

Subjective Vertical Conflict Theory and Space Motion Sickness

Wei Chen; Jian-Gang Chao; Jin-Kun Wang; Xue-Wen Chen; Cheng Tan

- BACKGROUND:** Space motion sickness (SMS) remains a troublesome problem during spaceflight. The subjective vertical (SV) conflict theory postulates that all motion sickness provoking situations are characterized by a condition in which the SV sensed from gravity and visual and idiotropic cues differs from the expected vertical. This theory has been successfully used to predict motion sickness in different vehicles on Earth.
- METHOD:** We have summarized the most outstanding and recent studies on the illusions and characteristics associated with spatial disorientation and SMS during weightlessness, such as cognitive map and mental rotation, the visual reorientation and inversion illusions, and orientation preferences between visual scenes and the internal z-axis of the body.
- RESULTS:** The relationships between the SV and the incidence of and susceptibility to SMS as well as spatial disorientation were addressed.
- CONCLUSION:** A consistent framework was presented to understand and explain SMS characteristics in more detail on the basis of the SV conflict theory, which is expected to be more advantageous in SMS prediction, prevention, and training.
- KEYWORDS:** space motion sickness, subjective vertical conflict, spatial disorientation.

Chen W, Chao J-G, Wang J-K, Chen X-W, Tan C. *Subjective vertical conflict theory and space motion sickness*. *Aerosp Med Hum Perform*. 2016; 87(2):128–136.

Space motion sickness (SMS) is usually referred to as a type of motion sickness produced when humans are exposed to microgravity during spaceflight. The physiological characteristics of SMS parallel those of motion sickness on the Earth in most symptoms, including stomach discomfort, vomiting, headache, lack of concentration, and drowsiness.^{54,60} SMS is experienced by 60–80% of astronauts during their first 2–3 d in microgravity and by a similar proportion during their first few days after returning to the Earth.^{22,55} SMS could induce potential risks to a crew's health, safety, and performance, which is the main disadvantage during the first critical days of spaceflight, particularly in unexpected situations such as vomiting while wearing a space suit during extravehicular activities. Spatial disorientation is likely to cause SMS during spaceflight and it can become a dangerous problem, making it difficult for the astronaut to move quickly through the vehicle.⁵⁸ These vestibular disturbances may also compromise the ability of astronauts to safely land a spacecraft during emergency reentry.^{18,55}

The sensory conflict theory is widely accepted as the most reasonable explanation for SMS. However, it is still not universally accepted because it does not provide sufficient predictive

power regarding who will display symptoms under which types of sensory conflict.^{44,55} Other explanations such as the fluid shift^{37,61} and otolith asymmetry^{24,46} hypotheses have merit in several aspects; however, they also have limitations, for example, in accounting for asymptomatic individuals. In addition, most validation attempts which involved prediction of SMS incidence or severity as observed under normal mission operations have not produced prospectively positive correlations.⁵⁰ This does not necessarily mean that the theory explanation is incorrect. Because of the challenging tasks and limited working hours, activities in orbit differ substantially between crewmembers; thus, comparable conditions for reliable prediction on Earth may simply not be possible. However, a fundamental

From the National Key Laboratory of Human Factors Engineering and the State Key Laboratory of Space Medicine Fundamentals and Application, China Astronaut Research and Training Center, Beijing, China.

This manuscript was received for review in March 2015. It was accepted for publication in November 2015.

Address correspondence to: Jian-Gang Chao, Ph.D., National Key Laboratory of Human Factors Engineering, China Astronaut Research and Training Center, Box 5132-22, Beijing 100094, China; xjtucjg@163.com.

Reprint & Copyright © by the Aerospace Medical Association, Alexandria, VA.

DOI: 10.3357/AMHP.4327.2016

point is that the applicability of a theory should correspond with provocative conditions and the tasks being performed.

A theory put forward by Bos and Bles postulates that only one type of sensory conflict regarding the internal representation of the subjective vertical (SV) is necessary and sufficient to explain most types of motion sickness.^{3,7} The SV conflict theory has been successfully used to predict motion sickness in several vehicles on Earth.^{8,63} SV is a subjective perception of one's own position and orientation, which is mainly determined by the sensory cues of gravity, vision, and the longitudinal axis of the body (the idiotropic cue). It is thought to be the most common probe used by our brains to judge spatial self-orientation¹ and conflict appears when it is at variance with the expected vertical from previous experiences. SV conflict occurs more often in microgravity than on Earth, because gravity, the predominant cue of verticality, is not present in microgravity and astronauts' postures and movements are more labile when they perform tasks and float in the spacecraft interior. Many astronauts maintain a local SV as shown by reports of inversion illusions and visual reorientation illusions. Instability of the SV in microgravity is thought to be a specific trigger for SMS.¹⁰ This conflict is the essence of spatial disorientation, so an internal relationship is constructed between the SV, spatial disorientation, and SMS. Although the SV conflict theory is not perfect in many respects, like the other theories, it may be meaningful to apply it to SMS and investigate the possibility that it can explain and predict SMS.

Here, various studies associated with spatial orientation and SMS have been carefully summarized to develop a consistent framework for understanding, explaining, and predicting SMS characteristics in more detail than before. This article is organized as follows: in the first section, the SV model is expounded and a theoretical framework involving vectors, cues, frames, and organs for the SV is built. Following this, the SV conflict theory is synthesized and its mathematical model is described. Much effort was made to describe the illusions and characteristics associated with SMS during weightlessness, which helped to clarify the relationships between SV conflict and SMS incidence and susceptibility.

