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Somato-vestibular interactions regarding spatial (dis)orientation

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TNO Human Factors
Soesterberg, The Netherlands

Somato-vestibular interactions regarding spatial (dis)orientation

J.E. Bos

SUMMARY

Purpose: Spatial (dis)orientation is determined by the visual, vestibular and non-vestibular proprioceptive systems. Knowledge of the vestibular and visual systems has already resulted in a model that can be used to predict spatial (dis)orientation. To improve these predictions the present report gives a first approximation of a (mathematical) description of the somato-vestibular interactions regarding spatial orientation.

Methods: A theoretical model is build upon a recapitulation of the current knowledge on the vestibular system and relevant observations concerning somato-vestibular responses: the somatogravic effect under different circumstances in normal subjects and patients without a functioning vestibular apparatus, and the Ferris wheel illusion.

Results: The model proposed does predict a number of observations that can not be predicted fully by vestibular signals only.

Conclusions: Humans do use somatosensory cues in addition to visual and vestibular cues to determine their sense of verticality. Irrespective the complexity of the somatosensory sub-systems involved, a simple collective model does already give satisfactory results.

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TNO Technische Menskunde
Soesterberg

Somato-vestibulaire interacties met betrekking tot ruimtelijke (des)oriëntatie

J.E. Bos

SAMENVATTING

Vraagstelling: Ruimtelijke (des)oriëntatie wordt bepaald door de visuele, vestibulaire en de niet-vestibulaire proprioceptieve systemen. Kennis van de vestibulaire en visuele systemen heeft al geresulteerd in een model dat gebruikt kan worden om ruimtelijke (des)oriëntatie te voorspellen. Om deze voorspellingen te kunnen verbeteren geeft het onderhavige rapport een eerste benadering van een (wiskundige) beschrijving van de somato-vestibulaire interacties met betrekking tot ruimtelijke oriëntatie.

Werkwijze: Een theoretisch model is gebaseerd op een overzicht van bestaande kennis over het vestibulaire systeem en relevante waarnemingen over somato-vestibulaire responsies: het somatogravische effect onder verschillende omstandigheden in gezonde proefpersonen en patiënten met een niet werkend evenwichtsorgaan en de reuzenrad-illusie.

Resultaten: Het voorgestelde model is in staat een aantal van de waarnemingen te voorspellen die met enkel een vestibulair model niet volledig voorspeld kunnen worden.

Conclusie: Mensen gebruiken somatosensorische informatie, aanvullend aan visuele en vestibulaire informatie, bij het bepalen van hun gevoel van verticaliteit. Ongeacht de complex-heid van de somatosensorische subsystemen die hierbij een rol spelen, geeft een enkelvoudig model al acceptabele voorspellingen.

1 INTRODUCTION

In flying an aircraft, a pilot's motion and attitude perception and his control behaviour is dependent upon the feedback of visual, somatosensory, vestibular, and in some extent to auditory stimulation due to the aircraft motions. In other reports the visual vestibular interaction has been elaborated (Bos et al., 2001, 2002). There, a general applicable model to explain and describe spatial orientation and motion sickness was explicated first, giving a framework to further elaborate the components necessary to describe and understand the complex of human spatial orientation behaviour in natural and unnatural conditions. As a second step in the search for a comprehensive integrative description of all components contributing to spatial orientation, the present report will focus on somatosensory-vestibular interactions. Because of the importance of the somatogravic effect in this respect (see below), this interaction will shortly be termed the somato-vestibular interaction accordingly.

In aviation, in military aviation even more than in civil aviation, high velocity and manoeuvrability are important factors, and as a consequence, (high) G-loads are inescapable then. It is evident by experience that the seat-of-the-pants "feeling" is one of the most clear-cut aspects when confronted with high G-loads. This reflects a somatosensory phenomenon, indicating it's importance here. The relevance of the somatosensory system regarding spatial orientation in general has already been noted by Mach (1875). Kornhuber (1974) makes a difference in this respect between "proprioceptive" (concerning all registrations of motion and/or pressure), vestibular (the inner ear only), and somatosensory (all other motion and pressure) sensors. Defined this way, proprioception equals the sum of vestibular and somatosensory information. For this reason, we would, for example, now term the somatogravic effect the proprioceptive effect in stead. There is, however, a problem in discriminating the effects due to the somatosensory and the vestibular system, because normally all accelerations exerted to the one are equal to those exerted to the other. Specifically regarding the flight environment, this problem was already discerned by Van Wulffte Palthe (1922). This is probably the main reason why so little is known on the functioning of the somatosensory system as a whole, as opposed to knowledge of the visual system, for example.

The best elaborated illusion regarding spatial disorientation, a matter not yet understood or settled completely, however, is the somatogravic effect: a false tilt sensation due to a horizontal acceleration that is added to the gravitational acceleration, like the forward acceleration during a takeoff, or the centripetal acceleration in a centrifuge. In the next section this illusion will be illustrated by experimental data from the literature and from additional experiments performed in a small arm centrifuge at TNO, and with the counter-rotation centrifuge of the Defence and Civil Institute of Environmental Medicine (DCIEM), Toronto, Canada. All these data are used to show that the effects observed in individual recordings cannot all be explained by processing of vestibular signals only. In addition, the data by Mittelstaedt et al. on the location of the extravestibular graviceptors is presented that show the relevance of the somatosensory system regarding spatial orientation (e.g. Mittelstaedt & Fricke, 1988). A last fact of importance with respect to somato-vestibular interactions concerns the final orientation obtained subjectively during the Ferris wheel illusion. Next to these facts, the subsequent section will describe how theoretically these facts can be combined into one model describing the somato-vestibular interactions regarding spatial orientation. Though part of these considerations have been described in the report on visual-vestibular interactions (Bos et al., 2002), they will be repeated here in order to realise an independent comprehensible document. For a proper understanding in this respect some basic principles of somato-vestibular sensory function will be dealt with first.

2 CURRENT KNOWLEDGE

2.1 Exafferents and reafferents

When we move there is a wide range of sources of information available to our central nervous system (CNS) to determine attitude (i.e. spatial orientation) and motion. When we are moved passively, visual, vestibular and somatosensory cues as suggested above already, are dominant. When we move ourselves, there is additional information available that can be inferred from self-generated motor commands, which are combined with experience (a process of learning), thus giving information on self-motion too. These processes are enhanced by somatosensory signals that give the possibility to check the accuracy of this information, and facilitate the process of learning. When walking, for example, the motion of the legs gives information on the amount of body-motion. As a result of the learning processes involved, stepping around over a rotating disk in the dark while keeping the body space fixed still gives a sense of self motion (e.g. Bles & Kotaka, 1986; Bles et al. 1984, 1983). Arthrokinetic information is used likewise (De Graaf et al., 1994). Signals coming from sensors are (medically) termed afferents. The afferents resulting from self generated action are called reafferents, and those resulting from external sources, e.g. due to aeroplane movement, are called exafferents (Von Holst, 1954). For the present purpose, interest will be confined to passive motion, for we do not really fly ourselves, and more specifically to changes in attitude perception due to forces exerted to, and accelerations experienced by the body as a whole (i.e. head, trunk and limbs). The remainder will consequently deal with somato-vestibular exafferents only.

