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## Research Report

# Insights into the control of arm movement during body motion as revealed by EMG analyses

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## ABSTRACT

Recent studies have revealed that vestibulomotor transformations contribute to maintain the hand stationary in space during trunk rotation. Here we tested whether these vestibulomotor transformations have the same latencies and whether they are subject to similar cognitive control than the visuomotor transformations during manual tracking of a visual target. We recorded hand displacement and shoulder-muscle activity in two tasks: a stabilization task in which subjects stabilized their hand during passive 30° body rotations, and a tracking task in which subjects tracked with their finger a visual target as it moved 30° around them. The EMG response times recorded in the stabilization task (~165 ms) were twice as short as those observed for the tracking task (~350 ms). Tested with the same paradigm, a deafferented subject showed EMG response times that closely matched those recorded in healthy subjects, thus, suggesting a vestibular origin of the arm movements. Providing advance information about the direction of the required arm movement reduced the response times in the tracking task (by ~115 ms) but had no significant effect in the stabilization task. Generally, when providing false information about movement direction in the tracking task, an EMG burst first appeared in the muscle moving the arm in the direction opposite to the actual target motion (i.e., in accord with the precueing). This behavior was rarely observed in the stabilization task. These results show that the sensorimotor transformations that move the arm relative to the trunk have shorter latencies when they originate from vestibular inputs than from visual information and that vestibulomotor transformations are more resistant to cognitive processes than visuomotor transformations.

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## 1. Introduction

Most of the hand movements performed by human and non-human primates are directed toward visual or somatosensory targets. In line with this, several behavioral and neurophysiological studies investigated the control of these daily actions. Specific effort has been devoted to understanding the processes leading to the transformation of the visual and/or somatosensory information of the spatial goal of the movement into the motor output required to reach that goal (Batista and Newsome, 2000; Bernier et al., 2009; Crawford et al., 2004; Sarlegna and Sainburg, 2007; Sober and Sabes, 2005).

Converging lines of evidence suggest that vestibular signals can also be involved in sensorimotor transformations during goal-directed hand movements. Providing information about the linear and angular displacements of the head/body in space, the vestibular inputs would be used to trigger the motor commands enabling stationary hand position/trajectory in space during body motion. Supports for such vestibulomotor transformations come from studies showing that galvanic stimulation of the vestibular apparatus (GVS) produces deviations of reaching or drawing movements that can be predicted by the side of the stimulated labyrinth (Bresciani et al., 2002a,b; Guerraz et al., 2003; Mars et al., 2003) and by the reduced capacity of individuals with vestibular lesions for maintaining the hand stationary during trunk motions (Raptis et al., 2007).

Compared to the wealth of information available on visually and somatosensory driven movements, much knowledge has yet to be acquired regarding the mechanisms through which vestibular information contributes to controlling arm movements. In this context, our goal was to shed light on the vestibulomotor transformations that permit individuals to stabilize their hand in space during body motions. More specifically, we tested whether these vestibulomotor transformations have the same latencies and whether they are subject to similar cognitive control than the visuomotor transformations associated with the manual tracking of a moving visual target. The rationale for comparing tracking arm movements and compensatory arm movements during body rotation is that both tasks require movements of the arm relative to the trunk that aim at reproducing the spatiotemporal characteristics of the stimulus (i.e., either target or body motion). However, there are reasons to believe that tracking and stabilization arm movements may involve processes widely differentiated above and beyond those merely related to early sensory processing of the stimuli.

Tracking arm movements are considered to depend largely on cognitive processes (Mrotek et al., 2006; Poulton, 1981). These processes would allow, for instance, the determination of the direction and velocity of the target motion. These time-consuming cognitive processes could explain the long response times of the manual tracking movements (i.e., ~350 ms, Masson et al., 1995). Conversely, well-known vestibular-driven motor responses (for instance, those involved in postural and ocular control) have short latencies and are relatively independent of cognitive information (Guerraz and Day, 2005; Keshner et al., 1995; Roy and Cullen, 2001). However, previous studies that have estimated the latency of the compensatory arm movements following vestibular

stimulation have reported divergent durations, ranging from very short (e.g., ~50 ms, Adamovitch et al., 2001; Tunik et al., 2003) to relatively long (e.g., ~300 ms, Bresciani et al., 2002a,b) latencies. It is worth mentioning that these estimations were obtained by determining the first significant change in the arm kinematics profile following the vestibular stimulation. Because muscular activity was not recorded, it is therefore not possible to establish whether the modifications in the arm's kinematics were due to the effect of the arm's inertia or rather to actual changes in the motor commands resulting from vestibulomotor transformations. For instance, in the study of Adamovitch et al. (2001), as the short latencies were observed after the mechanical braking of the subjects' trunk during trunk-assisted hand reaching, the fast kinematic changes may have resulted from (passive) interaction torques generated at the trunk arrest. On the other hand, in the study of Bresciani et al. (2002a,b), the long latencies for producing kinematic changes were observed after electric stimulation of the labyrinths was delivered while subjects produced rapid reaching movements towards a target. As a consequence, the time required for the stimulation to have a detectable effect on the arm kinematics was likely increased by the arm's inertia and interactive torque resisting to changes in the hand's trajectory.

Electromyographic (EMG) activity of the arm muscles following vestibular (galvanic) stimulation has already been identified and analyzed by Britton et al. (1993). Studying the vestibular control of equilibrium in absence of visual feedback, the authors found functional EMG responses in the brachial muscles having a latency of ~125–150 ms when the arm served to support the body. This EMG response appeared less stereotyped when visual feedback was available (Britton et al., 1993; see also Baldissera et al., 1990). However, as the muscle activation following vestibular stimulation is strongly task dependent (e.g., GVS-evoked EMG response of the leg muscles disappears in the absence of postural constraint (Fitzpatrick et al., 1994)), these studies cannot be used to determine the latencies of the vestibulomotor transformations during spatially oriented arm movements.

In the present study, we assessed the latency of the vestibulomotor transformations by determining the onset of the first burst of EMG activity in the brachial muscles when individuals stabilized their hand in space during whole-body rotation. This latency was compared with that computed in a visuo-manual tracking task wherein the motion of the visual target required similar motion of the arm with respect to the trunk. As whole-body rotations not only generate vestibular inputs but also induce massive somatosensory inflow, the use of proprioceptive and cutaneous information cannot be excluded. Thus, to determine the latency of the sensorimotor transformations when no other cues than those of vestibular origin are available for controlling arm movements, in addition to healthy subjects, we also tested a woman with a normal vestibular system but who is suffering from a severe loss of proprioception and cutaneous sense from the nose down to the feet.