Subjective Vertical

SV is generally regarded as a subjective judgment of the body vertical and is the internal representation of gravity. A comprehensive SV theory was first outlined by Mittelstaedt.^{39,40} In most circumstances, verticality of self or objects seems clear and unquestionable. However, when a roll-tilted subject is asked to align a small luminous line with the direction of gravity, a remarkable pattern of systematic errors arises, which is known as the A-effect. The large deviations of the SV from veridicality are attributed to a failure on the part of the gravity systems to correctly perform the necessary coordinate transformation on the visual system.^{39,67} Besides external visual and vestibular cues determining our sense of verticality, Mittelstaedt suggested that there is an internal cue, namely a tendency to shift the SV toward the person's own longitudinal axis ("idiotropic vector"). The vector model is illustrated in **Fig. 1** and

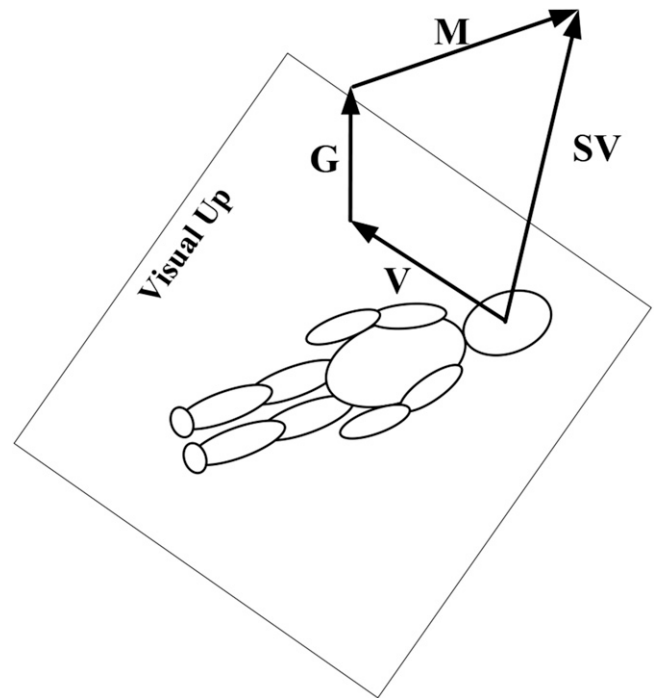


Fig. 1. A vector model for the subjective vertical (SV). V, M, and G represent the vectors of vision, idiotropic, and gravity, respectively. V is aligned with a visual pole supplied by a visual scene, M depends on the body posture and is aligned with the longitudinal axis of the body, and G includes the gravireceptor vector and the gravireceptor bias vector. The G direction is the reverse of the physical direction of gravity.

indicates that the SV is the nonlinear sum of three vectors, including gravity, visual vertical, and an intrinsic "idiotropic" tendency to perceive the vertical in a footward direction.

The gravity vector represents the resulting gravireceptor cues and gravireceptor bias. Gravireceptor cues originate from a gravito-inertial stimulus to the otoliths, whereas gravireceptor bias is produced by the extr vestibular system. Extr vestibular gravity information, which assists in the perception of orientation, was thought to originate from somatic and visceral receptors; however, it was subsequently demonstrated that the effect is mediated by mechanoreceptors in the kidneys and the large blood vessels of the abdomen.^{41,64,65} A notable characteristic of gravity is that it is indistinguishable from forces caused by inertial acceleration, so mechanoreceptors cannot discriminate between tilt and translation.⁴² Obviously this is not the case, since the ambiguity can be resolved by combining otolith signals with estimates of head rotation from semicircular canal, visual, and/or proprioceptive cues.²⁹

The visual vector contributes to the perceived visual vertical, which is abstracted from stimulus signals from visual scene (VS) frames and polarity cues, such as trees, buildings, people, a box on a shelf, or an object hanging on a string, which provide a second source of information. Note that frame and polarity cues are perceptual and depend on visual attention, expectations, and prior experiences of the observer.⁵²

The idiotropic vector is usually considered a unitary vector, to supplement the tendency of aligning the vertical with the

z-axis of the body pointing to the headward direction, independent of the rotation angle sensed by the vestibular system.³⁹ This tendency can explain the A-effect, i.e., a general tendency of subjects to underestimate the amount of self-tilt when subjected to physical lateral tilt.¹⁰ In addition, it has been shown that even in space, where there is no net force acting on the body, subjects do still have a sense of verticality.⁶⁸ Mittelstaedt³⁹ suggested that the idiotropic vector is not part of a specific sensory system, but rather a central nervous system (CNS) agent that is recruited when the SV must be computed. It is also important to note that this vector is not defined physically, but is reckoned by the perceived direction of the z-axis of the body and it is constant in a given individual.³² Interpretation of the idiotropic vector remains unclear. Eggert proposed an interesting reinterpretation that the brain partly relies on a prior assumption that SV is related to the long body axis.²⁶

SV Conflict Theory

Sensory conflict theory. The sensory conflict theory is the primary basis for understanding motion sickness and states that motion sickness is a conflict between actual and anticipated sensory signals,⁵⁷ such as the eyes, the vestibular systems, and the nonvestibular proprioceptors. It is widely accepted and can be used to anticipate whether some combination of stimuli is likely to induce motion sickness. It also predicts that SMS should occur during weightlessness.⁵⁴ Otolith organs do not function normally during weightlessness, while cues from other sensory organs remain unchanged during weightlessness; therefore, information used for orientation and motion perception does not match previously stored neural models in 1 g, and sensory conflict may occur. In a recent review work Thornton proposed an etiology of SMS and argued that the primary sensory conflict in weightlessness occurs within a single sensory modality (otolith organs) and is unique to SMS. He also proposed a second component contributing to SMS: the bimodal conflict between otolith sensors and angular motion sensors that can occur during head movements that produce symptoms consistent with motion sickness.^{59,60}

Oman extended Reason's hypothesis by adding emetic linkage output pathway dynamics and synthesized a mathematical model based on the observer theory from control engineering.⁴⁸ His model states that motion sickness is related to the vector difference between a vector representing all available afferent sensory information and a vector representing expected sensory information, and the chance of motion sickness and the severity of the motion sickness increase with the vector difference.

An underlying neural mechanism of sensory conflict theory also postulated by Oman^{49,53} is that the conflicting signals for sickness originate in neurons in the central vestibular system subserving spatial orientation, which respond to a variety of cues, including proprioceptive and visual ones in addition to direct inputs from the vestibular afferents; these neurons can link to the "emetic brain" (the brainstem vomiting center), eventually producing symptoms and signs of motion sickness. Recently Cullen and coworkers have supplied some new evidences from brainstem and cerebellar sensory processing.^{12,20,21}

They identified a subclass of neurons in the vestibular nuclei and deep cerebellar nuclei that respond preferentially to passive head movements, whereas the inputs to these neurons during active head movement are inhibited by the cerebellar reafference cancellation mechanism (comparing the expected consequences of self-generated movement with the actual sensory feedback). This mechanism explains the distinct difference in susceptibility of drivers and passengers, human immunity to normal self-generated movement, and why the unexpected change of body posture is relatively provocative.

