotation-induced signals may have allowed the brain to compute an estimate of the perturbing torques applied on her arm and to change the motor commands accordingly.

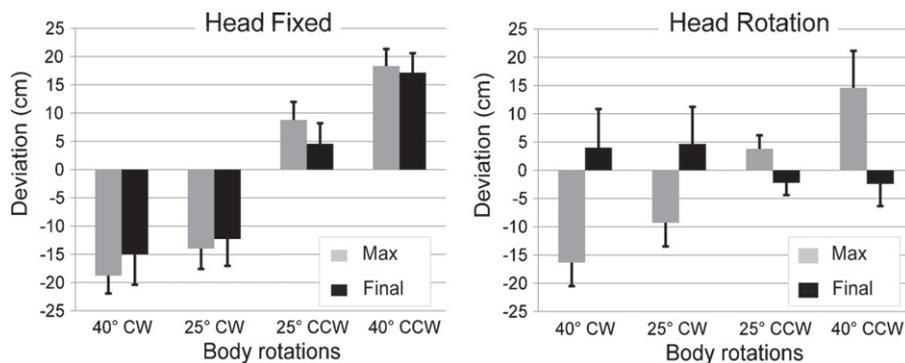


Fig. 3. Deafferented patient's mean maximal lateral hand deviations (gray bars) and mean final hand deviations (black bars) in the Head Fixed (left panel) and Head-Rotation (right panel) conditions, for the 25° and 40° rotation amplitudes. Error bars indicate between-trials standard deviations.

Consistent with this proposal, we found that the deviations of the hand were uncorrected when the patient's head remained fixed in space during her trunk rotations. In this condition, the patient's perception of the torso rotations was greatly degraded by the absence of rotation-induced vestibular signals and by her loss of somatosensory information of the cervical region. In the absence of feedback signaling torso rotation, the prediction of the perturbing forces on the arm during the reaching movements turned out to be impossible.

Previous studies have shown that vestibular (Bockisch & Haslwanter, 2007) and visually evoked (Cohn, DiZio, & Lackner, 2000) information of (illusory) body rotation can be used to alert the brain that external forces may perturb forthcoming reaching movements. However, thus far the level of accuracy of this prediction was not known. Indeed, the healthy subjects tested in previous studies were endowed with somatosensory signals from the reaching arm. These signals provide information on hand position with respect to the body and on the presence of forces perturbing the movements. Then the small deviations (i.e., ≤ 4 cm) observed in these studies during either the vestibular or visually induced self-motion illusion may not be representative of the brain's actual estimate of the external torques acting on the arm during the reaching. By showing that a patient deprived of somatosensory information can compensate for the rotation-induced perturbing torques, the present study provides experimental evidence that the central prediction of these torques from vestibular information is accurate and can be used to control goal-directed arm movements.

It is worth noting that the perturbing torques evoked by body rotations are not only a function of the trunk angular velocity but are also proportional to the mass of the arm and the velocity of the reaching movement. The large automatic hand path corrections that were observed during the patient's movements therefore highlight the capacity of the brain to dynamically use both body rotation information and information related to the kinematics of the arm movements. The present results are then consistent with current models in which the motor commands are produced according to an internal prediction of the dynamics of the task (Cohn et al., 2000; Kurtzer, Pruszynski, & Scott, 2008; Papaxanthi, Pozzo, & McIntyre, 2005; Wolpert & Flanagan, 2001). According to these models, the brain would use internal models capable of performing the complex computations required to capture the relationship between the context in which the movement is produced (which includes the additional arm joint torques due to body rotations) and the effect of the motor commands on the arm. Converging lines of evidence suggest that the latter can be estimated using efference copy issued from movement preparation (Desmurget & Grafton, 2000; Wolpert & Flanagan, 2001). The long latencies of the trajectories corrections (~ 570 ms) give support to the idea that the trajectories corrections were not issued from direct vestibulospinal pathways.

Our findings provide compelling indications that internal models were largely preserved in the patient despite the absence of somatosensory information. Internal models in the patient could be updated, during daily activities, by integrating visual and vestibular signals and motor commands. However, the fact that the patients produced variable and relatively slow movements (~ 1.5 s) may indicate that these internal models were not completely unimpaired. Indeed, producing slow movements may correspond to a strategy of the patient for avoiding large interaction torques between shoulder and elbow joints. These interaction torques increase with the velocity of the movements (Gribble & Ostry, 1999) and they are known to be difficult to compensate for in absence of proprioception (Sainburg et al., 1993). Although the maximal deviations of the hand produced by the torso rotations did not significantly differ between the HF and HR conditions, the movements produced by the patient were slower in the Head rotation condition than in the Head-fixed condition. This could also represent a viable strategy for the patient to reduce the rotation-induced inertial torques in the condition where she was clearly aware of body rotations.

The neural mechanisms for capturing the relationship between the motor system and the physical environment are currently investigated. There is converging evidence that the cerebellum has an essential role into these mechanisms. Indeed, this fundamental brain structure for motor control is considered to contain internal model(s) of the motor apparatus (Wolpert, Miall, & Kawato, 1998) and to play an important role for predicting movements outcomes (Blakemore & Sirigu, 2003; Bastian, 2006). Finally, thanks to its tight connection with the vestibular apparatus, the cerebellum may contribute in building internal models of self-motion (Angelaki et al., 2004).