2.2 Somato-vestibular cues

By Newton's second law we know that a mass m moved with an acceleration $\mathbf{a} = d^2\mathbf{x}/dt^2$ (with $\mathbf{x}$ representing position) is subject to a force $\mathbf{F} = m\mathbf{a}$, or, any mass m to which a force $\mathbf{F}$ is applied tends to move with an acceleration $\mathbf{a}$ (and hence, the ratio $\mathbf{F}/\mathbf{a}$ is a constant m). If two masses are involved (e.g. one of yourself, and the other being the huge mass of earth), these will attract each other with a force proportional to both these masses (Newton's gravitational law). As before, this force provokes an acceleration specifically denoted by $\mathbf{g}$. So, when moving on earth we only "feel" the resultant of these accelerations, $\mathbf{f} = \mathbf{a} + \mathbf{g}$, where the specific force $\mathbf{f}$ is also called the gravito-inertial acceleration (GIA).

There are several sensors within the human body sensitive to the specific force $\mathbf{f}$. Most importantly, we are equipped with a vestibular apparatus, in which the otoliths serve as linear accelerometers. Throughout the body, including our organs, there are mechanoreceptors that measure the forces acting on them. If we are in contact with an external surface, skin-receptors will also measure the forces exerted on them. Lastly, fluid flows and pooling are sensed too (Mittelstaedt, 1992, 1996; Vaitl et al., 1997), but we will not consider these cardiovascular effects here separately. The first three sources of information are shown in Figure 1.

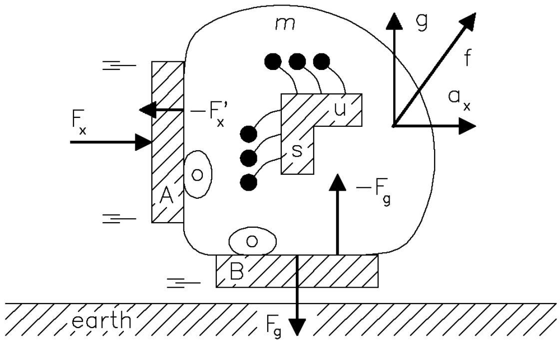

Fig. 1 A jelly sphere including horizontal (u) and vertical (s) accelerometers and organs (o) supported by surfaces (A and B) moved over the earth's surface (see text for further explanation).

Suppose some jelly spherical body with a mass *m* moves horizontally over the earth's surface. Figure 1 then shows the forces and accelerations at stake. Suppose that the motion itself is driven by a force $\mathbf{F}_x$ pushing the body by means of some surface (A in Fig. 1). The body will then both exert a reaction force $-\mathbf{F}_x$' due to inertia, but, most importantly, it will move in the direction of the exerted force $\mathbf{F}_x$. By Newton's second law the resultant acceleration is then given by $\mathbf{a}_x = (\mathbf{F}_x - \mathbf{F}_x')/m$. Force sensors at the body surface will sense the pressure, and somatosensors within the body will sense the body distortion. We will suppose that these surface and somatosensory signals are all combined into one percept of the force exerted on the body. Along the vertical axis the following is happening. Here gravity attracts the body, and hence the body is pulled down by the force $\mathbf{F}_g$. But, because the supporting surface (B in Fig. 1) can't move down, this surface exerts a force on the body $-\mathbf{F}_g$ (Newton's third law). Hence, in the vertical (*z*-) direction the body is at rest ($|\mathbf{F}_g| = |-\mathbf{F}_g|$). Due to the weight of the body (*mg*) it will be deformed, and this distortion is also sensed by somatosensory (force) sensors. This reasoning also holds for the organs within our body (o in Fig. 1). There may be, however, a difference between the stimulation of the sensors at the surface of the body, and those inside the body. Suppose, for example, someone totally submerged in water, such that his weight is equal to that of the water and he is floating. The pressure exerted by the water on the skin will then be equal all over the body, and therefore the net specific force as sensed by the skin somatosensors will be zero. Observed effects of the elimination of these skin somatosensory cues vary from minor to marked (Brown, 1961; Stone & Letko, 1964; Nelson, 1968; Wade, 1973; Mayne, 1974; Jarchow & Mast, 1999). However, all organs within the body are still attracted by the gravitational force, and this net force equals that of gravity.

Within the body (more specifically the head) we also assume a set of accelerometers (the otolith organs) to be present. If the body under consideration here would be an upright head, these otoliths would be the utricles along the horizontal axis (u in Fig. 1), and the saccules along the vertical axis (s in Fig. 1). Each of these organs consists of layers of hair cells with crystals (the actual otoliths) on top, which crystals have a higher density than the surrounding fluid. These otoliths function as more or less perfect three-dimensional DC-accelerometers (Merfeld et al., 1993). We therefore take the transfer function of these otoliths to be the identity, i.e.

$$\mathbf{f}_o = \mathbf{f}_h \,. \tag{1}$$

In Figure 1 the utricles will signal proportional to the acceleration $\mathbf{a}_x$, and the saccules will signal proportional to the gravitational acceleration, and this acceleration will point upwards. Hence, the resultant of the accelerations involved here add to the specific force or gravito-inertial acceleration $\mathbf{f} = \mathbf{a} + \mathbf{g}$.

The vestibular apparatus is also composed of the semi-circular canals (SCC), a set of three more or less orthogonal canals within each inner ear. The otolithic membranes are part of the SCC configuration. Each canal contains fluid (endolymph) that will lag head rotations due to inertia. Each fluid flow is sensed by some sort of valve (the cupula) with the same density as the endolymph so as to be insensitive to linear motion. These SCC act as angular acceleration sensors, be it that their output is proportional to angular velocity in the frequency range of naturally made head and body movements (Steinhausen, 1931, 1933; Van Egmond et al., 1949; Groen, 1956, 1957; Robinson, 1977; Raphan et al., 1979). By approximation the transfer function of the SCC may therefore be given, with $\boldsymbol{\omega}_h$ the head angular velocity and τ_c = 10 s, by

$$\boldsymbol{\omega}_s = \frac{\tau_c s}{\tau_c s + 1} \boldsymbol{\omega}_h \,. \tag{2}$$

There will, of course, be differences in static and dynamic behaviour between the vestibular and the extra-vestibular proprioceptive subsystems, and these differences may be utilised by our CNS to obtain additional information on motion and gravity. Von Gierke & Parker (1994) even attributed the difference in dynamics of somatogravic and vestibular sensors to cause people to get sick. Nevertheless, there remains a fundamental problem concerning the indistinguishability of the accelerations due to motion and due to gravity, and this will be explained in the next section.