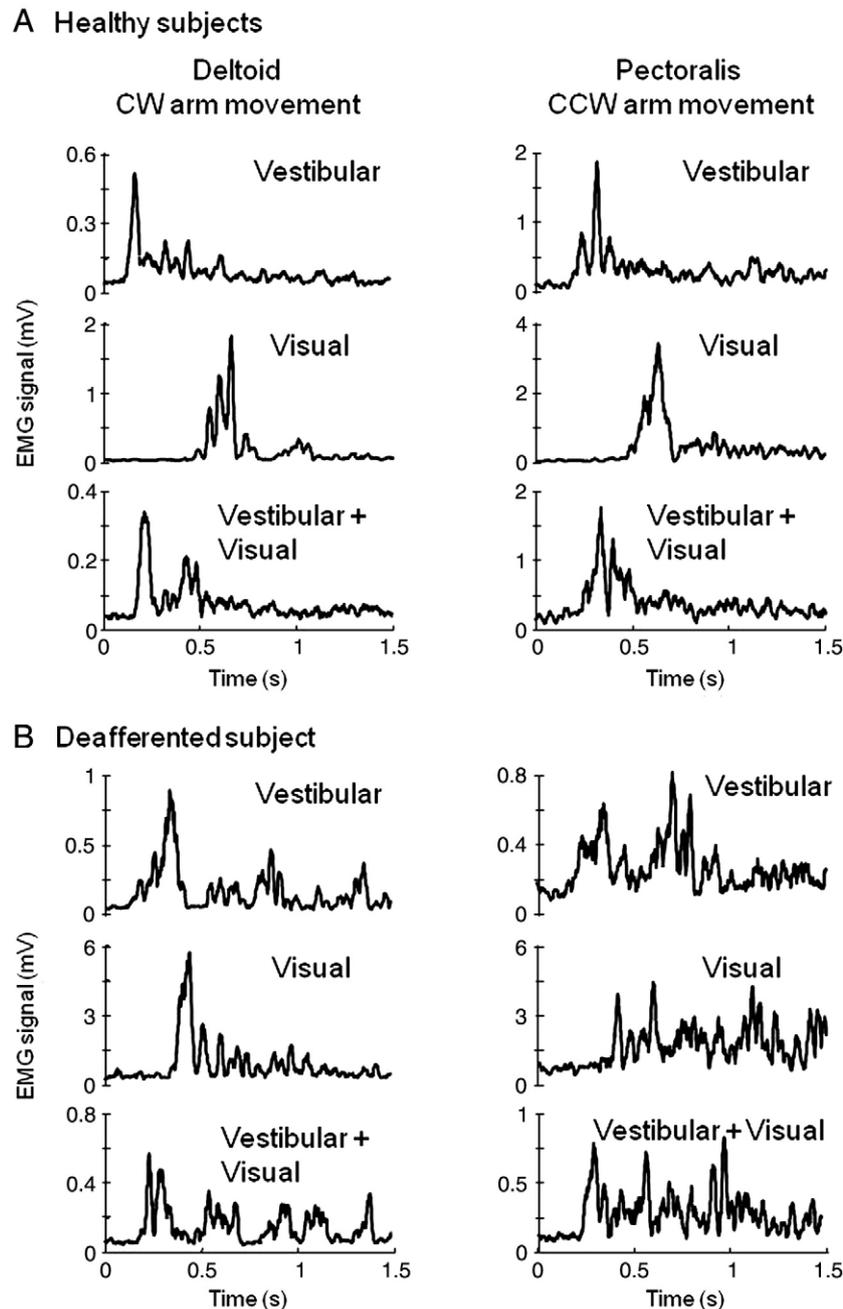
The vestibular signals can be processed for cognitive processes such as those involved in the perception of self-motion (Blouin et al., 1995a; Bresciani et al., 2002b; Israël et al., 1999; Seemungal et al., 2008). Such cognitive factors could be involved in the control of the compensatory arm movements that allow keeping the hand stationary during body motion. In

a second experiment, we compared the influence of cognitive processes on the control of arm movements in the stabilization and tracking tasks. For this purpose, before each trial, we provided subjects with information about the direction of the movement required either to keep the hand stationary in space during the whole-body rotations or to track the moving visual target. If stabilizing the hand in space requires little cognitive processes as several other vestibular-evoked movements (e.g., postural and ocular movements), then information about the forthcoming movement should have negligible

effects on the EMG response times (RTs). Conversely, we should observe reduced EMG RTs when participants tracked the visual stimulus if this task requires a great deal of cognitive processes (Masson et al., 1995; Poulton, 1981).

## 2. Results

Examples of EMG signals of the posterior deltoid and the pectoralis major muscles during chair and target rotations are



**Fig. 1** – EMG recordings (smoothed over 25 samples moving average) from representative trials by a healthy subject (upper panel) and by the deafferented subject (lower panel). The stimulus onset occurred at 0 s. Irrespective of whether the goal of the movement was to stabilize the hand during body rotation or to track the moving target with the finger, clear EMG bursts occurred in the posterior deltoid during CW arm movements and in the pectoralis major during CCW movements.

shown in Fig. 1 for one healthy subject and the deafferented subject. In all conditions and for all subjects, movements of the arm relative to the trunk were associated with clear phasic EMG activities of the shoulder muscles. When subjects were instructed to keep the hand stationary in space, EMG bursts were found in the pectoralis muscle (muscle contributing to CCW arm movements) during CW body rotations and in the posterior deltoid muscle (muscle contributing to CW arm movements) during CCW rotations. In addition, EMG activities were found in the pectoral and deltoid muscles when the tracked visual target moved CCW and CW, respectively. As such, these results confirm that the compensatory arm movements observed during body rotations were actively controlled by the CNS through muscular torques and did not only arise from passive forces (e.g., arm inertia).

