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Psychophysiological correlates of the inter-individual variability of head movement control in seated humans

N. Vibert [a,*], T. Hoang [b], D.P.D. Gilchrist [c], H.G. MacDougall [c], A.M. Burgess [c], R.D. Roberts [c], P.P. Vidal [a], I.S. Curthoys [c]

[a] *Laboratoire de Neurobiologie des Réseaux Sensorimoteurs, CNRS UMR 7060-Université René Descartes (Paris 5), Centre Universitaire des Saints-Pères, 45 rue des Saints-Pères, 75270 Paris Cedex 06, France*
[b] *Laboratoire de Statistique Médicale, CNRS FRE 2428-Université René Descartes (Paris 5), 45 rue des Saints-Pères, 75270 Paris Cedex 06, France*
[c] *School of Psychology, University of Sydney, NSW 2006, Australia*

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Abstract

We recently conducted experiments where 24 seated participants were subjected (with eyes closed) to small amplitude, high-jerk impulses of linear acceleration. Responses were distributed as a continuum between two extremes. The ''stiff'' participants showed little movement of the head relative to the trunk, whereas the ''floppy'' participants showed a large head rotation in the direction opposite the sled movement. We hypothesized that the stiff behavior resulted from the spontaneous use of an imagined visual frame of reference and undertook this larger-scale study to test that idea. The distribution along the ''stiff–floppy'' continuum was compared with the scores on psychophysiological tests measuring vividness of imagery, visual field-dependence and motion sickness susceptibility. Multivariate regression analysis revealed that the ''stiffness'' of individuals was loosely, but significantly related to the vividness of their imagery. However, ''stiffness'' was not linked to visual field-dependence or motion sickness susceptibility. Even if it explains only 20% of the variance of the data, the increase of ''stiffness'' with vividness of imagery fits our hypothesis. With eyes closed, stiff people may use imagined external visual cues to stabilize their head and trunk. Floppy people, who are poorer imagers, may rely more on ''egocentric'', proprioceptive and vestibular inputs.
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1. Introduction

When seated humans experience passive body movement, the head lags behind the body because of its inertia, and somatosensory inputs from the trunk and/or neck are the main source of sensory information for 40–70 ms [1–3]. These inputs generate reflex motor responses, which together with mechanical properties of the head–neck system determine the initial movement of the head [1,3]. The head movement initiates vestibulo-collic reflexes and visually related modulation of the ongoing postural responses, and after about 100 ms voluntary control mechanisms will also play a role [2–6]. When stance is perturbed in standing humans, the patterns of muscle contractions triggered by early proprioceptive information show inter-individual variability, which appears to reflect the use of different, pre-programmed motor synergies for postural stabilization [7–9]. There is evidence that similar variation exists in the head stabilization strategies used by seated humans [4,6].

We recently conducted experiments where seated participants were subjected (with eyes closed) to high-jerk, small-amplitude pulses of linear acceleration [10]. The head movements triggered by the impulse were distributed along a continuum between two extreme patterns. The ''stiff'' participants showed little movement of the head relative to the trunk. In contrast, the ''floppy'' participants showed a large head rotation in the direction opposite the sled movement. EMG recordings showed that most of the stiff participants were not contracting superficial neck or back

* Corresponding author. Tel.: +33 1 42 86 33 91; fax: +33 1 42 86 33 99.
E-mail address: nivi@ccr.jussieu.fr (N. Vibert).

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muscles. In contrast, about half of the floppy participants were actively but involuntarily pulling their head in the direction of inertia, opposite the sled movement [10]. This inter-individual variability was not due to differences in the level of anticipation or attention, nor to voluntary cognitive control. We proposed that the different motor responses of seated participants reflected deeply rooted individual strategies of postural control (see Ref. [10] for details).

Some people spontaneously use external visual cues to stabilize their posture, while other individuals do not [11–13] and instead rely on gravitational and/or ''egocentric'', vestibular and proprioceptive cues [9,14]. As pointed out by Keshner [6], such a mental set may be sufficient to modify the cervico-collic reflex and other initial responses to trunk translation, and the modulation of head movement by vestibular and visual inputs. Consistent with that view, we showed in eight people [10] that visualization of an imaginary target during sideways impulses reduced the head roll of floppy participants, but did not modify the head movement of stiff participants. This outcome suggested that spontaneous reference to an internal image of the external visual world, rather than merely to vestibular and proprioceptive information, might be associated with the stiff behavior.

The variability of the efficiency of imaginary targets previously used to modulate head stabilization or vestibulo-ocular responses in humans suggests inter-individual differences in the ability to visualize and use imaginary visual cues [4,5,15–17]. Mast et al. [18] demonstrated that visual mental imagery might have the same effect as true visual input on head stabilization and postural control. Jeka et al. [19] demonstrated that head stabilization in standing humans is much worse in congenitally blind individuals than in sighted people with eyes closed. Sighted persons may use their visual experience during motion even when visual information is absent [18,20]. Altogether, differences in visual imagery capacity may affect the way participants spontaneously stabilize their head in response to sled impulses, depending on how well participants visualize the experimental room with eyes closed. People with better imagery capabilities may use the ''image'' of the external world as a reference when the impulse begins and thus be stiffer.

The fact that some people rely on visual rather than vestibular and proprioceptive cues led to studies that linked inter-individual differences in postural stabilization while standing, with visual field-dependence or independence [13,21,22]. The perception of field-dependent people is dominated by the overall organization of the background visual field and for them, the different parts of the field are difficult to separate. In contrast, field-independent people experience the different parts of the visual field as discrete entities easily separated from one another [23]. We postulated that field-dependent people might be more likely to use a visual frame of reference (and be stiffer) than field-independent individuals.