2.3 GIF resolution

To move about on earth in a controlled manner, knowledge of self-motion is a prerequisite. Here, also the human CNS has to deal with Einstein's equivalence principle. By path integration we may calculate position from acceleration. If we would then not discern gravity as such, we might feel like an astronaut within five minutes ($\Delta x = \iint g dt^2 = \frac{1}{2} g t^2 \approx 440$ km, with $g = 9.81$ m/s^2 and $\Delta t = 300$ s). The fact that we don't "feel" this indicates that our CNS employs some algorithm to successfully filter out gravity. Mayne (1974) suggested that a simple low-pass filter may describe this CNS-action because gravity is always constant, while (self generated) accelerations are variable. This idea was incited by the somatogravic effect (see the introduction). As described above also, the otoliths respond linearly to the specific force $\mathbf{f} = \mathbf{a} + \mathbf{g}$. Because the otoliths are head fixed while gravity is earth fixed, the acceleration $\mathbf{a}$ needed for proper path integration should hence be calculated by

$$\mathbf{a}_e = \mathrm{R}_\omega(\mathbf{f}_h) - \mathbf{g}_e . \qquad \textbf{(3)}$$

Here, the rotation matrix R_ω can be obtained by SCC signals, as well as by vision, and this has been explicated elsewhere (Bos et al., 2002). Because angular motion is determined explicitly by the SCC and by vision, while somatosensory signals are all directly related to specific force, it is assumed here that no somatosensory cues are used for the rotation R_ω in (3), even though angular motion could, theoretically, be determined by comparison of several somatosensory cues. The matrix R_ω thus rotates the head-referenced otolith sensed $\mathbf{f}_h$ into an earth-referenced vector. In the resulting earth fixed frame of reference, gravity can accordingly be estimated by a low-pass filter. Let us denote the perceptions of gravity and motion by $\tilde{\mathbf{g}}_e$ and $\tilde{\mathbf{a}}_e$, respectively. In Laplace notation we then have

$$\tilde{\mathbf{g}}_e = \frac{1}{\tau_g s + 1}\mathbf{f}_e \quad \text{and} \quad \tilde{\mathbf{a}}_e = \frac{\tau_g s}{\tau_g s + 1}\mathbf{f}_e , \qquad \textbf{(4)}$$

such that always $\tilde{\mathbf{a}} + \tilde{\mathbf{g}} = \mathbf{f}$. Here τ_g = 5s is taken according Bos & Bles, 2002). Equation 4 implies that the acceleration of self-motion perception is just the counterpart (i.e. a high-pass response) of the sensed vertical, as we have observed indeed (Bos & Bles, 1998, 2002). The scheme by which we assume gravity is estimated by our CNS is shown in Figure 2 (after Bles & De Graaf, 1993). Here, otolith signals are rotated first to get an earth-referenced vector, because gravity is only constant in an earth fixed frame of reference. Only then can a low-pass filter estimate gravity. An inverse rotation next gives the head referenced gravity vector as we "feel" it.

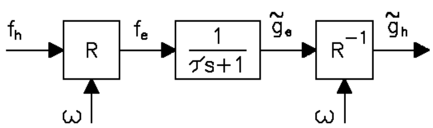

Fig. 2 Functional signal flow from head referenced otolith ($\mathbf{f}_h$) and canal ($\boldsymbol{\omega}$) signals via earth referenced signals ($\mathbf{f}_e$ and $\tilde{\mathbf{g}}_e$) to the head referenced sensed vertical ($\tilde{\mathbf{g}}_h$).

It has previously been shown (Bos & Bles, 2001) that the mathematical equivalent of this model can be written as a three-dimensional differential equation yielding an estimation of gravity $\tilde{\mathbf{g}}$ (or subjective vertical SV)

$$\frac{d\tilde{\mathbf{g}}}{dt} = \frac{1}{\tau_g}(\mathbf{f} - \tilde{\mathbf{g}}) - \boldsymbol{\omega} \times \tilde{\mathbf{g}} , \qquad \textbf{(5)}$$

where the head-referencing index "h" has been omitted. Because this equation is the three-dimensional equivalent of a two-dimensional model by Mayne (1974), we previously suggested to call this the Mayne equation. Hence, by (5) the CNS is capable of solving the specific force resolution problem. Note that the Mayne equation is written explicitly in the time domain, whereas its equivalent according to Figure 2 in the Laplace domain, would require two rotations, which is computationally awkward, and unusual in the Laplace domain.

3 EXPERIMENTAL DATA

3.1 Somatogravic effect

When simulating the catapult launch on an aircraft carrier, for example, centrifuges are used, applying the centripetal acceleration to mimic a high, possibly longer lasting linear forward acceleration (e.g. Cohen et al., 1973). When a subject is fixed to the end of a centrifuge arm (a distance *r* from the centre) and he is rapidly brought to a constant angular velocity (ω) about an earth vertical axis, he will experience a centripetal acceleration ($\omega^2 r$) which is perpendicular to the gravitational acceleration (see Fig. 3). The resultant specific force, or gravito-inertial acceleration, hence tilts ramp-wise with respect to the subject. It is observed, however, that the sense of verticality, or subjective vertical (SV) only approaches the direction of the specific force asymptotically within a period of (decades of) seconds. This apparent tilt during centrifugation was termed the somatogravic effect (Graybiel et al., 1947). Figure 4 shows some results of Graybiel & Clark (1965) on both healthy subjects and in patients without a functioning vestibular apparatus (labyrinthine-defective, LD), indicating the significance of both vestibular and extravestibular sensors regarding this effect.

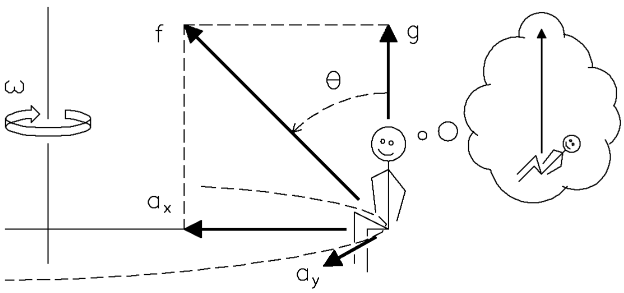

Fig. 3 Human subject facing the centre of rotation (angular velocity ω), experiencing a forward linear centripetal acceleration (a_x), a lateral tangential acceleration (a_y) during on- and offset only, and an upward gravitational acceleration (g), which accelerations add to form the specific force (f). As a result of sustained rotation, the subject will feel tilted (approximating θ), which phenomenon is termed the somatogravic effect.