SV conflict theory. Bos and Bles⁷ tried to recognize the special role of gravity in motion sickness. Focusing on the observation that people get sick when there is an apparent change of gravity with respect to their head, they assumed that it is only the sensory difference between gravity components that correlates with motion sickness and redefined Oman's theory on the basis of an SV conflict model, which is referred to as the "subjective vertical conflict theory." He stated that "all situations which provoke motion sickness are characterized by a condition in which the sensed vertical is at variance with the subjective vertical as expected from previous experience" and "Subjects develop motion sickness preferably when their subjective vertical is at stake,"⁷³ indicating that motion sickness arises when the conflict concerns the internal representation of SV.

The SV conflict theory is not a replacement of the sensory conflict theory, but a simplification and evolvement. Here, the essential cause of motion sickness is still the multisensory conflict, but Bos and Bles propose that it originates not at the first stage of vestibular processing but at subsequent levels of processing as a result of competing internal estimates of orientation derived from different senses.^{7,53} The sensed SV acts at a higher level constructed on the basis of multisensory information, while the expected SV is constructed by an internal model of the body state based on previous experience.^{7,15} Thus, it has an advantage in application in that there is no longer a need to classify conflicts into different types and apply different weight factors for various situations. Considering Oman's orientation-emetic linkage mechanisms, a heuristic neural conjecture might be helpful. At the earliest stages of sensory processing, the information from vestibular and extr vestibular signals converge in the vestibular cerebellum, which distinguishes between active and passive motion,¹² while the computation of orientation and posture control is a subsequent higher-order vestibular function.^{20,21} Thus, the pivotal issue is to determine the physiological locus and operational phase of the sensory conflict neurons or the internal model. However, this needs more evidence.

By adding an appropriate nonlinear transfer function to quantify the relationship between the SV conflicts and motion sickness incidence, an integrated SV conflict model (see Fig. 2) based on Oman's model⁴⁸ is summarized.^{7,10,11} A global overview of the model is shown in Fig. 2A. Inputs to the model were passive head movements and the state of SV was obtained after these inputs were passed through the spatial orientation model, which is derived from the model of visual-vestibular interaction¹¹ (see Fig. 2B). The vector difference (c) between the sensed

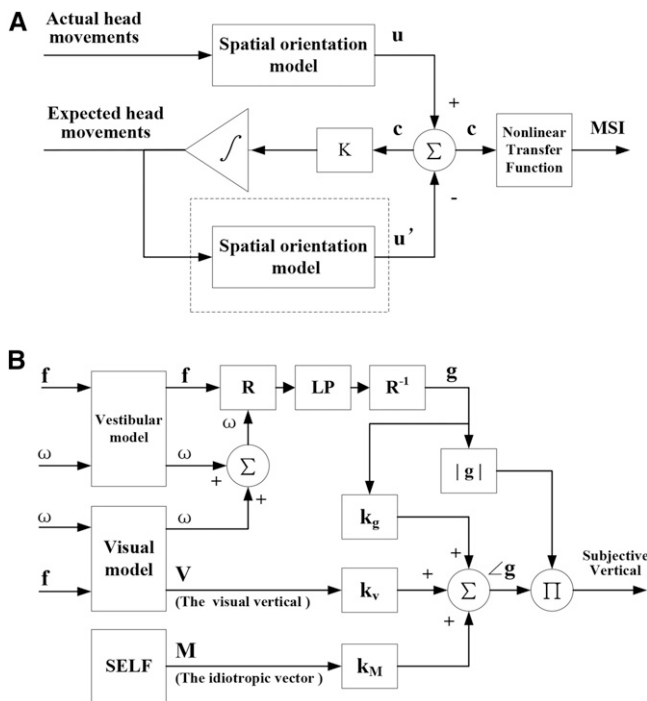


Fig. 2. An integrated model for the SV conflict theory.^{7,10,11} A) Global overview of the SV conflict model. K , internal feedback (or Kalman) gain; c , vector difference between u , the sensed and u' , the expected SV; MSI, motion sickness incidence. B) Spatial orientation model derived from the extended model of visual-vestibular interaction. Inputs are specific force f and angular velocity ω . R , transformation matrix; LP, low-pass filter; R^{-1} , inverse matrix of R ; g , gravity; $|g|$, magnitude and $\angle g$, direction of gravity; k_g , k_v , and k_M , weights for the gravity, visual, and idiotropic vectors, respectively. Functional signal flow from head-referenced otoliths and canal signals were manipulated via earth-referenced signals to the head-referenced sensed vertical. k_g , k_v , and k_M are weights for different cues.

(u) and the expected (u') SV is the conflict vector for generating motion sickness. The relationship between motion sickness incidence and the magnitude of the vector difference is nonlinear, and its transfer function consists of logarithmic functions and a leaking integrator, which model the trigger, cumulation, and adaptation.⁷ However, the model is still being developed and how exactly the feedback is organized by sensed SV still cannot be fully explained by this model.

The spatial orientation model shown in Fig. 2B produces the SV vector by means of integrated vestibular and visual inputs, together with the idiotropic vector. As stated previously, this verticality is essentially the estimation of gravity, including the magnitude ($|g|$) and direction ($\angle g$). In order to extract gravity out of the gravitoinertial force (f , sensed by the otoliths in the vestibular system), a mechanism which works like low-pass filtering is used by our CNS.⁴⁵ However, gravity is constant in an Earth-fixed frame of reference, whereas these neural signals come from sensors in a head-fixed frame of reference (otoliths). Hence, angular information (of vestibular and visual origin) is required to transpose the acceleration information into Earth coordinates (transformation matrix R) before low-pass filtering can be applied. Then the estimation of magnitude can be obtained. On the other hand, the direction of estimated gravity

is determined by k_g , k_v , and k_M , which are weights, respectively, for the gravity, visual, and idiotropic vectors. The magnitude is only sensed by the vestibular system and the visual and idiotropic vectors can only indicate orientation. Consequently, the estimated gravity was derived as the SV vector, which represents the sensed SV (u) in the path of actual head movements and the expected SV (u') of expected head movements. Usually the expected SV is constructed under conditions of natural body motion on Earth and the time constant of the low-pass filter is optimized based on this condition. For unnatural motions, a typical conflict may be caused by the various delays of the filter in the sensed SV. The incidence of SMS in microgravity can also be explained by this model.