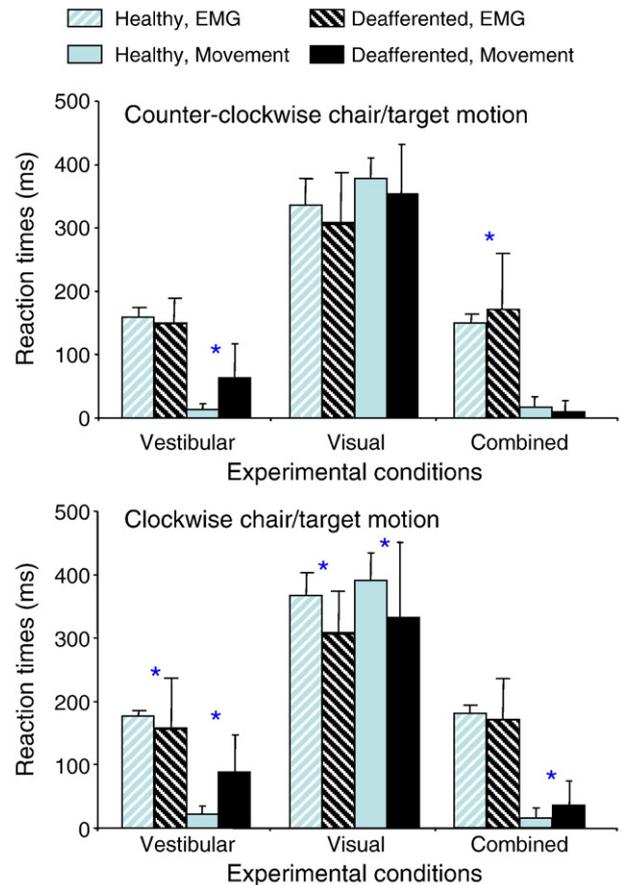
### 2.1. Experiment 1: EMG and movement response times

The healthy subjects' EMG and movement RTs were considerably longer in the Visual condition (352 ms and 384 ms, respectively) than in both the Vestibular (167 ms and 17 ms, respectively) and the Combined (164 ms and 16 ms, respectively) conditions (see Fig. 2). This was confirmed by a significant main effect of condition (two-way repeated measures ANOVA,  $F_{2,8}=8.7$ ,  $P<0.0001$ ). Importantly, the EMG and movement RTs in the Vestibular and Combined conditions, which both involved body rotations, were not significantly different ( $P>0.05$ ). The ANOVA also revealed a significant Condition (Vestibular, Visual, Combined)  $\times$  Response Time (EMG, Movement) interaction ( $F_{2,8}=132.28$ ,  $P<0.0001$ ). The breakdown of the interaction (Student–Newman–Keuls test) showed that the onsets of EMG activities preceded hand movement onsets by 32 ms (electromechanical delay) in the Visual condition ( $P<0.01$ ) but occurred after hand movement in both the Vestibular and Combined conditions (global mean 149 ms,  $P_s<0.001$ ). Because motion of the arm relative to the trunk started before the burst of EMG activity, the early phase of the hand movements with respect to the trunk in both conditions with body rotations likely resulted from passive forces (e.g., arm inertia) rather than muscular torque.

The deafferented subject's RTs were substantially smaller in both the Vestibular and Combined conditions (global mean=162 ms) than in the Visual condition (global mean=309 ms). Most importantly, despite her severe deprivation of somatosensory information, the deafferented subject's EMG and movement RTs closely matched those of the healthy subjects. For instance, the patient's mean EMG RTs fell within the healthy subjects' 95% confidence intervals in 3 of the 6 condition/direction combinations (see Fig. 2). Generally, the mean RTs remained relatively close to the confidence intervals when falling outside and were either shorter or longer than the means obtained by the healthy subjects.

### 2.2. Experiment 1: Movement accuracy

In all conditions, the healthy subjects were able to produce the arm-to-trunk movements required to maintain the unseen finger on the target during the target-body relative motion. On average, at the end of their arm movements, subjects underestimated the amplitude of the relative target-body motion by

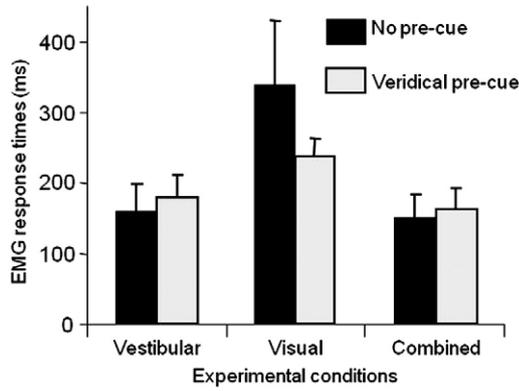


**Fig. 2 – Healthy and deafferented subjects' mean EMG and movement RTs. The error bars represent the between-subject standard deviations for the healthy subjects and the within-subject standard deviations for the deafferented subject. \*The mean obtained by the deafferented patient fell outside the 95% confidence interval computed for the healthy subjects.**

only  $1.06^\circ$  ( $SD=2.3^\circ$ ). The angular final errors were not significantly different between the three experimental conditions (one-way ANOVA,  $F_{2,8}=3.35$ ,  $P>0.05$ ). The deafferented subject also showed small error after both body or target motions (on average,  $0.89^\circ$ ). However, these small errors are not so meaningful in view of the visual feedback that the deafferented subject had on her hand position as specified in the Experimental procedures section.

### 2.3. Experiment 2: Effect of prior information on EMG activity

Providing healthy subjects with prior information about the arm movement direction had clear effects on the EMG responses in the Visual condition but had negligible consequences in both the Vestibular and Combined conditions (Fig. 3). A between-subjects ANOVA performed on the EMG RTs revealed a significant Experiment (Exp. 1, Exp. 2)  $\times$  Condition (Vestibular, Visual, Combined) interaction ( $F_{2,8}=8.73$ ,  $P<0.001$ ). The breakdown of the interaction revealed that EMG RTs recorded in the Visual condition, which were  $\sim 350$  ms in