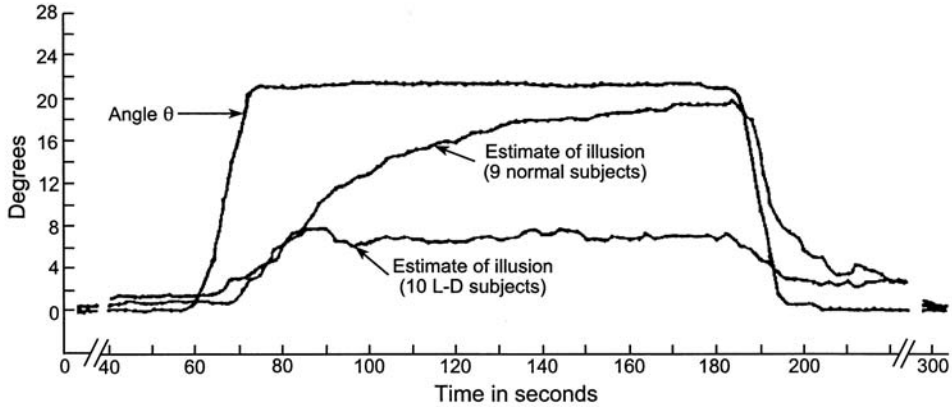

Fig. 4 Average estimated angle of tilt (θ) as observed by 9 normal subjects and 10 labyrinthine defective (L-D subjects), experiencing a centripetal acceleration of approximately 0.4g in a 1.9 m centrifuge from t=±60 to t=±185 s (after Graybiel & Clark, 1965).

3.2 Additional data

In 1999 we performed a series of experiments, analogous to those by Graybiel et al., including centrifugation on a small arm centrifuge (Bos, 2000). This centrifuge consisted of a chair mounted 0.64 m from the centre of rotation, facing the direction of rotation which was about an earth vertical axis. Subjects were accelerated CCW with 90°/s^2 to 180°/s in one trial and to 225°/s in another. This resulted in centripetal accelerations of 6.3 m/s^2 and 9.8 m/s^2, respectively, and tilts of the GIA of 33° and 45°, respectively. After 90 s of constant velocity rotation, deceleration was realised with 2°/s^2 in order to minimise motion sickness. Subjects had to indicate their sense of verticality by means of a joystick, a metal rod, 1 cm of diameter and 10 cm long, that could rotate about the roll-axis, positioned at the subject's right hand. Subjects were instructed to keep the joystick always upright, i.e. parallel to the earth vertical. A 10 s baseline interval at stand still was always recorded in advance of the centrifuge runs. To their SV-data we fitted a function according

$$f_i = A\left(1 - e^{-t_i'/\tau}\right) + y_0, \tag{6}$$

where y_0 represents the last sample of the pre-centrifuge run, i.e. a base-line value.

$$t_i' = (t_i - T)(t \geq T) \quad \text{with} \quad \begin{cases} (t_i \geq T) = 0 & \text{for} \quad t_i < 0 \\ (t_i \geq T) = 1 & \text{for} \quad t_i \geq 0 \end{cases}. \tag{7}$$

The parameters A, τ and T have been found by minimising S with

$$S = \sum_i (f_i - y_i)^2 . \tag{8}$$

In Figure 5, results of three (of the sixteen participating) subjects are shown.

From these data it can be seen that in general the function given by (6) adequately describes the observed behaviour, irrespective the large variability observed. Amplitudes (A), time constants (τ), as well as the initial delays (T), vary considerably. We conclude that this must be at least partially due to somato-vestibular interactions. At the time we described this experiment (Bos, 2000), it was suggested to include a high-pass filtered acceleration signal as sensed by the somatosensory system in (5) to determine the sensed or subjective vertical. We will return on this, however, below.

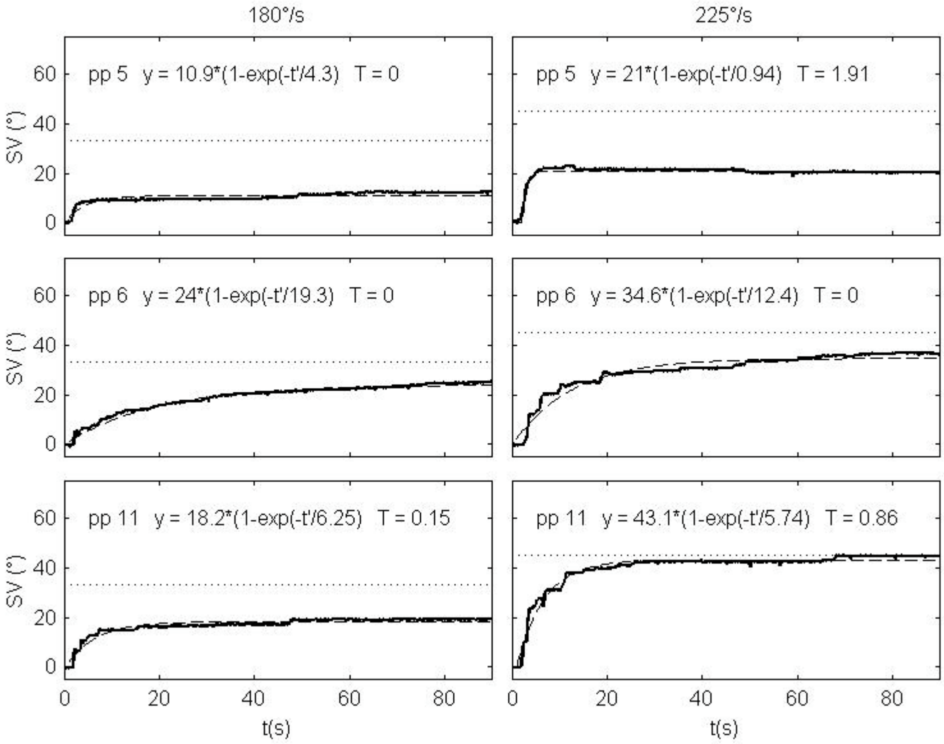

Fig. 5 Somatogravic effect in three subjects using a small arm centrifuge. Solid lines represent the observed data, dashed lines the mathematical fit given by (6), and dotted lines the angle of GIA-tilt. For details see text.

3.3 Counter-rotation

In 2000, we performed another centrifuge experiment, in collaboration with Dr. Cheung from the DCIEM in Canada (Bos et al., 2001). The purpose of this experiment was to confirm the low-pass filter characteristic of the otolith driven orientation mechanism as described by (5). Because in (5) angular information is at stake when using a fixed arm centrifuge, we built upon the idea that had been applied before (Graybiel & Johnson, 1963; Benson & Barnes, 1970) to use a so-called counter-rotation (or CORO) platform. When the subject is centrifuged *and* rotated at the end of the centrifuge arm contrary to the centrifuge rotation at the same time, such that his physical orientation remains earth fixed, there is a net centripetal acceleration that rotates about the subject. Here, however, there is *no* concomitant angular motion as sensed by the SCC (see Fig. 6).

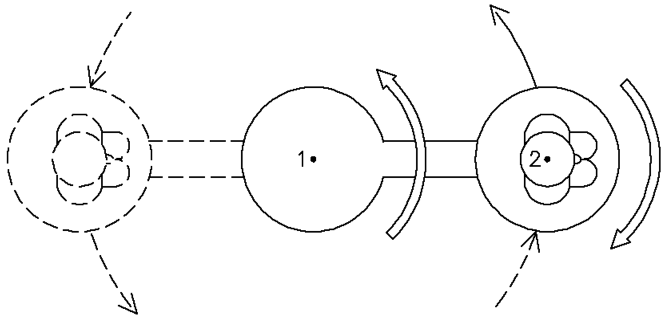

Fig. 6 Counter-rotation paradigm. Top view of a subject rotating about two parallel axes of rotation (1 and 2) such that the net rotation is zero, while only the linear centripetal acceleration rotates about the subject.