Motion sickness susceptibility is another parameter, which has been linked with postural control [24]. Motion sickness may be triggered by sensory mismatch between vestibular, visual and somatosensory inputs in unusual situations [25]. Inter-individual differences in motion sickness susceptibility may result from differences in the weighting of visual with respect to vestibular and proprioceptive signals. Individuals who rely on vision for balance would not be able to disregard erroneous visual cues as easily as the others and may have higher motion sickness susceptibility [25]. Actually, motion sickness susceptibility and visual field-dependence appear to be correlated [26], so we expected individuals prone to motion sickness to be stiffer.

To check the above hypotheses, we undertook a large-scale study on 108 participants. We tested whether ''stiffness'' was correlated with scores on psychophysiological tests measuring the vividness of imagery, the level of visual field-dependence and motion sickness susceptibility.

2. Material and methods

One hundred eight healthy volunteers (58 females and 50 males) gave informed consent to participate in the experiments. The mean age ($\pm$standard deviation) of participants was 26.2 ± 10.7 years (females were aged 12–57 years, males 8–60 years). For the three minors, experiments were performed with the informed consent of the legal guardian. The Human Ethics Committee of the University of Sydney approved all procedures adopted.

The visual field dependence of participants was tested using the rod-and-frame test (RFT). In complete darkness, the participant has to align with the gravitational vertical a rod that is presented alone or in the center of a square frame. With the frame, the field-dependent participants tend to set the rod towards the side to which the frame is tilted [27]. A LabVIEW® 4.1 (National Instruments, Austin, Texas) program was used to generate the rod-and-frame displays and record the settings of the participant. Subjects sat in complete darkness 1 m away from a translucent screen on which the displays (covering 21° of visual field) were back projected, with their head maintained in a vertical position. The test session included 24 trials in pseudo-random order. The rod was presented alone or with the frame tilted 15° to the right or left [28]. Means of eight settings were obtained in each condition. The frame effect was calculated in degrees of angle according to Ref. [29]. The leftward and rightward frame effects were computed separately, and were summed to obtain the RFT score.

The Embedded Figures Test (Consulting Psychologists Press, Palo Alto, California) evaluates visual field dependence/independence in a broader sense. The participant must locate a previously seen simple figure within a larger, complex figure in which the sought-after simple figure is embedded [23,30]. The typical test session includes 12 trials and the mean solution time per item is the participant's score.

The vividness of imagery of participants was assessed using two self-assessment questionnaires, the vividness of visual imagery questionnaire (VVIQ, [31]) and the vividness of motor imagery questionnaire (VMIQ, [32]). Both require the participants to rate the vividness of images that written descriptions of scenes evoke in their mind, using a five-point scale. The VVIQ contains 16 items describing still visual scenes, rated once with eyes open and once with eyes closed. The sums of the ratings with eyes open (VVIO) and eyes closed (VVIC) were computed separately. The VMIQ uses a similar format but is composed of 24 items relevant to body movement imagery. Participants must image each item once from an external viewpoint (watching someone else doing the movement) and once from an internal viewpoint (imaging the sensations associated with doing the movement themselves). The sums of the ratings obtained when imagining someone else (VMIOT) and oneself (VMISE) doing the movement were computed separately.

The susceptibility to motion sickness was evaluated using an updated version of the self-assessment questionnaire (MSSQ) of Reason & Brand (see Ref. [33] for details). The motion sickness susceptibility (MSS) score increases with susceptibility from 0 (if one never experienced motion sickness) to a theoretical 380.

The procedures used to deliver high-jerk linear accelerations to seated humans, and to analyze the head and trunk movements were described elsewhere (see Ref. [10] for details). Briefly, participants were asked to sit with eyes closed in a relaxed position, without any instruction unless otherwise stated. Sharp onset pulses (peak jerk 256 m s^{-3}, Fig. 1A2) of linear acceleration (peak value 5.6 m s^{-2}) were delivered either sideways or in the fore–aft direction (Fig. 1). Movements of the head and trunk were measured using Optotrak® (Northern Digital, Waterloo, Ontario, Canada) sampling at 200 Hz. The testing session consisted of 10 sideways impulses, 5 towards the left and 5 towards the right. Eighty-one of the 108 participants were also tested with 10 fore–aft linear sled impulses, 5 directed forwards and 5 directed backwards.

The amplitude of the head re trunk movements triggered by sideways impulses (see Ref. [10]; Fig. 1) was characterized by measuring the initial head roll (HRA, Fig. 1A2, upper panel) and head re trunk translation in the direction opposite the acceleration (head re trunk displacement (HVTD), Fig. 1A2, lower panel). Similar parameters, namely head pitch amplitude (HPA) and HVTD2, were used for fore–aft impulses (Fig. 1B).

The effects of visualization of an imagined target located about 4 m in front of the participants were investigated during sideways impulses.

- Sixty-one of the 108 participants tested without instruction (34 females) were tested a second time within the same session while instructed to close their eyes, but to keep their "internal" gaze fixated on the virtual target. This target was supposed to move with them and the sled during the impulse (sled-fixed target).
- A representative sample of 12 participants was then selected. They underwent a distinct, single test session where sideways impulses were delivered in four situations: without any instruction, while imagining a sled-fixed target as above, while imagining a virtual target that stayed still in space instead of moving with the sled (earth-fixed target), and while asked to actively minimize their head re trunk movement (i.e. to "stiffen up" their neck).