Application and disputation. The SV conflict theory explains the different contributions of head movement in provoking motion sickness. Unambiguous observations have shown that pitch and roll head movements for an upright sitting subject are more provocative than those of yaw, regardless of physical perceptions or visual inducement in a virtual reality environment.^{37,60} This is because these head movements change vertical perception relative to the direction of gravity, whereas yaw motion does not. Similarly, pitch and yaw head movements are provocative with the subject in a supine position, whereas roll motion is not. Based on this theory, a control model was developed and has been successfully used to take into account all six degrees of freedom of vessel motion for the prediction of motion sickness.^{35,63}

It can also be used to interpret the underlying conflict of SMS simulation on Earth. It was thought that the susceptibility to the sickness induced by centrifugation (i.e., after a 1-h centrifuge run from 3 G to 1 G) shares the same underlying conflict with SMS induced from the transition from 1 to 0 G, since they both result from the conflict between a sensed and expected vertical.^{4,45} The supine position is often used to simulate a weightless sensory context^{27,38} because gravity is orientation-irrelevant when the supine subjects are observing the visual scene in parallel with the frontal plane, and therefore SV is determined as in microgravity.

Some findings could be better explained by the SV conflict theory. Bles et al. referred to the findings of visually induced motion sickness by several European research groups, using optokinetic drum stimulation, in which the incidence of motion sickness was estimated to be <1% despite the absence of corresponding vestibular information.²⁵ These findings do not agree with the sensory conflict theory because optokinetic stimuli create clear differences between sensed and expected sensory information; however, the low incidence was in accordance with their SV conflict model because the stimulus was neutral with respect to gravity.

However, this explanation is controversial. Cheung and Vaitkus noted that this European research showed a low motion sickness incidence because the vestibular system responds to acceleration only, and constant vection from optokinetic drum stimulation does not create a visual-vestibular sensory mismatch because this is the natural stimulus to constant velocity

rotation.¹⁶ In contrast, the results obtained by Hu *et al.*³³ showed that optokinetic drum stimulation leads to motion sickness in approximately 60% of individuals. Bles *et al.* ascribed these discrepancies to the use of nonrigid optokinetic drums (in fact Hu's drum is relatively rigid), which result in incorrect alignment of the drum and may introduce a wobble or sway, leading to discrepancies between the sensed and expected SV.⁹ Although no study has directly compared rigid and nonrigid optokinetic drums, the finding that optokinetic drum tilt significantly increases the level of motion sickness suggests that the higher incidence of motion sickness may be caused, at least in part, by misalignment.¹³

There is other evidence about rigid optokinetic drums to refute Bles' claim that the SV conflict is not the sole causal factor responsible for motion sickness. According to SV conflict theory, motion sickness should not occur in response to optokinetic stimuli when: 1) the drum rotates on an Earth-vertical axis; 2) the subject's head is immobilized and centered at the rotation axis; and 3) vertical stripes are used in the drum's interior. However, under these experimental conditions, Bonato and Bubka have confirmed that intermittently changing rotation direction or velocity^{5,14} can hasten motion sickness onset; while the sensed and expected gravitational verticals are in agreement, an increase in visual and vestibular sensory conflict does occur and is more predictive than SV conflict. Bos and Bles responded to these facts and stated that it is possible in Bonato and Bubka's experiments that people perceive the center of rotation erroneously (like the rod and frame effects) or may 'think' they are viewing lateral motion, and both effects may result in tilts of the perceived vertical.¹⁰ Further investigations are needed to clarify whether these variables in Bonato and Bubka's experiments, including their recent result that blurring the stripes with a frosted acetate filter can also hasten motion sickness onset,⁶ possibly affect the perceived vertical. The rationale of SMS proposed by Thornton^{59,60} stated that the absence of gravity is a singularity in the range of gravitational environments and produces a singular conflict in the otolith sensors, and the etiologies of SMS and motion sickness are different in this way. However, the SV conflict theory explains it in another way: SMS can be attributed to a single cause as all other motion sicknesses, the discrepancy between the altered otolith signals and the expected signals by the brain, which change the prior model of constructing SV and produce conflicts.

Explanation and Prediction for SMS Based on the SV Conflict Theory

According to the SV conflict model illustrated in Fig. 2, there exist two unique forms of conflicts when entering space. One is the magnitude conflict due to the unloading of the otoliths. Because gravity is absent, the estimated magnitude of the SV is basically lost and then the conflicts of magnitude between sensed SV and expected SV from experiences on Earth appear. Another is the orientation conflict. Otolith sensors indicate change in orientation of the SV everywhere on Earth, which is detected by means of weight-loaded hair cells in the otolith organ.⁵⁹ Its contribution is represented as K_g in Fig. 2B. When

weight is removed, orientation signals from the otoliths are absent, since all the cells stay in their neutral positions. Thus, in weightlessness there are only visual and idiotropic cues left (K_V and K_M) to determine orientation. The two forms of conflicts can be attributed to a single cause: the discrepancy between the altered SV and the expected SV by the brain. On the other hand, the effects of these conflicts are principally expressed in two typical phenomena: spatial disorientation and orientation preference. The first describes how SMS occurs and the second explains why SMS occurs variously between individuals.