According to the model description (equation 5 as explained below), the SV will deviate from and rotate in a cone about the true vertical (see Fig. 7). According to (5) the SV should lag the GIA, and we wanted to quantify this lag.

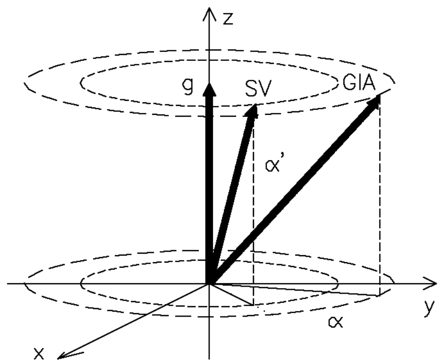

Fig. 7 In the CORO-paradigm, the subjective vertical (SV) will deviate from and rotate about a veridical vertical axis.

The centrifuge we used for this experiment had an arm length of 1.8 m, and we used 10, 15, and 20 RPM that resulted in centripetal accelerations of 1.9, 4.3, and 7.7 m/s^2, and associated tilts of the GIA with respect to the earth vertical of 11, 24, and 38°, respectively. The SV was measured again with a device equal to that in the experiment used above, however with two degrees of freedom now, i.e. it could rotate about the roll and pitch axes. To look for possible asymmetries in roll and pitch indications we also asked subjects to indicate a perfect circle with the joystick of 10, 20, and 45° when otherwise stationary. A typical example (one of 16 subjects) is shown in Figure 8.

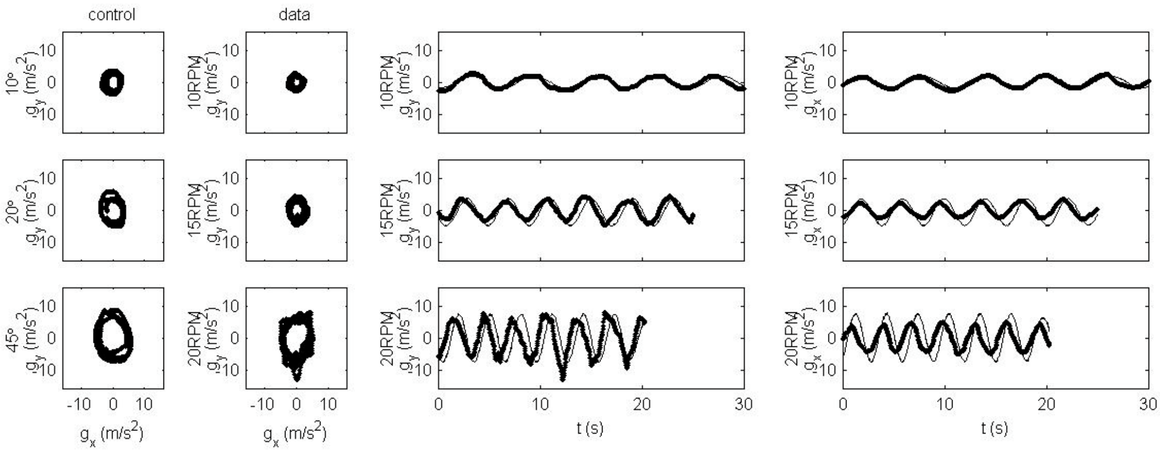

Fig. 8 CORO SV-indications. Left: xy-plots of stationary control data at 10, 20, and 45°. Second left: xy-plots of SV-data during counter-rotation at 10, 15, and 20 RPM. Note that in the left two columns the plots mimic a top view with the subject looking to the right. Second right: time plot of lateral SV-component during counter-rotation (thin lines = stimulus, thick lines = SV-component). Right: time plot of for-aft SV-component during counter-rotation.

These CORO-data reveal that again a large variability was present in observed behaviour. This concerns asymmetries in for-aft and lateral SV-amplitude indications, and most interestingly, in observed phase lags *and* leads. On average, the phase difference was about zero, indicating a symmetric distribution among the observed phase differences, which were in the range of ±150°. Phase leads had also been observed by Benson & Barnes (1970). In the experiments we performed in 2000, subjects mentioned a strong sensation of being tossed around, with a high somatosensory component. Also in the report on these data (Bos et al., 2001) we suggested to include a high-pass filtered somatosensory acceleration signal to explain these data, because a high-pass filter does induce a phase lead. Individual differences in weighting of vestibular and somatosensory cues could thus explain the observed variability in phase lags *and* leads. We will now return on this explanation in the theoretical considerations section.

3.4 The centre of graviception

The role of extra-vestibular mechanoreceptors in the determination of spatial orientation has first been addressed by Mittelstaedt & Fricke (1988). They let subjects, including some LD-patients, laying on their side, vary their position on a centrifuge such that they were subjectively horizontal. The idea behind these experiments was that the information of all force-sensors is weighted, and the result determines the final direction that is interpreted as the direction of gravity (see Fig. 9). It was observed then that subjects did feel horizontal with the head being positioned away from the centre, indicating that extravestibular graviceptor information is used in determining subjective orientation in addition to vestibular signals. Furthermore, there were considerable differences between subjects (average distance of the centre of the head to the centrifuge axis = 25.2 cm, ranging from 3.5 to 50.4 cm), indicating that the weighting of vestibular and extravestibular signals varies considerably between subjects. Because LD-patients show a centre of graviception located considerably lower in the body as compared to the control subjects, they concluded that this centre is located somewhere in the trunk. On the basis of additional experiments with paraplegic and nephrectomised patients, Mittelstaedt (1992) concluded that the centre of graviception is likely located in the kidneys.

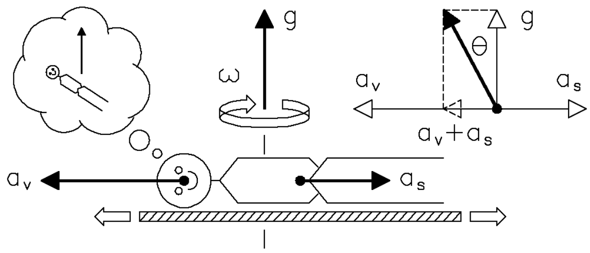

Fig. 9 Human subject laying on his side, capable of shifting his position such that the (weighted) resultant centripetal accelerations (vestibular, $a_v=\omega^2 r_v$, and somatosensory, $a_s=\omega^2 r_s$) add to zero, and the subjective perception results in a horizontal posture.

3.5 Ferris wheel illusion

Here, it will prove essential to also consider the following observations. Despite the fact that these are interesting, they have not yet been elaborated systematically, and references to the literature are therefore scarce. These observations concern the following.