Statistical analysis of the data was conducted using the SPLUS 2000 (Insightful Inc., Seattle, Washington) software. All means are given with standard deviation (mean ± S.D.). The gender dependence of parameters (Table 1) was assessed using two-tailed, unpaired *t*-tests. Correlation between the four parameters measuring the "stiffness" (HRA, HVTD, HPA and HVTD2) was assessed using non-parametric, Spearman rank correlation tests with Bonferroni adjustment. The relation of these parameters with sex, age

Table 1
Descriptive statistics

Type of test	Parameter	Mean ± S.D. (all participants)	Mean ± S.D. (females)	Mean ± S.D. (males)	Significance of difference
Sideways impulses	HRA (°)	**8.0 ± 5.2**	6.9 ± 4.1 ($n = 58$)	9.4 ± 6.1 ($n = 50$)	**0.015**
	HVTD (mm)	**35 ± 19**	29 ± 14 ($n = 58$)	42 ± 21 ($n = 50$)	**<0.001**
Fore–aft impulses	HPA (°)	**9.3 ± 5.5**	8.1 ± 4.5 ($n = 41$)	10.6 ± 6.1 ($n = 40$)	**0.04**
	HVTD2 (mm)	**44 ± 16**	39 ± 12 ($n = 41$)	50 ± 17 ($n = 40$)	**0.001**
Psychophysical parameters	RFT score (°)	**2.54 ± 2.32**	1.88 ± 2.84 ($n = 50$)	1.16 ± 1.50 ($n = 44$)	0.13
	Emb Fig score (s)	**27.3 ± 15.1**	30.6 ± 14.6 ($n = 48$)	23.5 ± 14.9 ($n = 41$)	**0.025**
	VVIO score	**39.6 ± 12.5**	38.8 ± 11.3 ($n = 50$)	40.5 ± 13.8 ($n = 44$)	0.53
	VVIC score	**37.0 ± 12.6**	35.6 ± 12.9 ($n = 50$)	38.6 ± 12.2 ($n = 44$)	0.24
	VMIOT score	**53.9 ± 17.9**	53.7 ± 18.3 ($n = 50$)	54.2 ± 17.8 ($n = 44$)	0.89
	VMISE score	**57.4 ± 18.8**	59.5 ± 19.1 ($n = 50$)	55.0 ± 18.4 ($n = 44$)	0.25
	MSS score	**42.7 ± 34.2**	48.3 ± 35.7 ($n = 52$)	36.4 ± 31.6 ($n = 47$)	0.08

Means ± S.D. obtained for each variable quantified in this study. Differences between genders are in bold when significant ($p < 0.05$). HRA, head roll amplitude; HVTD and HVTD2, head re trunk displacement (sideways and fore–aft impulses); HPA, head pitch amplitude; RFT, rod-and-frame test; Emb Fig, embedded figures test; VVIO, vividness of visual imagery with eyes open; VVIC, vividness of visual imagery with eyes closed; VMIOT, vividness of movement imagery imagining others; VMISE, vividness of movement imagery imagining oneself; MSS, motion sickness susceptibility.