Spatial disorientation in microgravity can be described using two illusions: visual reorientation illusions (VRIs) and inversion illusions (IIs). Since the SV is not anchored by gravity, its direction is unstable in microgravity. This instability of the SV can trigger disorientation.²⁸ Spatial disorientation usually occurs first after SV conflicts and it is the main provoker of SMS.^{37,58} The typical situation that elicits SMS is when crewmembers are moving around in a spacecraft quickly. A reasonable explanation is that the direction of the SV is labile during transition from one spacecraft module to another, since these modules (especially in the ISS) usually do not have a continuous floor to ceiling relationship and are connected by a tunnel with no well-defined floor, walls, or ceiling. Thus, crewmembers' SV may frequently shift when they move around in modules (VRIs), and SV conflicts occur because of the subconscious assumption carried from life on the Earth that people are normally upright and the SV remains unchanged. Another example is that many astronauts in spaceflight have experienced the sudden feeling of being upside-down after the onset of microgravity (IIs). These changes in perceived orientation are provocative, but without any concomitant vestibular cue.⁵⁰

Orientation preference consists of rest frame preference and bias preference. In order to compensate for the absence of orientation signals from gravity, astronauts increase reliance on visual or idiotropic cues when sensing SV during microgravity. Harm and colleagues analyzed several Shuttle astronauts' in-flight verbal reports and postflight debriefing to determine microgravity orientation types based on the selection of rest frames.³¹ Preference appears because astronauts use alternative rest frames with respect to the VS cues and the body's internal z-axis (IZ), which correlates with susceptibility to SMS. Russian researchers also investigated cosmonauts' orientation illusions and observed similar orientation preferences.³⁶ Another preference that was first proved by Mittelstaedt and Glasauer⁴³ is that an individual's gravireceptor bias has an alternative selection: the headward bias or the footward bias. This bias preference correlates with susceptibility to inversion illusions. The explanation for orientation preference is given in the following section. To clarify these theories, the above phenomena have been disentangled and reconstructed with regard to specific illusions and characteristics, which are discussed and explained using the SV conflict theory.

The expected SV: cognitive map. The brain's mechanism for the maintenance of expected SV can be thought of as a cognitive map, which originates from an internal model, including

mental organization of spatial knowledge or awareness of a familiar environment.⁶² The CNS spontaneously compares the sensed SV and the cognitive map of the corresponding environment, and the map is continuously updated through visual cue experiences or representations (e.g., written descriptions) of them.² Thus, a cognitive map is a manifestation of a human adapting and learning in an unusual environment. Its neural mechanism may be explained by the place cells in the hippocampus that create an internal neural map representing a particular environment and provide the brain with a spatial reference map system.⁴⁷

A cognitive map is updated and maintained on the basis of the allocentric coordinates of our environment.^{2,19} An allocentric reference frame is defined by gravity and visual scene polarity, whereas the egocentric reference frame is defined by the eye, head, or internal z-axis. A recognition task is performed in an allocentric reference frame and perception is performed in an egocentric reference frame, so a reference shift is usually needed to build SV, which is called mental rotation.² Mental rotation is the capacity to mentally rotate objects and visual scenes (as opposed to oneself) and to make judgments or recognize them as they are reoriented. The egocentric reference frame under terrestrial conditions maintains the body's vertical axis aligned with the allocentric vertical axis.⁶⁶ Therefore, shifting from an egocentric to an allocentric frame of reference, on the basis of yaw rotation along the vertical axis, would be advantageous.¹⁵ In contrast, the variability of body orientation and the inconsistency of the modules' visual verticals during spaceflight in the absence of gravity may involve more rotations, including pitch and roll rotations that conflict with the SV experienced on land. It may be assumed that a persisting conflict triggers our CNS to reorganize its cognitive map (or recalculate its parameters) in order to reduce this conflict before the symptoms of motion sickness appear. Difficulties in acquiring and maintaining an integrated cognitive map of the entire spacecraft are thought to be a major disadvantage in orientation and navigation and may induce SMS.^{17,52} Mental rotation ability may thus be important for mitigating SMS and for effective performance in microgravity, particularly for visually dependent subjects.¹⁹

Spatial disorientation: inversion illusions and visual reorientation illusions. II was first reported by Cosmonaut Titov in 1961. It has been described as the sensation of "hanging upside down," which usually occurs immediately after the onset of microgravity and persists for minutes to hours.⁵⁴ The affected individual feels continuously inverted with respect to an external gravitational reference frame, the orientation of which is then determined by body orientation (aligning with the idiotropic vector).⁵² The majority of crewmembers do not experience inversion illusion; however, those who do describe it as very provocative and would experience SMS and even vomiting.⁵⁴ Mittelstaedt and Glasauer⁴³ proved that this illusion is related to gravireceptor bias, which was tested by comparing joint bias measurements of six astronauts in normal gravity with those in spaceflight. The results showed that subjects who suffered the longest from emesis also had the most headward

bias and the longest lasting IIs, whereas subjects with the most footward bias had strong illusions of uprightness, except for an initially reduced appetite, which was free from space malaise. Based on the SV conflict theory, this is easy to understand, because the footward bias of gravireceptors aligns the direction of SV with the idiotropic vector, while the headward bias would weaken the idiotropic vector, which may make the judgment of SV less convincing. It can be concluded that the body's gravireceptors are unweighted during microgravity, while an individual's headward or footward bias presumably remains. Moreover, the fluid shift may increase the bias toward the headward direction; therefore, astronauts with a headward bias on the Earth should experience persistent IIs and be more susceptible to SMS,^{17,43,50} although the effect may only last a few days. This relationship suggests that gravireceptor bias is a predictor of SMS susceptibility.

Another phenomenon that often occurs is VRI. VRI was first described by Skylab and Spacelab crews and was named by Oman.⁵⁴ It describes an astronauts' illusion that the surface nearest the feet seems like the "floor" and that the surface parallel to the body seems like the "wall." Susceptibility to VRI can persist for months, or even throughout the entire flight. Oman⁵¹ concluded that VRIs are caused by a sudden change or uncertainty in perceived allocentric orientation and that this occurs without concurrent movement commands or vestibular and proprioceptive cues. Inconsistency in the visual verticals of those intersecting modules is thought to be one of the major causes.^{19,51} Unlike the inversion illusion, a VRI is a visual attention dependent change, resulting from an angular reorientation of the mental allocentric reference frame used for perception of orientation and place.⁵² A more complete explanation is that VRI contributes to the mismatch between the judgment of present self-orientation and previous visual orientation experiences or how various objects and surfaces are arranged with respect to each other; therefore, it can be concluded that VRI occurs with the updating of cognitive maps or a shift in SV.