When a subject is rotated with a constant angular velocity in yaw about an earth horizontal axis (barbecue spit rotation) and closed eyes, he will first perceive the veridical motion. But when his canal afferents have returned to their resting value, normally corresponding with zero angular velocity, he will only feel a linear acceleration (Fig. 10). Because the horizontal component of this linear acceleration is 90° out of phase with the vertical component, and there is no canal angular velocity signal, this is interpreted as a circular motion with some fixed orientation (Mayne, 1974; Mittelstaedt et al., 1989). The resulting subjective motion equals that of a gondola of a Ferris wheel, for which reason this illusion is also called the Ferris wheel illusion.

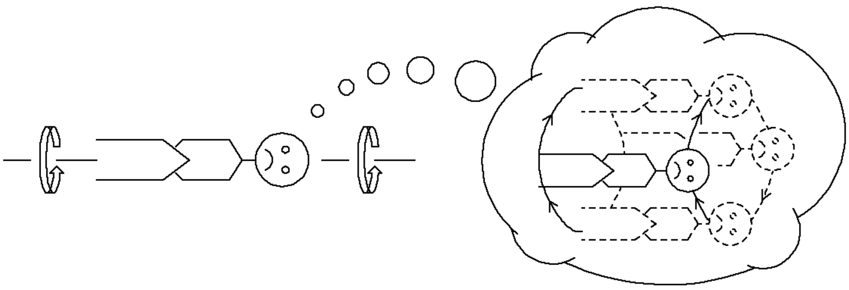

Fig. 10 Ferris wheel illusion. A subject rotating with a constant angular velocity about an earth horizontal axis (left) perceives a motion like a gondola of a Ferris wheel after his canal signals have returned to their rest value (right).

The final orientation during this illusion is dependent upon path integration of canal afferents, the idiotropic vector (Mittelstaedt, 1983), cognition, and somatosensory cues. For example, pressure applied to the feet will result in an upward orientation, which is reasonable, because this would also be the case when the same circular motion is made when standing upright (personal observations; Lackner & Graybiel, 1978; Mittelstaedt et al., 1989). If pressure is applied to the head, subjects perceive an inverted orientation, which makes sense for equal reasoning. Young et al. (1996) also noted that during the first days in space, pressure to the feet gives a strong sensation of being "upright". The interesting conclusion that may be drawn from these observations is that apparently, the external force exerted to the body is interpreted by our CNS as one indicating the direction of gravity, and not as a force associated with motion. This will be an essential fact that can be used in the modelling approach that follows in the next section on theoretical considerations regarding somato-vestibular interactions.

4 THEORETICAL CONSIDERATIONS

4.1 Modelling approach

We previously presented a model to explain the basic characteristics of human spatial orientation and motion sickness in general (Bos & Bles, 2002; Bos et al., 2002). The development of this model was inspired by our attempts to set up a model to predict motion sickness (Bos & Bles, 1998). The relationship between motion perception and motion sickness results from the assumption that motion sickness is the outcome of a discrepancy between the gravitational vertical as determined by integrated sensory information and a vertical as expected based on previous experience (Bles et al., 1998, 2000). This relationship will be explicated here first, also to put the question under consideration within a broader view. To this end, Figure 11 shows the observer model of Bos & Bles (2002) which describes the control of body motion. Here, a desired body state ($\mathbf{u}_d$) directs a controller (C) generating motor commands (**m**) that subsequently drive the muscles in our body to fulfil the desire. Together with external perturbations (**ext**, by a car, ship or aeroplane e.g.), this results in the actual body state (**u**). This state is sensed by visual, vestibular (inner ear labyrinth), somatosensory (surface and subsurface force and deflection sensors), and to some degree also by auditory sensors, all confined in the block S of Figure 11. After some central nervous system (CNS) processing and delay, this results in signals representing the state of the body ($\mathbf{u}_s$). Parallel to this primary path of signal flow, akin signals are supposed to be generated by a copy of the primary path ($\hat{\mathrm{B}}$ and $\hat{\mathrm{S}}$), together called an internal model or neural store which is supposed to be created by previous experiences. The input of this internal model is a copy of the motor commands (also called an efference copy). Here the output $\hat{\mathbf{u}}$ should be a better estimate of the body state as compared to the output $\mathbf{u}_s$, and it is this estimate that is compared with the desired state $\mathbf{u}_d$ to generate the error signal (**e**). Optimally, the output of the internal model $\hat{\mathbf{u}}_s$ should be equal to that of the primary path $\mathbf{u}_s$. If, for example, an external perturbation is present, these signals will not be equal. The difference or conflict $\mathbf{c} = \mathbf{u}_s - \hat{\mathbf{u}}_s$ may then give rise to an additional feedback signal, weighted by K, and used by the internal model to drive the difference towards zero. In terms of Kalman filtering, this conflict (**c**) is also called the "innovation". Now the body state **u** has several components, e.g. angular velocity ($\boldsymbol{\omega}$), linear acceleration (**a**), and gravity (**g**). Oman (1982) suggested that the resulting multi-vectorial conflict (**c**) is correlated with motion sickness (**s**) as conceptually postulated by Reason & Brand (1975). However, it can be shown that by only the difference between the gravity components in **c**, transformed by some function H, motion sickness can be predicted successfully as it has been observed in a quantitative way (Bos & Bles, 1998). This observer theoretical approach is also applicable more generally, as has been shown by others in addition (Glasauer, 1992; Glasauer & Merfeld, 1997; Merfeld, 1995).

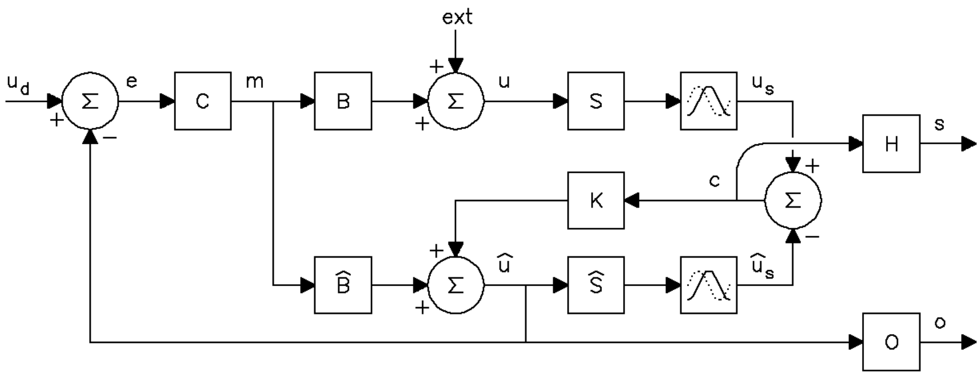

Fig. 11 Spatial orientation and motion sickness model (from Bos & Bles, 2002; see text for details).