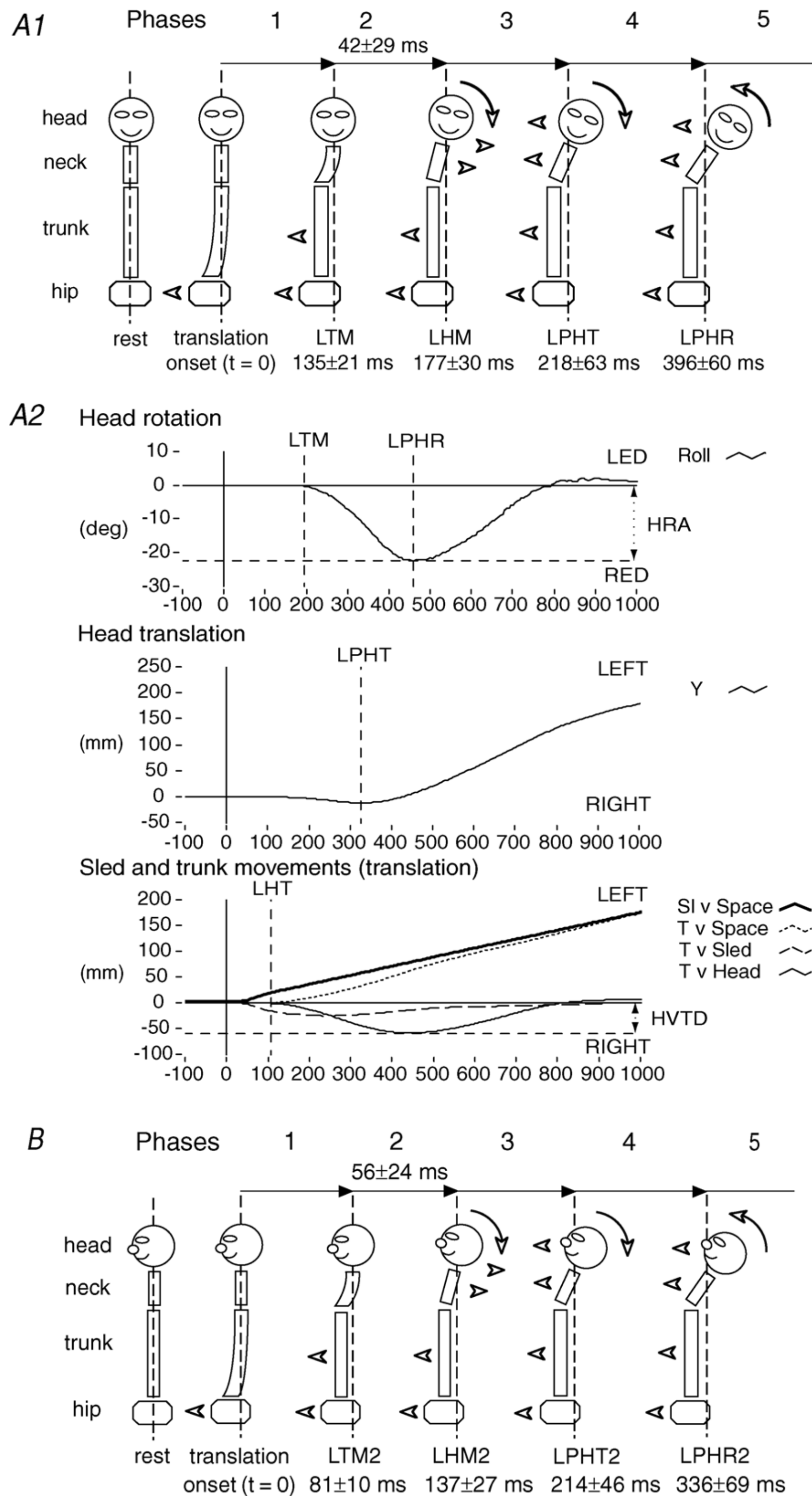

Fig. 1. Typical head and trunk movements triggered by sideways and fore–aft accelerations (adapted from Ref. [10]). (A1) Schematic drawings showing the sequence of trunk and head movements displayed by seated participants during sideways impulses. The values given for phase duration and latencies are the average values (±S.D.) obtained for 108 participants. LTM, latency of the initial trunk movement in space; LHM, latency of the initial head movement in space; LPHT, latency to the peak of the initial head translation in the direction opposite the sled; LPHR, latency to the peak of the initial head roll. (A2) Example of head and trunk movements triggered by a sideways impulse in a ''floppy'' participant, as displayed by our LabVIEW® program. In the head rotation panel, LED and RED stand for ''left ear down'' and ''right ear down'', while HRA shows the measure of the head roll amplitude. The traces showing head movements in pitch and yaw have been removed for sake of clarity. In the head translation panel, Y corresponds to head movements along the inter-aural axis, and the other

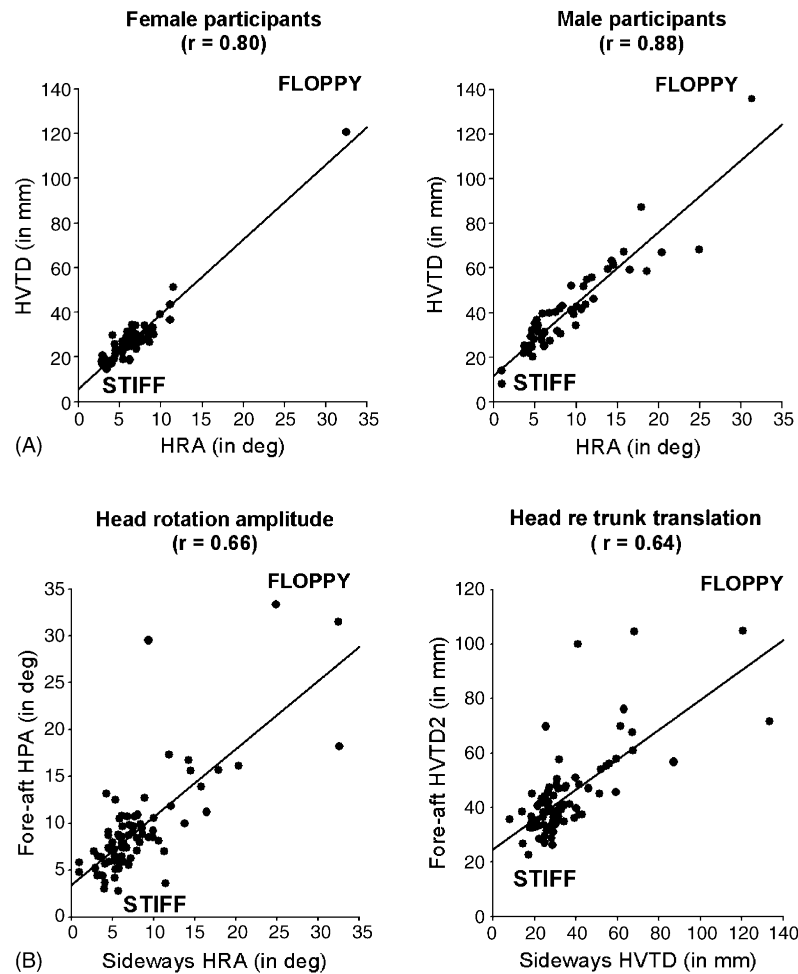

Fig. 2. Distribution of participants along the stiff–floppy axis and correlation between sideways and fore–aft impulses. (A) Graphs showing the distribution of female and male participants along the stiff–floppy axis in response to sideways impulses. In each case, r is the Spearman coefficient of correlation between the two parameters characterizing the amplitude of the head re trunk movements triggered by the sled acceleration (HRA and HVTD). Note the overall higher "stiffness" of females. (B) Graphs demonstrating the correlation between the head re trunk movements triggered by sideways and fore–aft impulses in 81 participants. The coefficient of correlation is 0.66 for the head rotation amplitude (HRA vs. HPA), and 0.64 for the head re trunk translation amplitude (HVTD vs. HVTD2).