Acknowledgments

This research was supported by Natural Sciences and Engineering Research Council of Canada and the French Centre National d'Etudes Spatiales. We thank Franck Buloup and Gabriel Gauthier for their help.

References

- Angelaki, D. E., Shaikh, A. G., Green, A. M., & Dickman, J. D. (2004). Neurons compute internal models of the physical laws of motion. *Nature*, 430, 560–564.
- Bastian, A. J. (2006). Learning to predict the future: The cerebellum adapts feedforward movement control. *Current Opinion in Neurobiology*, 16, 645–649.
- Blakemore, S. J., & Sirigu, A. (2003). Action prediction in the cerebellum and in the parietal lobe. *Experimental Brain Research*, 153, 239–245.
- Bloin, J., Teasdale, N., & Mouchino, L. (2007). Vestibular signal processing in a subject with somatosensory deafferentation: The case of sitting posture. *BMC Neurology*, 7, 25.

- Blouin, J., Vercher, J. L., Gauthier, G. M., Paillard, J., Bard, C., & Lamarre, Y. (1995). Perception of passive whole-body rotations in the absence of neck and body proprioception. *Journal of Neurophysiology*, *74*, 2216–2219.
- Bockisch, C. J., & Haslwanter, T. (2007). Vestibular contribution to the planning of reach trajectories. *Experimental Brain Research*, *182*, 387–397.
- Bresciani, J. P., Blouin, J., Sarlegna, F., Bourdin, C., Vercher, J.-L., & Gauthier, G. M. (2002). On-line versus off-line vestibular-evoked control of goal-directed arm movements. *Neuroreport*, *13*, 1563–1566.
- Bresciani, J. P., Gauthier, G. M., Vercher, J.-L., & Blouin, J. (2005). On the nature of the vestibular control of arm-reaching movements during whole-body rotations. *Experimental Brain Research*, *164*, 431–441.
- Cohn, J. V., DiZio, P., & Lackner, J. R. (2000). Reaching during virtual rotation: Context specific compensations for expected coriolis forces. *Journal of Neurophysiology*, *83*, 3230–3240.
- Desmurget, M., & Grafton, S. (2000). Forward modeling allows feedback control for fast reaching movements. *Trends in Cognitive Sciences*, *4*, 423–431.
- Desmurget, M., Jordan, M., Prablanc, C., & Jeannerod, M. (1997). Constrained and unconstrained movements involve different control strategies. *Journal of Neurophysiology*, *77*, 1644–1650.
- Dizio, P., & Lackner, J. R. (1995). Motor adaptation to Coriolis force perturbations of reaching movements: Endpoint but not trajectory adaptation transfers to the nonexposed arm. *Journal of Neurophysiology*, *74*, 1782–1787.
- Forget, R., & Lamarre, Y. (1995). Postural adjustments associated with different unloadings of the forearm: Effects of proprioceptive and cutaneous afferent deprivation. *Canadian Journal of Physiology and Pharmacology*, *73*, 285–294.
- Gribble, P. L., & Ostry, D. J. (1999). Compensation for interaction torques during single- and multi-joint limb movement. *Journal of Neurophysiology*, *82*, 2310–2326.
- Guillaud, E., Simoneau, M., Gauthier, G., & Blouin, J. (2006). Controlling reaching movements during self-motion: Body-fixed versus Earth-fixed targets. *Motor Control*, *10*, 330–347.
- Kurtzer, I. L., Pruszynski, J. A., & Scott, S. H. (2008). Long-latency reflexes of the human arm reflect an internal model of limb dynamics. *Current Biology*, *18*, 449–453.
- Merfeld, D. M., Zupan, L., & Peterka, R. J. (1999). Humans use internal models to estimate gravity and linear acceleration. *Nature*, *398*, 615–618.
- Papaxanthis, C., Pozzo, T., & McIntyre, J. (2005). Kinematic and dynamic processes for the control of pointing movements in humans revealed by short-term exposure to microgravity. *Neuroscience*, *135*, 371–383.
- Pigeon, P., Bortolami, S. B., DiZio, P., & Lackner, J. R. (2003). Coordinated turn-and-reach movements. I. Anticipatory compensation for self-generated coriolis and interaction torques. *Journal of Neurophysiology*, *89*, 276–289.
- Sainburg, R. L., Poizner, H., & Ghez, C. (1993). Loss of proprioception produces deficits in interjoint coordination. *Journal of Neurophysiology*, *70*, 2136–2147.
- Sarlegna, F., Gauthier, G. M., Bourdin, C., Vercher, J.-L., & Blouin, J. (2006). Internally driven control of reaching movements: A study on a proprioceptively deafferented subject. *Brain Research Bulletin*, *69*, 404–415.
- Scott, S. H., Gribble, P. L., Graham, K. M., & Cabel, D. W. (2001). Dissociation between hand motion and population vectors from neural activity in motor cortex. *Nature*, *413*, 161–165.
- Wolpert, D. M., & Flanagan, J. R. (2001). Motor prediction. *Current Biology*, *11*, R729–732.
- Wolpert, D. M., Miall, R. C., & Kawato, M. (1998). Internal models in the cerebellum. *Trends in Cognitive Sciences*, *2*, 338–347.