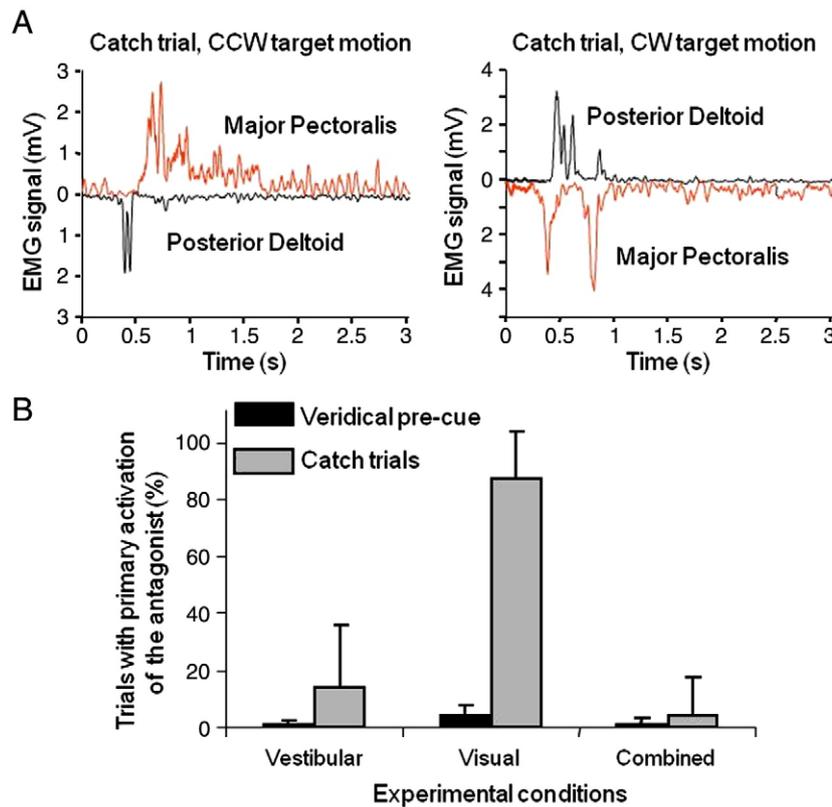


**Fig. 3 – EMG response times with and without prior information about movement direction. The histograms present the mean response times of both the pectoralis major and posterior deltoid muscles. The means reported for the conditions without prior information are those obtained in Experiment 1. Vertical bars indicate between-subject standard deviations.**

Experiment 1, dropped to 235 ms when subjects received precue about the veridical movement direction before the onset of the stimuli (mean reduction of ~115 ms,  $P < 0.001$ ). Remarkably, the precueing had no significant effect on the

EMG RTs in both the Vestibular and the Combined conditions ( $P_s > 0.05$ ).

Using the same procedure as in Experiment 1 to detect the onset of the EMG bursts, we found that in 86% of the catch trials of the Visual condition (Fig. 4B), a burst appeared first in the antagonist muscle (i.e., the muscle moving the arm in the direction opposite to the actual target motion) and then in the agonist muscles (Fig. 4A). For instance, when the target moved in the CCW direction, subjects first contracted the posterior deltoid, a muscle that contributes to CW arm movements. Likewise, when the target moved CW, an EMG burst was initially found in the pectoralis major, which contributes to CCW arm movements. Interestingly, the RTs recorded in the catch trials were much smaller when the initial bursts occurred in the antagonist muscle (202 ms) than when they appeared in the agonist muscle (332 ms;  $t = 2.77$ ,  $df = 16$ ,  $P < 0.05$ ). In the former case, the RTs were not significantly different from those in the Vestibular and Combined conditions ( $P > 0.05$  for all t-tests performed to test muscle and direction effects). On the other hand, the fact that the RTs approached those for the trials without precueing (~350 ms) when the EMG burst first occurred in the agonist muscle suggests that, for these few catch trials, subjects paid little attention to the (false) instruction they received and initiated their movement based on visual information of the target motion.



**Fig. 4 – (A) EMG recordings for representative trials where subjects received false prior information about the direction of the movement required to track the moving target with the hand. The stimulus onset occurred at 0 s. (B) Percentage of the trials with false and veridical precueing in which an EMG burst first appeared in the antagonist muscle, that is, in the muscle moving the arm in the direction opposite to the motion of the target with respect to the trunk. Vertical bars in panel B indicate between-subject standard deviations.**

A completely different picture emerged when the goal of the arm movements was to compensate for body rotations. Indeed, an EMG burst occurred in the antagonist muscle in only 13% of the catch trials in the Vestibular condition and in 4% of the catch trials performed in the Combined condition. Hence, subjects generally activated the appropriate muscle to stabilize their hand in space despite the false precueing they received about the required movement direction. This was true regardless of whether vision or no vision of the target was provided during the body rotations. In most catch trials for all conditions, subjects rapidly stopped their initial response and informed the experimenter that the prior information they received did not correspond to the actual required movement. Subjects were told that a programming mistake was probably responsible for the wrong information they received.

We integrated the normalized EMG signals recorded from the muscles acting as antagonists to the actual required movement to measure the amount of EMG activity in these muscles and to test whether this activity was statistically different between the experimental conditions. As Fig. 5 illustrates, the information provided in the catch trials had virtually no effect on the EMG integrals (iEMG) of the antagonist muscles in both the Vestibular and Combined conditions. Note that the iEMG for the muscle antagonist of the actual required movement was not null, suggesting that the activation of this muscle was necessary to maintain the arm extended against the gravity. Conversely, in the Visual condition, a large increase of activity was found in the muscle moving the arm in the direction opposite to the actual target displacement. Two-way ANOVAs revealed significant Condition (vestibular, visual, combined)  $\times$  Precueing (veridical, false) interactions for both the pectoral ( $F_{2,24}=7.65$ ,  $P<0.01$ ) and the deltoid muscles ( $F_{2,24}=32.90$ ,  $P<0.001$ ). The breakdown of the

interactions confirmed that the iEMG of the antagonist was increased by the catch trials in the visual condition ( $P_s<0.01$ ) but not in both the Vestibular and the Combined conditions ( $P_s>0.05$ ).

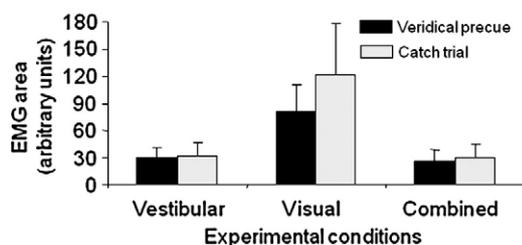
### 3. Discussion

Rotating healthy subjects about the vertical axis generated bursts of muscular activation in the brachial muscles with a latency of  $\sim 165$  ms. This activation induced arm movements relative to the trunk which enabled the subjects to stabilize their hand in space during body motion. We found that the EMG latencies of the responses to the rotations were more than twice as short as those observed when the subjects tracked the moving target with the finger ( $\sim 350$  ms). Most importantly, in the absence of cutaneous and proprioceptive information, the EMG response times of the deafferented subject closely matched those recorded in healthy subjects in all tested conditions. Moreover, for the normal and deafferented subjects, when the illumination of the Earth-fixed target permitted subjects to control their movements through visual feedback during the rotation, the EMG RTs corresponded to those recorded in the Vestibular condition, where no visual feedback was available.