and the seven psychophysiological scores (Table 1) was assessed using multivariate regression analysis. HRA and HVTD on one hand, and HPA and HVTD2 on the other hand, were jointly regressed on nine variables: sex, age, RFT, embedded figures, VVIO, VVIC, VMIOT, VMISE and MSS scores, to generate full linear models. The variables having a significant influence on stiffness were then sequentially selected to generate the final models presented below. The effects of visualization of a sled-fixed target were assessed using paired t-tests. The effects of visualization of an earth-fixed target or of active "stiffening up" of the neck were assessed using paired, non-parametric tests (Friedman ANOVA and Wilcoxon signed-rank tests) because of the small number of participants tested.

3. Results

The amplitude of the initial head movement was highly variable. As in Ref. [10], the head movements of participants were distributed between the stiff and floppy extremes (Fig. 2). We confirmed that females were stiffer than males (Fig. 2; Table 1) and that within each gender stiffness was unrelated to the weight or height of participants. The two parameters describing the amplitude of the initial head movement were highly correlated for both sideways (Fig. 2A) and fore–aft ($r = 0.76$) impulses. As in Ref. [10], there was a high correlation between the amplitude of head movement triggered by fore–aft and sideways stimulation (Fig. 2B).

components have been removed for sake of clarity. In the sled and trunk movement panel, HVTD shows head re trunk displacement amplitude. Sl v space, sled re space; T v space, trunk re space; T v sled, trunk re sled; T v head, trunk re head; accel, acceleration of the sled and chair. (B) Schematic drawings showing the sequence of trunk and head movements displayed by seated participants during a backward impulse. The values given for phase duration and latencies are the average values (±S.D.) obtained for 81 participants. LTM2, latency of the initial trunk movement in space; LHM2, latency of the initial head movement in space; LPHT2, latency to the peak of the initial head translation in the direction opposite the sled; LPHR2, latency to the peak of the initial head roll.

Both the rod-and-frame test and the embedded figures revealed large inter-individual differences. The RFT score ranged from 0.04° to 16.65°, the embedded figures score from 1.5 to 70.2 s. Females were more visual field-dependent than men, but this trend was significant only for the embedded figures.

The three questionnaires also revealed large differences between participants. Both the VVIO and VVIC scores ranged from 16 to 80, while the VMIOT and VMISE scores ranged from 24 to 119 and 24 to 115, respectively. The motion sickness susceptibility score varied from 0 to 137.8. The vividness of imagery and motion sickness susceptibility did not depend on the gender of participants. The scores characterizing the vividness of imagery (VVIO VVIC, VMISE and VMIOT) were highly correlated, with coefficients ranging from 0.46 to 0.64. Similarly, the two measures of visual field-dependence (rod-and-frame and embedded figures) were significantly correlated ($r = 0.28$ and $p = 0.009$). There was no correlation between the vividness of imagery, the visual field-dependence and the motion sickness susceptibility of participants.

Separate linear models were established for the two sets of variables measuring the head movements triggered by sideways (HRA and HVTD) and fore–aft (HPA and HVTD2) impulses. In both cases, only two variables influenced the stiffness of participants: gender and vividness