VRIs are expected to be provocative, but only during their onset.^{19,51} Early Shuttle crews made an important observation that VRI onset could trigger an immediate increase in nausea and occasionally cause vomiting during the first several days of weightlessness. VRIs are a more significant SMS stimulus than IIs because they occur often, e.g., when the crewmembers leave their seats and move about in all degrees of freedom, or some EVA astronauts have experienced height vertigo, apparently triggered by a VRI.¹⁹ However, the illusion episodes continue to occur on long-duration flights after SMS symptoms eventually subside, and crewmembers appear to be immune to the development of further symptoms.¹⁷ This may be an adaptation mechanism as the brain rebuilds a new cognitive map and can sustain SV conflicts after being exposed to an unfamiliar environment for a particular amount of time.

VRIs usually occur spontaneously. However, many crewmembers report that they can initiate VRI during microgravity by cognitively altering the SV without any physical movement or change in the visual scene content.⁵² It is assumed that the

brain increases the weight of the visual polarity vector and automatically manipulates the direction of the SV.

Orientation preference: visual scene or internal Z-axis vectors.

The rest frame is defined as a particular reference frame that the observer considers to be stationary and it was suggested that people select an internal “rest frame” to create the subjective sense of spatial orientation.^{31,56} The selection of a rest frame can be attributed to individual preference when people build SV determined by the interaction among gravireceptor, visual, and idiotropic cues. Gravity is dominant in most situations on the Earth; therefore, preference for the other two cues may be inconspicuous. However, tilting the head away from a gravitationally erect position may enhance the effect of visual cues.³⁴ Depending on relative weighting, SV points in an intermediate direction when there are minor directional differences between these cues, as illustrated in Fig. 1. However, one sensory modality or the other typically captures the SV if there are large differences.⁵¹ The body’s gravireceptors are unweighted in microgravity and the SV is captured by the VS cues or the body’s IZ (the idiotropic cue). In this case, preference would appear to be due to variable weightings of the two cues between individuals. Harm suggested that one astronaut’s rest frame can always be located on a continuum determined by VS and IZ,^{30,31} and this may be because the CNS wants to minimize the calculations for spatial orientation.

Usually rest frame preference remains stable when entering an unfamiliar environment. Oman *et al.* developed an experiment to quantify how frame and visual polarity cues affect spatial orientation during the STS-90 Neurolab mission.⁵¹ They measured the SVs of four astronauts to test their orientation preferences. The results showed that one astronaut, who was strongly visually dependent prior to the flight, remained so in orbit and two of the three who were idiotropic dependent preflight also remained idiotropic dependent. The other became more visually dependent during flight, but then returned to his preflight characteristics after coming back to Earth. Although the test population was small, the results indicate the apparently consistent differences between individuals in relative weighting assigned to visual and body cues regardless of gravitational conditions. De Winkel’s experiment, which was conducted under simulated lunar and Martian gravity conditions using partial gravity parabolic flight, indicated that subjects determine their orientation only by their body longitudinal axis when gravity is below a certain threshold.²³ However, this result did not agree with observations made in orbit.

Rest frame preference was confirmed to be related to an astronaut’s susceptibility to SMS and could be a potential predictive factor. Harm and colleagues compared several astronauts’ questionnaires regarding SMS symptoms during and postflight, and found that VS astronauts had greater symptoms than IZ astronauts. Similar findings were reported by Clément and Reschke¹⁹ that astronauts who are more “body oriented” exhibit fewer visual reorientation illusions and spatial disorientation than those depending predominantly on visual cues, even in the absence of visual cues for vertical orientation. This

can be explained using the SV conflict theory. IZ astronauts in orbit construct their SV in alignment with the body axis and VS astronauts align their SV with one of the principal environmental axes of symmetry, depending on the orientation of polarized objects in the visual scene. Hence, SMS does not occur if everyone remains upright with respect to the module. However, if a VS astronaut floats through modules with inconsistent visual verticals or finds another astronaut upside down, he will experience a sudden change in the SV direction and these unanticipated perception changes may contribute to VRIs and consequently SMS. However, it can be speculated that the IZ astronauts should be less prone to SMS because they always “take the world around with them” and develop a sense of well-being in any orientation, and they even tend to attribute actual self-motion to their surroundings or the spacecraft.^{19,53}

Conclusion

SV represents a self-judgment indicating the direction of our estimate of spatial orientation, which is not determined by any single receptor or body location but is the sum of three vectors: gravity, visual vertical, and idiotropic. Instability in the SV direction can trigger spatial disorientation and then SMS. SV direction is labile in the absence of gravity, and it may change either with body rotation or simply by cognitively initiating VRIs. Individual bias preference (headward or footward) can result in different susceptibilities to inversion illusions. Furthermore, this instability varies with an individual’s alternative selection of orientation rest frame (idiotropic cues or visual vertical) and this preference is relative to SMS susceptibility and could be a potential predictive factor. However, why orientation preference differs between individuals remains an open question.

Development of SMS relates to numerous factors and the SV conflict theory is still incomplete. More experiments are required to determine the parameters before the model is used to predict SMS. Some mechanisms remain unclear, e.g., how the idiotropic cue and gravireceptor bias interact when they both act on the direction of the body’s longitudinal axis.

ACKNOWLEDGMENTS

This study was sponsored by the Independent Research Fund of the National Key Laboratory of Human Factors Engineering (HF2013-Z-B-03).

The authors declare that they have no conflicts of interest.

Authors and affiliations: Wei Chen, M.D., B.S., Jian-Gang Chao, Ph.D., M.D., Jin-Kun Wang, M.D., B.S., and Xue-Wen Chen, M.D., B.S., National Key Laboratory of Human Factors Engineering, and Cheng Tan, M.D., B.S., State Key Laboratory of Space Medicine Fundamentals and Application, China Astronaut Research and Training Center, Beijing, China.