Previously, we showed that the combination of a low-pass filter in both the primary path of sensor afferents *and* in the internal model is essential for explaining motion sickness as it has been observed (Bos & Bles, 1998, 2002). Only then does the conflict **c** behave like a second order derivative of the external perturbations, and a peak in sickness severity is predicted as it has been observed, i.e. about 0.16 Hz. The next paragraph will consequently deal with the elaboration of the perception model (blocks S and $\hat{S}$ in Fig. 11).

4.2 Somato-vestibular interactions

For the present purpose of modelling somato-vestibular interactions, it is essential to reckon that people *without* a functioning vestibular apparatus do *not* get sick from motions (James, 1982; Reynolds, 1884; Reason & Brand, 1975; Money, 1970). If this fact is combined with the former conclusion about the low-pass filtering, it can be concluded that somatosensory afferents are *not* included *before* the low-pass filtering as described by (5), but only *after* that. Then it may be questioned how the somatosensory signals are separated in the gravity and motion components, like those of the vestibular afferents. The data of Jongkees & Groen (1950) and by Guedry & Harris (1963) are essential here. They observed that labyrinthine defective subjects when translated horizontally do not perceive a linear motion, but merely perceive tilt. Due to these observations and regarding the Ferris wheel illusion, it is assumed here that the somatosensory system is an ignorant one and the somatically sensed specific force is transformed by a simple filter to estimate gravity (see below). Hence, somatosensory afferents are probably added linearly to the vestibularly and CNS-processed estimation of gravity. Because it has been shown that a large variability exists in individual behaviours under the different conditions, an individual specific weighting is required here (see also Howard, 1997) as we did in describing the visual-vestibular interactions (Bos et al., 2002):

$$\tilde{\mathbf{g}} = \frac{w_v \tilde{\mathbf{g}}_v + w_s \tilde{\mathbf{g}}_s}{w_v + w_s} \,. \tag{9}$$

This then results in the submodel as sketched in Figure 12, showing the somatosensory interactions at stake regarding spatial orientation.

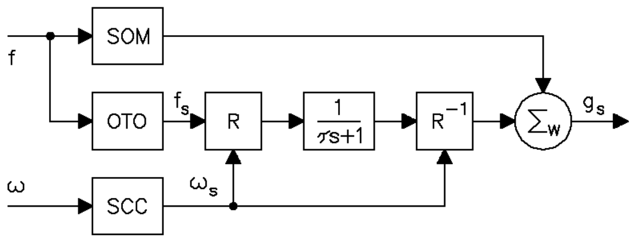

Fig. 12 Determining the subjective vertical based on vestibular and somatosensory information.

4.3 Somatosensory gravity estimation

As indicated by Lechner-Steinleiter (1978), people do adapt to forces exerted to the skin and this probably also holds for the somatosensors within the body. In a first order approximation, it is therefore assumed here that the somatosensory system functions as a high-pass filter acting on the specific force $\mathbf{f}_b$ as sensed with respect to the body, i.e.

$$\mathbf{f}_s' = \frac{\tau_s s}{\tau_s s + 1} \mathbf{f}_b \,. \tag{10}$$

Because the sensation of pressure release takes some seconds, but is complete within a minute, it may be assumed that τ_s is in the order of 20 s. Then (10) would imply that after a while no sense of force perception would be present at all. This, however, is contrary to experience. While sitting on a chair, we are still aware of the pressure exerted by the seat to our bottom, even after hours of sitting. It is therefore also assumed that an another signal

$$\mathbf{f}_s'' = \frac{k_s}{\tau_s s + 1} \mathbf{f}_b \tag{11}$$

is added linearly to the high-pass component. Because there is no reason to assume that the time constant here should be different from that of the high-pass τ_s is taken equal to that of (10). The value of k_s may vary considerably between subjects, as long as $0 < k_s < 1$. Combining (10) and (11) we then have

$$\mathbf{f}_s = \mathbf{f}_s' + \mathbf{f}_s'' = \frac{\tau_s s + k_s}{\tau_s s + 1} \mathbf{f}_b \,. \tag{12}$$

In order to estimate gravity from somatosensory signals too, a low pass filter is essential here, as it was in estimating gravity from vestibular afferents. It is furthermore hypothesised that the somatosensory system does *not* reckon inertial rotations as such (i.e. rotations of the body as a whole with respect to space), and it is therefore assumed that the additional low-pass filter simply operates on the signal represented by (12), *without* performing the rotation operation conform (3). Of course we feel the tilt during rotation about a horizontal axis, but it is hypothesised here that this tilt is *not* accompanied by a somatosensory signal representing angular velocity. It is for good reason that the vestibular apparatus is equipped with linear *and* angular motion sensors! By assuming this simple low-pass filter, short lasting forces exerted to the body and sensed by the somatosensory system will not be interpreted as a change of attitude, but just as a "push". The final somatosensory sense of gravity is then given by

$$\tilde{\mathbf{g}}_s = \frac{\tau_s s + k_s}{\tau_s s + 1}\mathbf{f}_s = \frac{\tau_s s + k_s}{(\tau_s s + 1)^2}\mathbf{f}_b, \qquad \textbf{(13)}$$

where, at first approximation, all time constants involved are assumed to be equal. The different components of this equation are graphically shown in Figure 13. Note that when the subject is initially upright, $\tilde{\mathbf{g}}_s(t=0)$ should be nonzero, and aligned with the true gravitational vector. Because the steady state condition is characterised by k_s, both integrators necessary to realise (13) should take an initial value of $k_s \cdot (0\ 0\ g)$. We will substitute (13) in the SOM-block of Figure 12 for further analysis.

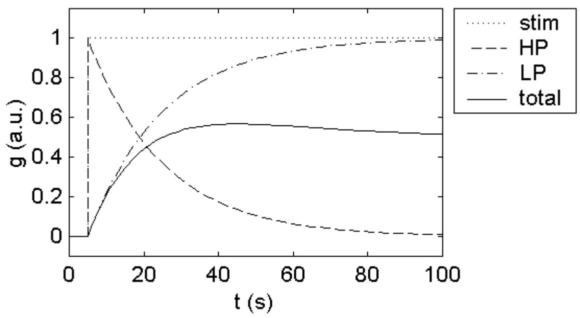

Fig. 13 Somatosensory and vestibular responses due to a unit acceleration step (stim). Shown are the transient high-pass component due to dynamic sensor signals (HP), a sustained low-pass response due to static sensor signals (LP), and the total hypothetical somatosensory response (total according 13 with $\tau_s = 20$ s, and $k_s = 0.5$).

4.4 Example

When all this information is combined, the somatogravic experiment by Graybiel & Clark (1965) can be run with this model, i.e. the model of Figure 12 with equation (13) substituted for the somatosensory system, (5) for the vestibular system, and (9) for the somato-vestibular weighting. The result of this simulation is shown in Figure 14, and will be discussed below, in view of the observed data as presented above in this report.