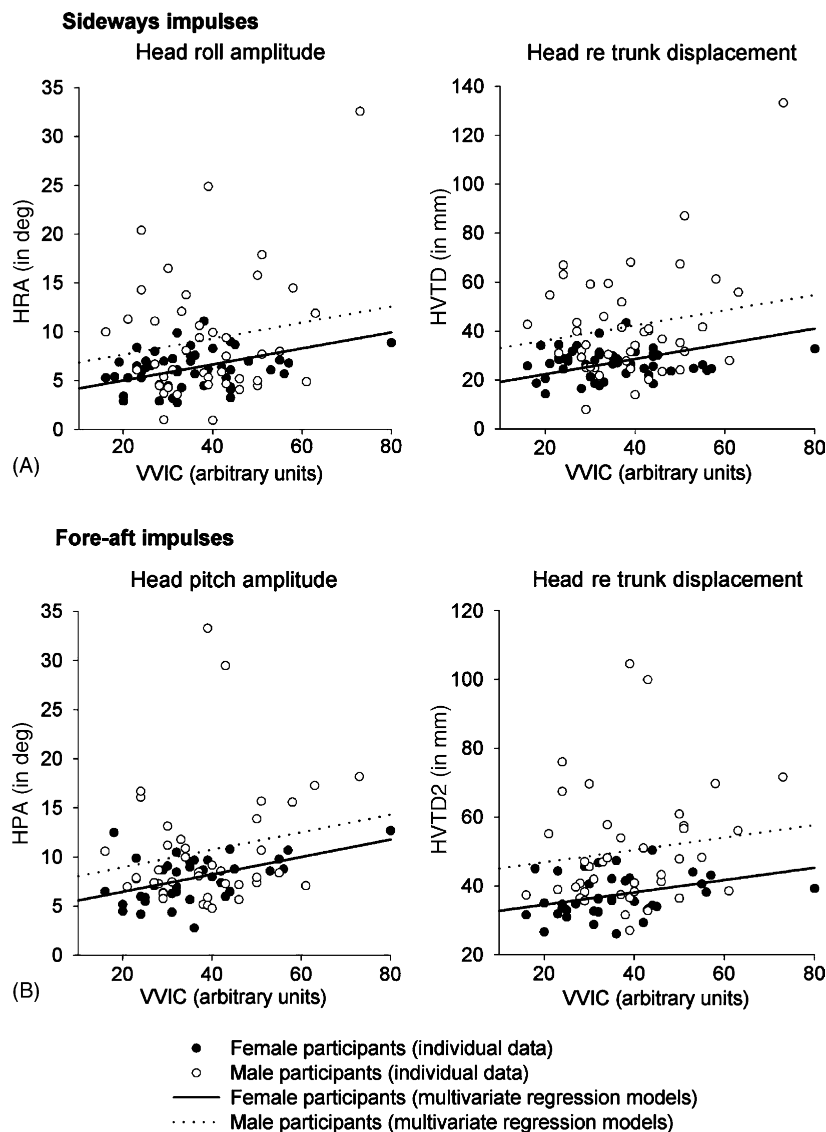

Fig. 3. Correlation between the "stiffness" in response to sideways and fore–aft impulses and the imagery capabilities in female and male participants. Each line corresponds to the models given by multivariate regression analysis that describes the relationship between either the HRA or HVTD (A, sideways impulses) or the HPA or HVTD2 (B, fore–aft impulses) and the VVIC score, in females ($n = 58$) and males ($n = 50$) participants. The black lines give the models obtained for females (with black circles representing individual data), the dotted lines give the models obtained for males (with empty circles representing individual data). Note that the lines corresponding to the models are not simple regression lines, since the multivariate models take into account several other factors beyond the vividness of visual imagery with eyes closed.

Table 2
Effects of target visualization and voluntary neck stiffening on the amplitude of the head re trunk movements elicited by sideways impulses in a representative sample of 12 participants

Participants	Instructions	HRA (°)	HVTD (mm)
Stiff participants ($n = 6$)	No instruction	4.3 ± 1.9	23.6 ± 10.1
	Sled-fixed imaginary target	3.6 ± 0.8	21.6 ± 6.8
	Earth-fixed imaginary target	3.9 ± 1.0	23.3 ± 6.1
	Voluntary neck stiffening	3.2 ± 1.1	**19.1 ± 7.1**#
Floppy participants ($n = 6$)	No instruction	14.3 ± 6.6	62.9 ± 31.2
	Sled-fixed imaginary target	**7.7 ± 3.3***	**40.9 ± 15.2***
	Earth-fixed imaginary target	**8.1 ± 3.6***	**45.7 ± 24.8***
	Voluntary neck stiffening	**4.6 ± 1.5***,#	**26.1 ± 8.8***,#

Bold values indicate those values that correspond to a significant difference indicated by either * or #. HRA, head roll amplitude; HVTD, head re trunk displacement.
* Indicate the values that were significantly different from control values ($p < 0.05$).
# Indicate significant differences between the neck stiffening and target visualization conditions ($p < 0.05$).

of visual imagery with eyes closed. There was no significant relation between the stiffness of individuals and their age or the six other psychophysiological variables.

The following model (where gender = 0 for females and 1 for males) was obtained for sideways impulses.

- HRA = 3.38 + 2.65 × gender + 0.082 × VVIC. Significance of the model is given by its F statistic: $F(2, 88) = 13.62$, $p < 0.001$ and the significance of the influence of VVIC on HRA is measured by a t-test ($p = 0.020$). The model explains 14% of the variance of HRA.
- HVTD = 16.23 + 13.73 × gender + 0.31 × VVIC ($F(2, 88) = 7.23$, $p = 0.001$ and there is a significant influence of VVIC on HVTD ($p = 0.036$)). The model explains 24% of the variance.

As expected from the high correlation between sideways and fore–aft impulses, a similar model was obtained for the HPA = 4.69 + 2.49 × gender + 0.089 × VVIC ($F(2, 74) = 6.00$, $p = 0.004$, 14% of variance explained) and HVTD2 = 30.92 + 12.34 × gender + 0.18 × VVIC ($F(2, 74) = 10.94$, $p < 0.001$, 23% of variance explained). There was a significant influence of VVIC on HPA ($p = 0.034$), but not on HVTD2 ($p = 0.13$).

These models reveal that floppiness increases significantly with the VVIC scores. As the highest scores correspond to the worst imagers, the stiffness of participants increases with the quality of their visual imagery. In addition, the linear relationships between the four parameters measuring head movements and VVIC depend on gender (Fig. 3).

As in Ref. [10], visualization of a sled-fixed imaginary target had different effects according to the ‘‘stiffness’’ of the 61 people tested. The 27 participants who showed head roll amplitudes larger than the median HRA obtained for the main sample of 108 participants (6.6°) were classified as floppy people, the 34 others as stiff people. Target visualization had no significant effect on the head movement of stiff participants, since their mean HRA decreased by only 8% ($p = 0.10$) and their HVTD by 2% ($p = 0.47$). By contrast, the amplitude of the initial head movement of floppy participants strongly decreased. Their average HRA dropped 38% ($p < 0.001$) and their mean HVTD 23% ($p < 0.001$).

Twelve participants, including six floppy and six stiff ones, were submitted to sideways impulses without instruction, while imagining a sled-fixed target, while imagining an earth-fixed target or while ‘‘stiffening up’’ their neck (see Section 2). Again, visualization of a sled-fixed target reduced the head movement of floppy participants, but had no effect on the responses of stiff participants (Table 2). The effects of visualization of an earth-fixed target were very similar to those of the sled-fixed target. When asked to ‘‘stiffen up’’ their neck, all participants were able to reduce their head re trunk movement to similar minimal levels (Table 2), and there was no longer a difference between the responses displayed by floppy and stiff participants.