REFERENCES

1. Barnett-Cowan M, Harris LR. Perceived self-orientation in allocentric and egocentric space: effects of visual and physical tilt on saccadic and tactile measures. *Brain Res.* 2008; 1242:231–243.

2. Benveniste D. Cognitive conflict in learning three-dimensional space station structures. [M.A. thesis.] Cambridge (MA): Massachusetts Institute of Technology; 2004.
3. Bles W, Bos JE, de Graaf B, Groen E, Wertheim AH. Motion sickness: only one provocative conflict? *Brain Res Bull.* 1998; 47(5):481–487.
4. Bles W, de Graaf B, Bos JE, Groen E, Krol JR. A sustained hyper-g load as a tool to simulate space sickness. *J Gravit Physiol.* 1997; 4(2):P1–P4.
5. Bonato F, Bubka A, Story M. Rotation direction change hastens motion sickness onset in an optokinetic drum. *Aviat Space Environ Med.* 2005; 76(9):823–827.
6. Bonato F, Bubka A, Thornton W. Visual blur and motion sickness in an optokinetic drum. *Aerosp Med Hum Perform.* 2015; 86(5):440–444.
7. Bos JE, Bles W. Modeling motion sickness and subjective vertical mismatch detailed for vertical motions. *Brain Res Bull.* 1998; 47(5): 537–542.
8. Bos JE, Bles W. Theoretical considerations on canal–otolith interaction and an observer model. *Biol Cybern.* 2002; 86(3):191–207.
9. Bos JE, Bles W. Motion sickness induced by optokinetic drums. *Aviat Space Environ Med.* 2004; 75(2):172–174.
10. Bos JE, Bles W, Groen EL. A theory on visually induced motion sickness. *Displays.* 2008; 29(2):47–57.
11. Bos JE, Bles W, Hosman R. Modeling human spatial orientation and motion perception. AIAA Modeling and Simulation Technologies Conference; 6–9 August 2001; Montreal, Canada. Reston (VA): AIAA; 2001.
12. Brooks JX, Cullen KE. Early vestibular processing does not discriminate active from passive self-motion if there is a discrepancy between predicted and actual proprioceptive feedback. *J Neurophysiol.* 2014; 111(12):2465–2478.
13. Bubka A, Bonato F. Optokinetic drum tilt hastens the onset of vection-induced motion sickness. *Aviat Space Environ Med.* 2003; 74(4):315–319.
14. Bubka A, Bonato F, Urmey S, Mycewicz D. Rotation velocity change hastens motion sickness onset in an optokinetic drum. *Aviat Space Environ Med.* 2006; 77(8):811–815.
15. Carrier J, DiZio P, Nougier V. Vertical frames of reference and control of body orientation. *Neurophysiol Clin.* 2008; 38(6):423–437.
16. Cheung B, Vaitkus P. Perspectives of electrogastrography and motion sickness. *Brain Res Bull.* 1998; 47(5):421–431.
17. Clément G. The neuro-sensory system in space. In: *Fundamentals of Space Medicine.* New York: Springer; 2011:95–142.
18. Clément G, Ngo-Anh JT. Space physiology II: adaptation of the central nervous system to space flight—past, current, and future studies. *Eur J Appl Physiol.* 2013; 113(7):1655–1672.
19. Clément G, Reschke MF. Spatial orientation. In: *Neuroscience in space.* New York: Springer; 2008:189–232.
20. Cullen KE. The neural encoding of self-generated and externally applied movement implications for the perception of self-motion and spatial memory. *Front Integr Neurosci.* 2014; 7:108.
21. Cullen KE, Brooks JX, Jamali M, Carrier J, Massot C. Internal models of self-motion: computations that suppress vestibular reafference in early vestibular processing. *Exp Brain Res.* 2011; 210(3–4):377–388.
22. Davis JR, Vanderploeg JM, Santy PA, Jennings RT, Stewart DF. Space motion sickness during 24 flights of the Space Shuttle. *Aviat Space Environ Med.* 1988; 59(12):1185–1189.
23. de Winkel KN, Clément G, Groen EL, Werkhoven PJ. The perception of verticality in lunar and Martian gravity conditions. *Neurosci Lett.* 2012; 529(1):7–11.
24. Diamond SG, Markham CH. Validating the hypothesis of otolith asymmetry as a cause of space motion sickness. *Ann N Y Acad Sci.* 1992; 656:725–731.
25. Diels C. Visually induced motion sickness. [Ph.D. thesis.] Loughborough, Leicestershire (UK): Loughborough University; 2008.
26. Eggert T. Der Einfluss orientierter Texturen auf die subjektive vertikale und seine systemtheoretische Analyse. Munich (Germany): Technical University of Munich; 1998.
27. Friederici AD, Levelt WJ. Spatial reference in weightlessness: perceptual factors and mental representations. *Percept Psychophys.* 1990; 47(3): 253–266.
28. Glasauer S, Mittelstaedt H. Perception of spatial orientation in microgravity. *Brain Res Brain Res Rev.* 1998; 28(1–2):185–193.
29. Green AM, Angelaki DE. Internal models and neural computation in the vestibular system. *Exp Brain Res.* 2010; 200(3–4):197–222.
30. Harm DL, Parker DE. Perceived self-orientation and self-motion in microgravity, after landing and during preflight adaptation training. *J Vestib Res.* 1993; 3(3):297–305.
31. Harm DL, Parker DE, Reschke MF. Relationship between selected orientation rest frame, circular vection and space motion sickness. *Brain Res Bull.* 1998; 47(5):497–501.
32. Howard IP, Hu G. Visually induced reorientation illusions. *Perception.* 2001; 30(5):583–600.
33. Hu S, Stern RM, Vasey MW, Koch KL. Motion sickness and gastric myoelectric activity as a function of speed of rotation of a circular vection drum. *Aviat Space Environ Med.* 1989; 60(5):411–414.
34. Jenkin HL, Dyde RT, Zacher JE, Zikovitz DC, Jenkin MR, et al. The relative role of visual and non-visual cues in determining the direction of “up”: Experiments in the parabolic flight. *Acta Astronaut.* 2005; 56(9–12):1025–1032.
35. Khalid H, Turan O, Bos JE, Incecik A. Application of the subjective vertical–horizontal–conflict physiological motion sickness model to the field trials of contemporary vessels. *Ocean Eng.* 2011; 38(1):22–33.
36. Kornilova LN, Grigorova V, Bodo F, Chernobyl'skiĭ LM. [Neurophysiological patterns of vestibular adaptation to microgravity.] *Aviakosm Ekolog Med.* 1995; 29(5):23–30 [in Russian].
37. Lackner JR, DiZio P. Space motion sickness. *Exp Brain Res.* 2006; 175(3):377–399.
38. Lucertini M, De Angelis C, Martelli M, Zolesi V, Tomao E. Subjective visual vertical in erect/supine subjects and under microgravity: effects of lower body negative pressure. *Eur. Arch. Eur Arch Otorhinolaryngol.* 2011; 268(7):1067–1075.
39. Mittelstaedt H. A new solution to the problem of the subjective vertical. *Naturwissenschaften.* 1983; 70(6):272–281.
40. Mittelstaedt H. Towards understanding the flow of information between objective and subjective space. *Neuroethology and Behavioral Physiology.* Berlin (Germany): Springer Heidelberg; 1983:382–402.
41. Mittelstaedt H. Somatic graviception. *Biol Psychol.* 1996; 42(1–2):53–74.
42. Mittelstaedt H. Origin and processing of postural information. *Neurosci Biobehav Rev.* 1998; 22(4):473–478.
43. Mittelstaedt H, Glasauer S. Illusions of verticality in weightlessness. *Clin Investig.* 1993; 71(9):732–739.
44. Muth ER. Motion and space sickness: intestinal and autonomic correlates. *Auton Neurosci.* 2006; 129(1–2):58–66.
45. Nooij SAE, Bos JE, Groen EL, Bles W, Ockels WJ. Space sickness on earth. *Microgravity Sci Technol.* 2007; 19(5):113–117.
46. Nooij SA, Vanspauwen R, Bos JE, Wuyts FL. A re-investigation of the role of utricular asymmetries in space motion sickness. *J Vestib Res.* 2011; 21(3):141–151.
47. O'Keefe J, Nadel L. The hippocampus as a cognitive map. Oxford (UK): Oxford University Press; 1978.
48. Oman CM. A heuristic mathematical model for the dynamics of sensory conflict and motion sickness hearing in classical musicians. *Acta Otolaryngol.* 1982; 94(Suppl. 392):4–44.
49. Oman CM. Motion sickness: a synthesis and evaluation of the sensory conflict theory. *Can J Physiol Pharmacol.* 1990; 68(2):294–303.
50. Oman CM. Sensory conflict theory and space sickness: our changing perspective. *J Vestib Res.* 1998; 8(1):51–56.
51. Oman CM. Human visual orientation in weightlessness. In: *Levels of perception.* New York: Springer; 2003:375–398.
52. Oman CM. Spatial processing in navigation, imagery and perception, Spatial orientation and navigation in microgravity. New York: Springer; 2007:209–247.
53. Oman CM, Cullen KE. Brainstem processing of vestibular sensory exafference: implications for motion sickness etiology. *Exp Brain Res.* 2014; 232(8):2483–2492.
54. Oman CM, Lichtenberg BK, Money KE, McCoy RK. M.I.T./Canadian vestibular experiments on the Spacelab-1 mission: 4. Space motion