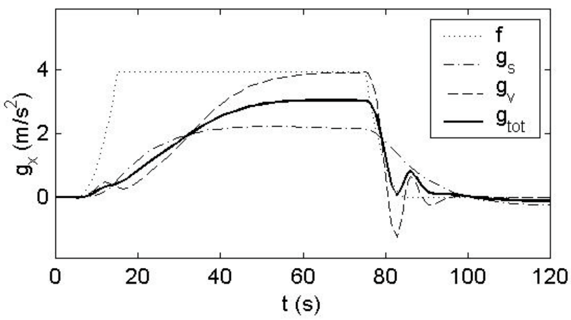

Fig. 14 Somatosensory and vestibular responses due to an acceleration step (stim) equal to that used by Graybiel & Clark (1965). Shown are acceleration components along the x-axis of the somatosensory system only (g_s), the vestibular system only (g_v), and the total after somatosensory weighting (g_{tot}). The model parameters were τ_s = 20 s, k_s = 0.5, and $w_s = w_v = 0.5$).

5 DISCUSSION AND CONCLUSIONS

Here, somato-vestibular interactions are described by means of some basic physics, current knowledge of the vestibular system, observed data on the somatogravic and related effects, and a theoretical consideration of these facts. Though it is known that the somatosensory system is a complex system spread all over the body, it does contribute in a specific way to our sense of verticality, and it is this subjective vertical that plays a key role in spatial (dis)orientation. The aim of this report has been to give an impulse to the (mathematical) description of somato-vestibular interactions in this respect. With a number of assumptions, observed data can successfully be described with more realism than by not taking into account the contribution of the somatosensory system.

The major assumption applied here concerns the pooling of all somatosensory subsystems into one transfer function which output adds to vestibular afferents in determining the subjective vertical. Irrespective this simplification, a realistic prediction could be calculated. Most interestingly, the model predicts an underestimation of the horizontal component of the acceleration vector that determines the subjective vertical (see Fig. 14). The vast majority of responses shown in this report, i.e. those by Graybiel & Clark (1965, Fig. 4), those of Figure 5, and the one shown in Figure 8, reveal an underestimation too. If it would be assumed that the vestibular afferents do give a proper sense of the magnitude of the experienced accelerations, then this underestimation is largely determined by the weighting of vestibular and somatosensory afferents, the latter indicating a reduced magnitude set by k_s in (13). This observation is in support of the model presented here. The dash-dot line in Figure 14, representing the output of the somatosensory subsystem, may as well be considered to represent the response of a patient without a functioning inner ear, i.e. a LD-patient as included in Graybiel & Clark (1965) their data. Because this trace comes close to the average of the observed LD-data (see Fig. 4), this is another fact in support of the model proposed here. It is, however, a reasonable assumption that LD-patients will adapt their somatosensory parameters in order to compensate for the deficient vestibular function.

From the example given in Figure 14, it can furthermore be seen that there is a strong asymmetry in the calculated responses regarding the centrifuge acceleration and deceleration. This asymmetry can be explained by the angular centrifuge motion and the canal-otolith interaction as given by (5), as has been elaborated before (Bos & Bles, 2002; Bos et al., 2002). There we also showed that the undershoot after the centrifuge deceleration can equally well be explained by the same description (5). From Figure 14 it is evident, however, that this undershoot is reduced considerably by the addition of somatosensory signals. The fact that an undershoot is not often observed in real centrifuge experiments, can therefore be interpreted as yet another proof of the involvement of the somatosensory system as described here.

In the present report, it is assumed that the somatosensory system is a naive or rudimentary one and the somatically sensed specific force is identified, more or less, with gravity. We previously proposed a model in which the vestibular afferents are separated in a gravitational component and a component due to motion (Bos et al., 2002). The question whether an equal separation holds for somatosensory afferents is yet unanswered. The observations by Jongkees & Groen (1950) and by Guedry & Harris (1963) are significant in this respect. They noted that LD-patients do not experience linear motion during true physical linear motion, but they only feel tilt. This validates the assumption that somatosensory signals are simply associated with gravity. This, of course, ignores other functions of the somatosensory system, like signalling pushes and pain, essential for (local) feedback purposes other than spatial orientation and motion perception. These responses can typically be used in tactile vests to aid the (fighter) pilot with localising targets or to prevent spatial disorientation in an indirect way (Rupert, 2000a,b). On the edge of local and global somatosensory function is the use of G-seats. Though meant to affect the global sense of spatial orientation and motion, these effects can only be realised by applying local pressure, because otherwise a true motion would occur. In this respect it can also be stated that onset-cues used in (flight) simulation are probably dominantly processed by the somatosensory system. If a small symmetrical acceleration is applied to the body, the head may even remain still in space due to its suspension on the trunk by the neck. It is furthermore interesting to note that Mann et al. (1949) found that SV-settings were significantly less precise when the non-labyrinthine proprioceptive cues are modified by the introduction of a well-padded seat. By specific support of the body, Nyborg (1971) also showed that people are capable of indicating the SV better than with diffuse support by rubber inflatable cushions.

Cheung et al. (1989) found that in LD-patients, circular (roll) vection about an earth horizontal axis was complete, i.e. these patients felt a complete head-over-heels rotation, despite the fact that they were sitting upright. Hence, when visual information is present, the somatosensory information is insignificant. This is different from visual-vestibular interactions, because most normal subjects will only feel tilted, and do not subjectively revolve completely. This speaks in advantage of a somato-vestibular weighting with an emphasis on vestibular signals. Together with the facts mentioned before, this also speaks in advantage of a dominance of vestibular cues in resolving the SV (see also Lechner-Steinleiter et al., 1979). However, Bisdorf et al. (1996), Ito & Gresty (1996, 1997), and Clark & Graybiel (1968) conclude that proprioception predominates (over visual and vestibular cues) in making a realistic appraisal of orientation regarding postural control and subjective vertical settings. These contradictory data may be considered a consequence of the large variability in somato-vestibular weighting as described in the present report. Based on experiments in space, Young et al. (1996) conclude analogous, that "there appear to be strong individual differences in the relative strength attached to different sensory modalities; there are visual people, tactile people, and those with a strong sense that their own trunk alignment defines 'down'."

Here, the effect of an internal model on the responses has been ignored, except for the fact that with the internal model motion sickness can be explained. Furthermore, the fact that people with a functioning somatosensory system but *without* a functioning vestibular apparatus do *not* get sick from motion has been used explicitly. It remains open for future research to study the effect of the internal model on the attitude output when somato-vestibular interactions are incorporated.

The somato-vestibular interaction model presented in this report does not pretend to be complete, far from that. However, it may be considered as a first and valuable approximation, and the data presented here, observed and predicted, give support to the appropriateness of the chosen approach.

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Soesterberg, 8 February 2002

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(Author, Project leader)

DECLARATION

The contractor, TNO Human Factors, hereby declares that, to the best of its knowledge and belief, the technical data delivered herewith under Contract No. F61775-01-WE085 is complete, accurate, and complies with all requirements of the contract.

DATE: ______________________
Name and Title of Authorised Official: _____________________________________

I certify that there were no subject inventions to declare as defined in FAR 52.227-13, during the performance of this contract.

DATE: ______________________
Name and Title of Authorised Official: _____________________________________