4. Discussion

This large-scale study confirmed and extended our initial findings [10]. The head movement responses of participants were variable and distributed along a continuum from stiff to floppy (Fig. 2). The ‘‘stiffness’’ of participants did not depend on age, and on average females were stiffer than males. Both stiff and floppy participants were able to ‘‘stiffen up’’ their neck with the same efficiency, which rules out the possibility that the inter-individual variability of responses might result from differences in the strength of neck muscles.

As in Ref. [10], visualization of a sled-fixed imaginary target reduced the amplitude of the head movement in floppy participants, but did not modify the head movement of stiff people. Similar effects were obtained with the earth-fixed imaginary target, which suggests that this increased stiffness resulted more from the fact that participants were forced to imagine an external visual space than from the exact nature of the imagined visual cue. Apparently, the forced adoption of a visual frame of reference before the impulse begins is associated with stiffer behavior. In general, visualization of an imaginary target improved the efficiency of head

stabilization during linear body translations as in former studies [4,6,17].

The average frame effect obtained in the rod-and-frame test was smaller than the values reported in the literature [13,22], which may be due to the small size of our rod-and-frame display and/or to the use of a digital, computer-generated projection. The embedded figure scores tended to be better than those reported [23], but were still in the normal range. In contrast with that suggested in the literature [25,26], there was no correlation between the visual field-dependence and motion sickness susceptibility, which argues against the idea that inter-individual differences in the MSS score arise simply from differences in the weighting of visual versus vestibular and/or proprioceptive signals.

Multivariate regression analysis did not reveal strong correlation between the psychophysiological variables and the variability in head movement control revealed by the impulses. The ‘‘stiffness’’ of individuals was loosely related to the vividness of their imagery with eyes closed, with the poor imagers being floppier than the good ones. However, this correlation explained only 20% of the variance in ‘‘stiffness’’. Our interpretation is that the best imagers may spontaneously visualize the experimental room with eyes closed and use this image as a visual frame of reference, thus reducing the movement of their head. In contrast, the worst imagers may not visualize the external world well enough to use it as a reference frame, and may instead spontaneously use an ‘‘egocentric’’, body-linked frame of reference and be likely to adopt the floppy strategy. They would rely on proprioceptive and/or vestibular inputs to control head and trunk movement, and thus would not care whether or not visualization of the external world is perturbed by a large head movement. The existence of a relationship between the ‘‘stiffness’’ of individuals and the vividness of their imagery supports the idea that ‘‘stiffness’’ might result partly from the frame of reference spontaneously chosen by each individual for postural stabilization.

However, this scheme is based on modest correlations, and should be viewed only as a working hypothesis. A large part of the inter-individual variability in stiffness cannot be explained by variations in vividness of imagery. According to Refs. [21,26], broader personality traits like the anxiety level should be taken into account. While basic anthropometric parameters like the height and weight did not influence stiffness, differences between subjects may well be due to the detailed morphology of their head–neck system. Indeed, movement of the head and neck is driven by interactions between biomechanical and neurally generated forces with complex kinematics [34]. Differences between the neck musculoskeletal organizations of each individual may profoundly alter head response dynamics [6]. Indeed, small variations in muscle insertions can produce large differences in moment arms and force generation [35] that cannot be deduced simply from passive observations, due to the complexity and obvious non-linearity of the system [36]. Imagining a visual target may induce subtle changes in the background tension and/or length of deep neck muscles that might strongly modify the biomechanical parameters of the head–neck system, and hence the amplitude and kinematics of head movements. Alternatively, differences in the reliance on an extrinsic frame of reference for postural control might still explain inter-individual variability, but the psychophysiological measures we used may not have adequately measured this dimension. In particular, the dynamic field-dependence measured by the rod-and-disc test (where the vertical is set on a rotating visual background) or in a moving visual environment [9,21,22,26] may correlate better with stiffness than the static field-dependence [22].

Interestingly, both floppy and stiff subjects were able to ‘‘stiffen up’’ their neck when asked to, which resulted in an almost perfect stabilization of the head. Why do not all the participants stiffen up to gain better head and gaze stability during the impulses? Since the vestibulo-ocular reflex stabilizes gaze in space within 10 ms of head movement, head stability per se is not critical for gaze stability. However, the exaggerated head movement displayed by some of the floppy participants, who actively pulled their head in the direction opposite the acceleration, is difficult to explain. It may increase the risk of whiplash injury during motor vehicle accidents (see Ref. [10]). We proposed [10] that the floppy response would have made sense if the participant had not been seated. When standing, moving the head back in the direction opposite the acceleration in response to an external trunk perturbation is functionally meaningful for balance, because it drives the center of mass of the body back within the participant's support polygon. Whatever their origin, the existence of inter-individual differences in high-level strategies of postural control suggests that using standardized test dummies and cadavers will not be sufficient for full understanding of the mechanisms of whiplash.

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References

[1] Allum JHJ, Gresty M, Keshner E, Shupert C. The control of head movements during human balance corrections. J Vest Res 1997;7:189–218.

[2] Kanaya T, Gresty MA, Bronstein AM, Buckwell D, Day B. Control of the head in response to tilt of the body in normal and labyrinthine-defective human subjects. J Physiol (Lond) 1995;489:895–910.

[3] Keshner EA. Head–trunk coordination during linear anterior–posterior translations. J Neurophysiol 2003;89:1891–901.