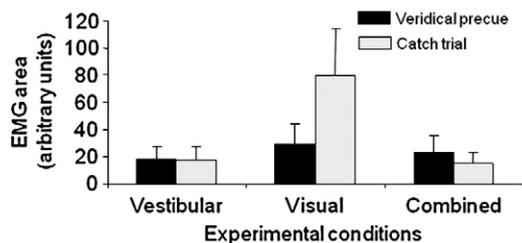
The results of a recent experiment refute the possibility that the deafferented subject used hypothetical residual somatosensory information to control her movements (Blouin et al., 2007a). In this experiment, the deafferented subject had to extend the arm to point straight-ahead in darkness while her torso was passively rotated (in a condition where her head was maintained fixed in space). Rotating the trunk while reaching for a target generates substantial Coriolis and centrifugal torques that deviate the arm in the direction opposite to the rotations (Bortolami et al., 2008; Pigeon et al., 2003). The deafferented subject was not aware of these arm deviations and did not correct for them. These results clearly show the impossibility for this patient to control arm movements through proprioceptive feedback and argue for vestibularly mediated compensatory movements during body rotation in the present experiment. Several studies have shown that the gain of vestibular-driven responses is greater when proprioceptive sense is deteriorated (Blouin et al., 1995b; Day and Cole, 2002; Horak and Hlavacka, 2001). Nevertheless, the latency of the motor responses to the vestibular stimulation appears unchanged for these patients with respect to that of healthy subjects.

Despite similar EMG response times for the deafferented and healthy subjects, one can still question the use of afferent inflow to trigger and guide the compensatory arm movements in healthy subjects. For instance, due to inertia, arm movements occurred prior to the onset of EMG bursts in both conditions with body rotation. For the healthy subjects, the stretch of the arm muscles during this interval generated proprioceptive signals which could have provided the brain with information about arm motion relative to the trunk. However, as the EMG latencies of proprioception-evoked responses to arm perturbations are shorter than 100 ms (Chernikoff and Taylor, 1952; Kurtzer et al., 2008; Marsden et al., 1976), the 165 ms EMG RTs recorded here appear too long

#### A Pectoral, CW target motion with respect to the trunk



#### B Deltoid, CCW target motion with respect to the trunk



**Fig. 5 – Integrals of the EMG signals computed in the antagonist muscles when subjects received veridical and false prior information about the required arm movement direction. Vertical bars indicate between-subject standard deviations.**

to involve muscular afferent signals. Moreover, as proprioceptive afferents do not directly provide information about body position/motion relative to space, they appear unsuitable for defining the spatiotemporal characteristics of arm movements required to stabilize the hand during body rotation. Therefore, the input signal used to define these characteristics was more likely to be vestibular in origin (as was vision in the tracking task). The 165 ms EMG RTs reported here would then correspond to the latency of the vestibulomotor transformations during the compensatory arm movements.

The latencies of brachial EMG responses to vestibular stimulation were in the same range as the functional EMG responses reported by Britton et al. (1993) following GVS in a task in which the arm served to support the body, but longer than those reported for vestibular-evoked eye (<20 ms, Ali et al., 2003) and lower limbs movements (100–120 ms; Britton et al., 1993; Fitzpatrick et al., 1994). The rather long 165 ms EMG latencies observed here following body rotations may reflect the complex neural processing related to the vestibulomotor transformation during the arm stabilization. Specifically, the transformations from vestibular signals to arm motor commands are presumably not as direct as the sensorimotor transformations that lead to vestibulo-ocular or vestibulospinal reflexes (albeit these reflexes also entail sensory integration). The control of arm movement during body motion is likely based on estimations of trunk rotation in space and of arm motion relative to the trunk. These estimations may involve complex and time consuming multisensory processing (e.g., vestibular, proprioception) and different frames of references (e.g., eye-, head-, trunk- and limb-based coordinates; see for instance, Angelaki and Cullen, 2008; Ivanenko et al., 1999). Therefore, compared to vestibulo-ocular or vestibulospinal reflexes, additional transformations may be required to define the spatiotemporal characteristics of the arm movements in order to stabilize the hand during body motion.

Typically, the mechanisms underlying the vestibular control of movement are thought to be quite resistant to cognitive processes (see however, Collewyn, 1989; Glasauer et al., 2007; Ventre-Dominey et al., 2003). For instance, artificial vestibular input induced by GVS still evokes a (non-required) postural response when the perturbation is made predictable by having subjects self-triggering the GVS (Guerraz and Day, 2005). In the present study, independence of the vestibulomotor transformations to cognitive processes is suggested by the lack of influence of neither the veridical and false prior information on impending body rotation on the EMG response latencies and on the selected agonist muscle. Conversely, prior knowledge of movement direction greatly influenced subjects' tracking behavior. Indeed, in the Visual condition, the EMG RTs decreased by ~115 ms when the incertitude about movement direction was alleviated before movement onset. Even more striking were the results obtained for the catch trials revealing that, in agreement with the false precueing, the subjects almost invariably contracted the muscle moving the arm in the direction opposite to the actual target displacement. These results confirm importance of cognitive processes in the manual tracking of a visual target (Masson et al., 1995; Poulton, 1981).

The present findings therefore suggest that vestibular-evoked movements are more immune to cognitive modulation than visually driven movements. A similar conclusion was reached by Barnes and Paige (2004) for the control of eye movements and by Guerraz and Day (2005) for the control of balance. Despite the fact that electrophysiological and neuroimaging studies have shown that the output of the vestibular apparatus projects either directly or indirectly to cortical regions of the brain (e.g., parietal and frontal cortices; Fasold et al., 2002), it is reasonable to speculate that (long) cortical loops are less involved in vestibulomotor processes than in visuomotor processes. The different role of cortical processes in the vestibular and visual control of movements could result from differences in the level of ambiguity of the information about self- and target motions provided by vestibular and visual signals (Guerraz and Day, 2005). Indeed, the vestibular system responds exclusively to body in space motions. Besides the rare occasions where individuals are submitted to high accelerations such as in a plane taking off, the vestibular system provides unambiguous information about body motion direction (Angelaki and Cullen, 2008; Merfeld et al., 1999; Snyder, 1999). This is not the case for visual stimulation which may arise either from self-motion or motion of the environment. As a consequence, as compared to vestibular stimulation, visual signals may entail additional processing to provide reliable information about body-environment relative motion (hence the long RTs in the Visual condition (~350 ms)). Prior information about the direction of the visual target certainly solved the problem of self- versus external motion in Experiment 2, leading to similar EMG RTs when the subjects first contracted the antagonist muscle in the catch trials of the tracking task (i.e., when subjects took into account the precue) and when they stabilized their hand during the body rotations.