- sickness: symptoms, stimuli, and predictability. *Exp Brain Res.* 1986; 64(2):316–334.
55. Ortega HJ, Harm DL. Space and entry motion sickness. In: *Principles of Clinical Medicine for Space Flight*. New York: Springer; 2008: 211–222.
 56. Prothero JD. The role of rest frames in vection, presence and motion sickness. [Ph.D. thesis]. Seattle (WA): University of Washington; 1998.
 57. Reason JT. Motion sickness adaptation: a neural mismatch model. *J R Soc Med.* 1978; 71(11):819–829.
 58. Stroud KJ. Mitigating vestibular disturbances during space flight using virtual reality training and reentry vehicle design guidelines. [Ph.D. thesis]. Boulder (CO): University of Colorado at Boulder; 2004.
 59. Thornton WE. A rationale for space motion sickness. *Aviat Space Environ Med.* 2011; 82(4):467–468.
 60. Thornton WE, Bonato F. Space motion sickness and motion sickness: symptoms and etiology. *Aviat Space Environ Med.* 2013; 84(7):716–721.
 61. Thornton WE, Moore TP, Pool SL. Fluid shifts in weightlessness. *Aviat Space Environ Med.* 1987; 58(9, Pt. 2):A86–A90.
 62. Tommasi L, Laeng B. Psychology of spatial cognition. *Wiley Interdiscip Rev Cogn Sci.* 2012; 3(6):565–580.
 63. Turan O, Verveniots C, Khalid H. Motion sickness onboard ships: subjective vertical theory and its application to full-scale trials. *J Mar Sci Technol.* 2009; 14(4):409–416.
 64. Vaitl D, Mittelstaedt H, Baisch F. Shifts in blood volume alter the perception of posture. *Int J Psychophysiol.* 1997; 27(2):99–105.
 65. Vaitl D, Mittelstaedt H, Saborowski R, Stark R, Baisch F. Shifts in blood volume alter the perception of posture: further evidence for somatic graviception. *Int J Psychophysiol.* 2002; 44(1):1–11.
 66. Vidal M, Amorim MA, Berthoz A. Navigating in a virtual three-dimensional maze: how do egocentric and allocentric reference frames interact? *Brain Res Cogn Brain Res.* 2004; 19(3):244–258.
 67. Vingerhoets RA, De Vrijer M, Van Gisbergen JA, Medendorp WP. Fusion of visual and vestibular tilt cues in the perception of visual vertical. *J Neurophysiol.* 2009; 101(3):1321–1333.
 68. Young LR. Vestibular reactions to spaceflight: human factors issues. *Aviat Space Environ Med.* 2000; 71(9, Suppl.):A100–A104.