[4] Guitton D, Kearney RE, Wereley N, Peterson BW. Visual, vestibular and voluntary contributions to human head stabilization. Exp Brain Res 1986;64:59–69.
[5] Keshner EA, Peterson BW. Mechanisms controlling human head stabilization. I. Head–neck dynamics during random rotations in the horizontal plane. J Neurophysiol 1995;73:2293–301.
[6] Keshner EA. Modulating active stiffness affects head stabilizing strategies in young and elderly adults during trunk rotations in the vertical plane. Gait Posture 2000;11:1–11.
[7] Horak FB, Nahsner LM. Central programming of postural movements: adaptation to altered support-surface configurations. J Neurophysiol 1986;55:1369–81.
[8] Keshner EA, Woollacott MH, Debu B. Neck, trunk and limb muscle responses during postural perturbations in humans. Exp Brain Res 1988;71:455–66.
[9] Keshner EA, Kenyon RV, Langston J. Postural responses exhibit multisensory dependencies with discordant visual and support surface motion. J Vest Res 2004;14:307–19.
[10] Vibert N, MacDougall HG, de Waele C, Gilchrist DPD, Burgess AM, Sidis A, et al. Variability in the control of head movements in seated humans: a link with whiplash injuries? J Physiol (Lond) 2001;532: 851–68.
[11] Collins JJ, De Luca CJ. The effects of visual input on open-loop and closed-loop postural control mechanisms. Exp Brain Res 1995;103: 151–63.
[12] Crémieux J, Mesure S. Differential sensitivity to static visual cues in the control of postural equilibrium in man. Percept Mot Skills 1994;78:67–74.
[13] Isableu B, Ohlmann T, Crémieux J, Amblard B. Selection of spatial frame of reference and postural control variability. Exp Brain Res 1997;114:584–9.
[14] Harm DL, Parker DE. Perceived self-orientation and self-motion in microgravity, after landing and during preflight adaptation training. J Vest Res 1993;3:297–305.
[15] Barnes GR, Eason RD. Effects of visual and non-visual mechanisms on the vestibulo-ocular reflex during pseudo-random head movements in man. J Physiol (Lond) 1988;395:383–400.
[16] Keshner EA, Chen KJ. Mechanisms controlling head stabilization in the elderly during random rotations in the vertical plane. J Mot Behav 1996;28:324–36.
[17] Baloh RW, Lyerly K, Yee RD, Honrubia V. Voluntary control of the human vestibulo-ocular reflex. Acta Otolaryngol 1984;97:1–6.
[18] Mast F, Kosslyn AM, Berthoz A. Visual mental imagery interferes with allocentric orientation judgements. Neuroreport 1999;10:3549–53.
[19] Jeka JJ, Easton RD, Bentzen BL, Lackner JR. Haptic cues for orientation and postural control in sighted and blind individuals. Percept Psychophys 1996;58:409–23.
[20] Vidal PP, Berthoz A, Millanvoye M. Difference between eye closure and visual stabilization in the control of posture in man. Aviat Space Environ Med 1982;53:166–70.
[21] Ehrenfried T, Guerraz M, Thilo KV, Yardley Y, Gresty MA. Posture and mental task performance when viewing a moving visual field. Cogn Brain Res 2003;17:140–53.
[22] Isableu B, Ohlmann T, Crémieux J, Amblard B. How dynamic visual field dependence-independence interacts with the visual contribution to postural control. Human Mov Sci 1998;17:367–91.
[23] Witkin HA, Oltman PK, Raskin E, Karp SA. A manual for the embedded figures tests. Palo Alto, California: Consulting Psychologists Press, 1971.
[24] Owen N, Leadbetter AG, Yardley L. Relationship between postural control and motion sickness in healthy subjects. Brain Res Bull 1998;47:471–4.
[25] Bles W, Bos JE, Kruit H. Motion sickness. Curr Opin Neurol 2000;13:19–25.
[26] Guerraz M, Yardley L, Bertholon P, Pollak L, Rudge P, Gresty MA, et al. Visual vertigo: symptom assessment, spatial orientation and postural control. Brain 2001;124:1646–56.
[27] Oltman PK. A portable rod-and-frame apparatus. Percept Mot Skills 1968;26:503–6.
[28] Zoccolotti P, Antonucci G, Spinelli D. The gap between rod and frame influences the rod-and-frame effect with small and large inducing displays. Percept Psychophys 1993;54:14–9.
[29] Nyborg H. A method for analysing performance in the rod-and-frame test I. Scand J Psychol 1974;15:119–23.
[30] Witkin HA. Individual differences in ease of perception of embedded figures. J Personal 1950;19:1–15.
[31] Marks DF. Visual imagery differences in the recall of pictures. Br J Psychol 1973;64:17–24.
[32] Isaac A, Marks DF, Russell DG. An instrument for assessing imagery of movement: the vividness of movement imagery questionnaire VMIQ. J Mental Imagery 1986;10:23–30.
[33] Golding JF. Motion sickness susceptibility questionnaire revised and its relationship to other forms of sickness. Brain Res Bull 1998;47: 507–16.
[34] Peterson BW, Choi H, Hain T, Keshner EA, Peng GCY. Dynamic and kinematic strategies for head movement control. Ann N Y Acad Sci 2001;942:381–93.
[35] Vasavada AN, Li S, Delp SL. Influence of muscle morphometry and moment arms on the moment-generating capacity of human neck muscles. Spine 1998;23:412–22.
[36] Peterson BW. Current approaches and future directions to understanding control of head movements. Prog Brain Res 2004;143: 369–81.