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#### 4. Conclusion

Here we demonstrated that the arm movements that allow individuals to compensate for the effects of body rotation on hand location are governed by mechanisms highly comparable to those involved in other motor responses driven by vestibular signals (e.g., ocular, postural, cephalic movements). As such, these findings point to a general principle underlying the contribution of vestibular signals to the control of movements. They also suggest possible generalization to motor behaviors that have not been investigated yet and which also require stabilization of a particular part of the body during motion (e.g., foot stabilization during body motion). These compensatory movements rely on rapid and efficient vestibulomotor transformations that involve negligible cognitive processes. Nevertheless, the delays in shoulder-muscle activation in response to passive body rotation are too long to be considered as reflexes. Most likely, movements range from the most to the least automatic (Prochazka et al., 2000). On such a continuum, the compensatory arm movements produced during body motion appear to be essentially controlled through automatic processes.

## 5. Experimental procedures

### 5.1. Ethics statement

This research was approved the Laval University biomedical ethics committee. Informed written consent was obtained from all subjects prior to the study.

### 5.2. Materials

All experiments were carried out in complete darkness. Subjects were seated in a chair that could be manually rotated about the vertical axis by the experimenter. They wore a rigid surgical collar which minimized head-on-trunk displacements. Chair angular displacement was measured with a potentiometer fixed at the center of rotation of the chair and with an accelerometer. The experimenter could also rotate a light-emitting diode (LED, 3 mm in diameter) about the vertical axis of the chair (i.e., around the subject). The LED was located in front of the right shoulder, ~70 cm from the subject (it was adjusted according to each subject's arm length) and 20 cm above a semi-reflecting glass board (1.5 × 1 m) resting horizontally at the participant's neck level. A board positioned between the subject and the LED prevented direct vision of the LED, which appeared as a virtual target 20 cm beneath the glass. Thus tactile contact with the targets was not possible. Light-emitting diodes (LED), placed on the floor behind the chair at 30° with respect to the subject, served to indicate to the experimenter the direction and magnitude of the chair or target rotations to be produced.

Another LED (fixation light) was fixed to the tip of an 80 cm rigid rod attached to the chair structure. The LED appeared in line with subjects' midline, at eye level. Participants were instructed to gaze at this chair-fixed LED during the rotations to minimize eye movements. To verify the ocular behavior in this experimental context, horizontal eye movements of the healthy subjects were recorded by means of an electro-oculographic device (AP623-4 Universal Bioelectric Amplifier, Biomedica Mangoni). To simplify the experimental procedure and reduce the duration of the experimental session with the patient, we did not record eye movements of the deafferented subject.

An LED fixed to the tip of the right finger could provide visual feedback about the position of the finger, which was detected by a 6-degree-of-freedom electromagnetic sensor (Flock of Birds, Ascension Technology Corporation) also taped on the tip of the finger. Another sensor and an accelerometer were fixed on the revolving target to record its displacement. Because magnetic fields are sensitive to metallic environments, all the elements positioned inside the working volume were made of wood or plastic. This precaution ensured good linearity of the recording system for each experimental condition (as tested before the experiment with chair and target rotations). With this system, the absolute position of the finger and the target could be measured with an accuracy of 1 mm and with a sampling rate of 100 Hz.

For security reasons, the semi-reflecting glass was removed when testing the deafferented subject. In this case, the visual target was positioned at shoulder level. As the arm and

both the target and chair-fixed LED were not separated by the semi-reflective glass, the arm of the deafferented subject was slightly illuminated by the LEDs in all conditions.

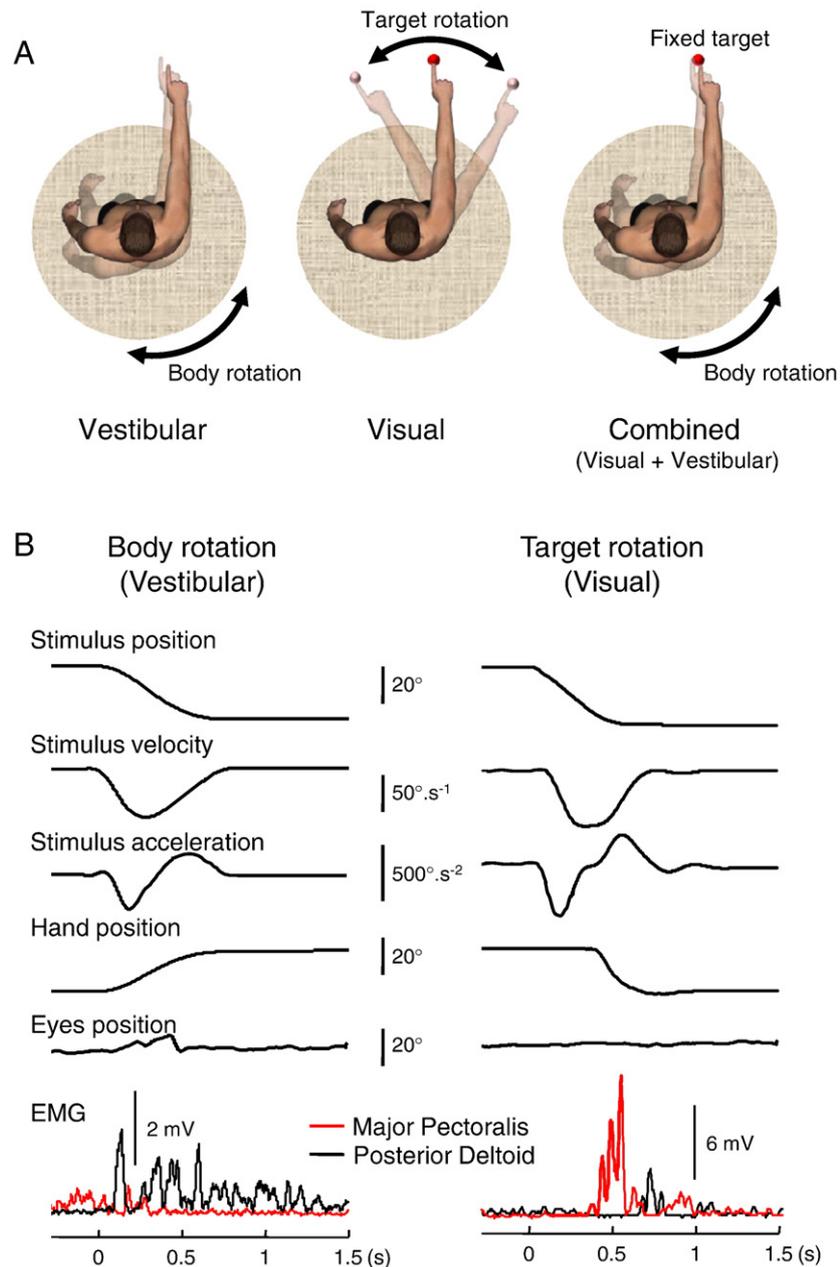
Prior to the experiments, pre-tests were carried out in which we recorded activity of several muscles acting on the arms (biceps and triceps brachial, posterior deltoids, pectoralis major) while stationary subjects rotated the extended arm horizontally around the shoulder joint (i.e., similarly to the movements required in the present study). These pre-tests clearly showed that the prime mover for rotating the extended arm clockwise was the posterior deltoid. On the other hand, the pectoralis major and the biceps were generally synchronously activated during counterclockwise movements at movement initiation. As the present study essentially focused on movement initiation, only EMG activities of pectoralis major and posterior deltoid, which both allow arm movement with respect to the shoulder joint, were recorded. To record these activities, bipolar AG-AgCl electrodes (2 cm center-to-center inter-electrodes spacing) were placed near the middle third of the muscles after cleaning the skin with alcohol, along a line parallel to the muscle fiber orientation (Cram and Kasman, 1998; Brindle et al., 2006). The EMG signals were pre-amplified (×1000) at the skin site and then digitally sampled at 1000 Hz using a Bortec AMT-8 system (Bortec Biomedical).

### 5.3. Experiment 1

Five healthy subjects (mean age 31 years, SD=7 years) and one deafferented subject (female, 59 year-old) participated in this experiment. None of the subjects had a history of vestibular or ocular disorders and all had normal or corrected-to-normal vision.

The deafferented subject suffered at the age of 31 years from a loss of the large myelinated fibers from her whole body after a severe sensory polyneuropathy. At this time, and since then, the deafferented subject has a severe loss of all somatosensory modalities (kinesthesia, tendon reflexes, touch, vibration, pressure) from the nose to the feet. The results of a sural nerve biopsy revealed a severe demyelination, affecting particularly the large fibers (Forget and 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 deafferented subject's vestibular nerves remained intact as confirmed by assessment of her vestibulo-ocular reflex (Blouin et al., 1995b). 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 et al., 2007b).

Three experimental conditions were used; two that involved rotating the subject about the yaw axis in front of an Earth-fixed target and one that involved rotating the target around the stationary subject (Fig. 6A). In all cases, the rotations were either counterclockwise (CCW) or clockwise (CW) and had an amplitude of 30°. In all conditions, the subject's task was to maintain the right index finger as accurately as possible on the target during the target-body relative motion. The initial target position was always directly in front of the right shoulder. Therefore, to maintain the finger on the target, subjects had to counter-rotate the shoulder joint by the same velocity of the stimulus. At the beginning of each



**Fig. 6 – (A) Schematic representation of the experimental conditions. (B) Examples of recorded time-series signals in the Vestibular and Visual conditions in Experiment 1.**

trial, both the finger LED and the target were lit to allow the subject to precisely position his/her finger on the target. From this starting point, the subsequent procedure varied according to the experimental conditions described below.

### 5.3.1. Vestibular condition

The finger LED and the target remained lit for 2.5 s. Two, 3, or 4 s after their extinction, the cue (not seen by the subject) indicating the required rotations was presented to the experimenter who rotated the chair accordingly. The time between extinction of the LED and rotation onset varied in order to prevent prediction by the subject of the rotation onset. During the rotations, the subjects had to keep the unseen index finger on the extinguished LED target. Rotating healthy

subjects in yaw activates mainly the horizontal semi-circular canals of the vestibular system and somatosensory receptors (e.g., cutaneous). For the deafferented subject, as she was severely deprived of all somatosensory information below the nose, the required compensatory arm movements during the passive body rotations were derived from vestibular information.

### 5.3.2. Visual condition

The finger LED was switched off 2.5 s after its illumination (i.e., when the finger was at the starting position) but the target remained visible. Two, 3 or 4 s after the extinction of the finger LED, the experimenter rotated the visual target. The subject, while still fixating the straight-ahead fixation LED, had to

track with the finger the target whose image swept the peripheral retina. Here, for the healthy and the deafferented subjects, information about the arm movement required to keep the finger on the target was derived from retinal signals.

### 5.3.3. Combined condition

We designed this condition to determine the latency of the sensorimotor transformations when both visual and vestibular information is available to control the arm movement. The procedure used here was identical to that used for the vestibular condition, except that the Earth-fixed target remained visible during body rotation. Therefore, the motion of the target on the retina during body rotation was similar to that of the Visual condition and the vestibular stimulation was similar to that of the Vestibular condition. Hence, the retinal and vestibular information was available to control the arm movement.

Each condition consisted of 20 trials for the healthy subjects, i.e., 10 trials per stimulus direction (i.e., for chair and target rotations). The order of presentation of the conditions was randomized across subjects and the order of presentation of the stimulus directions was randomized within each condition. For the deafferented subject, the conditions counted 30 trials (15 trials for each stimulus direction).

Details of the rotational stimuli are presented in Fig. 6B and Table 1. The body and target rotations had bell-shaped velocity profiles. The rotational dynamics were largely above the threshold of the vestibular system for detecting head motion and the body rotation velocity profiles fell within the velocity of natural active head rotations (Blouin et al., 1998; Guitton and Volle, 1987). Although the experimenter tried to produce similar rotational velocities in all subjects and conditions, some variations inevitably occurred. Despite that the vestibular and visual systems have evolved to respond to a large range of stimulations, a possibility remains that the variation observed here in the dynamic of the rotational stimuli could have brought variations in the EMG RTs for the healthy subject and the deafferented subject. To test this possibility, we plotted EMG response times against peak acceleration of either the target or the body rotation and computed the linear regression for each subject. The coefficients of determination ( $r^2$ ) were very low for all healthy subjects (ranging between 0.01 and 0.31 for all subjects and conditions) and for the deafferented subject ( $r^2=0.02$ , 0.01 and 0.01 for the visual, vestibular and combined conditions, respectively). These analyses confirm that if variations in the dynamics of the rotational stimuli (variations that also characterize natural head free movements, Fuller, 1992) have an effect on EMG response times; these variations were not large enough in the present experiment to show such an effect.

In both the Vestibular and Combined conditions, analyses of the healthy subjects' eye movements showed classic vestibular-evoked eye movements in the opposite direction of the rotations despite that subjects were instructed to fixate on the chair-fixed LED (see Fig. 6B). The maximal deviation of the eyes was relatively small (global means of 8.75° and 9.10° for the Vestibular and Combined conditions, respectively). After reaching these maximal deviations, the eyes returned toward their primary central position (i.e., the chair-fixed LED)

**Table 1 – Peak velocity/acceleration of the rotational stimuli (i.e., body or target) for the healthy subjects and the deafferented subject in the three experimental conditions.**

	Velocity (°s <sup>-1</sup> )	Acceleration (°s <sup>-2</sup> )
<i>Healthy subjects</i>		
Vestibular	99 (±6, ±7)	486 (±35, ±39)
Vision	139 (±19, ±21)	594 (±55, ±83)
Combined	100 (±6, ±5)	474 (±34, ±35)
<i>Deafferented subject</i>		
Vestibular	101 (±17)	468 (±128)
Vision	82 (±30)	307 (±142)
Combined	100 (±16)	430 (±77)

Values in parentheses represent for the healthy subjects the within- and between-subject standard deviations. For the deafferented subject, the values in the parentheses represent the within-subject standard deviation.

with a latency of 389 ms and 363 ms, for the Vestibular and Combined conditions, respectively (that is long before the rotational stimuli offset). Because the head did not rotate in the visual condition and because subjects fixated an Earth-fixed target, no eye motion occurred in this condition and these variables could not be computed.

### 5.4. Experiment 2

Eleven different healthy subjects (mean age 23 years, SD=2 years) participated in this experiment which was designed to compare the influence of cognition on the vestibulomotor and visuomotor transformations. To do so, the effect of providing prior information about the direction of the forthcoming arm movement on the EMG responses was measured. All three conditions of Experiment 1 were repeated (see Table 2 for kinematic details of the rotational stimuli). The only difference with respect to Experiment 1 was that additional LEDs located at eye level and at 30° on either side of the subject indicated the direction of the impending required arm movement. These LEDs, which served as the precues, were switched on for 2.5 s at the start of each trial (i.e., when both the finger LED and the target were lit). Subjects were instructed that the left and right lights indicated respectively CCW and CW arm movements relative to the trunk. Each condition was composed of 28 trials (14 trials for each direction). Four catch trials were randomly introduced (2 for each direction) in which subjects received false information about the direction of the required movement. Providing prior

**Table 2 – Peak velocity and acceleration of the rotational stimuli (i.e., body or target) of Experiment 2.**

Conditions	Velocity (°s <sup>-1</sup> )	Acceleration (°s <sup>-2</sup> )
Vestibular	94 (±18, ±2)	485 (±31, ±22)
Vision	130 (±14, ±3)	653 (±65, ±19)
Combined	97 (±6, ±3)	492 (±37, ±20)

Values in parentheses represent the within- and between-subject standard deviations.

information about an upcoming movement is known to be beneficial to the preparation of movements that largely depend upon cognitive processes (Goodman and Kelso, 1980; Rosenbaum, 1980; Terao et al., 2007). In particular, movement RT is reduced when subjects know in advance the direction of the movement they will have to produce in response to a stimulus (Bonnet and MacKay, 1989; Carson et al., 1995; Terao et al., 2007). As tracking a moving target with the finger is largely under cognitive control (Masson et al., 1995; Poulton, 1981), we expected that giving directional information in advance should decrease the EMG burst RT in the Visual condition. These bursts should invariably occur in the agonist muscle for veridical prior information, while for the catch trials the EMG bursts could be observed first in the antagonist muscle, that is, in the muscle moving the arm in the direction opposite to the actual target displacement. In contrast, according to the hypothesis that vestibulomotor transformations are largely independent of cognitive control, neither veridical nor false information about forthcoming movements should have a significant effect on the EMG activity in the Vestibular and possibly the Combined conditions.

## 5.5. Measured variables

### 5.5.1. EMG response times

EMG RTs were computed on the basis of both rotation (target or chair) and EMG burst onset times. The EMG signals were first rectified and smoothed over 25 samples. The threshold voltage indicating the onset of muscle activity was defined as 2 SD above a baseline activity, which was measured on a trial-by-trial basis, as the mean activity during a 1 s window, selected 0.5 to 1.5 s after the extinction of the finger LED (i.e., between 0.5 s and 3.5 s before the movement, depending on the trials). The EMG signals voltage had to remain above the threshold value for 24 ms to be identified as valid EMG bursts. All muscle activity onsets were visually inspected to eliminate pre-movement artifacts falsely identified as EMG bursts. Any such misidentification was corrected manually. Target and chair rotation onsets were determined using a  $5^\circ\text{s}^{-2}$  criterion (backward search from peak acceleration).

### 5.5.2. Movement response times

Hand RTs were calculated on the basis of both hand angular movement and (target or chair) rotation onset times. Movement onsets were detected using a  $5^\circ\text{s}^{-2}$  criterion (backward search from peak acceleration).

### 5.5.3. Movement accuracy

In all conditions, finger and target position signals with respect to the trunk were measured. The final hand angular error was defined as the angle between the target and the index finger, after hand movement offset (i.e., when hand velocity dropped  $<1^\circ\text{s}^{-1}$ ). We used the Cartesian coordinates of the sensors to compute the angle, with the platform rotation axis as origin (which coincided with the vertical axis of the subject's head).

### 5.5.4. EMG bursts

In Experiment 2, the integral of the normalized EMG signals recorded from the muscle acting as antagonist was computed

to assess the effect of providing veridical or false prior information about the direction of the required forthcoming arm movement. To quantify the EMG bursts, we first rectified and low pass filtered the EMG signals to generate envelopes. We used a zero-phase forward and reverse digital low-pass Butterworth filter, 4th rank and 7 Hz cutoff frequency which provides a good assessment of the total energy in the signal (Brindle et al., 2006; Gram and Kasman, 1998). To allow between-subject comparisons, the EMG signals were first normalized, by dividing the signals by the maximal EMG amplitude observed in each subject's experimental session (always occurring in the Visual condition). Moreover, as the kinematics of the chair/target rotations varied between trials and conditions, in order to compare the EMG bursts between conditions, we further normalized the EMG signal amplitudes by dividing the signals recorded in each trial of a given condition by the peak acceleration of the stimulus of that trial. Peak acceleration was used for the normalization because the burst of agonist activity is most highly correlated with the peak of acceleration (Hoffman and Strick, 1990). The amount of EMG activities was determined for each muscle by computing the integral of the normalized EMG signal (iEMG) in a time window spanning between 100 ms before to 300 ms after arm movement onset.

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