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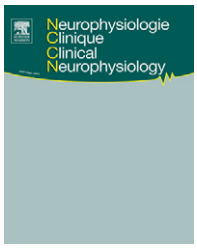

REVIEW/MISE AU POINT

Vestibular syndrome: A change in internal spatial representation

Le syndrome vestibulaire : un changement de représentation interne de l'espace

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Summary The vestibular system contributes to a wide range of functions from reflexes to spatial representation. This paper reviews behavioral, perceptive, and cognitive data that highlight the role of changes in internal spatial representation on the vestibular syndrome. Firstly, we review how visual vertical perception and postural orientation depend on multiple reference frames and multisensory integration and how reference frames are selected according to the status of the peripheral vestibular system (i.e., unilateral or bilateral hyporeflexia), the environmental constraints (i.e., sensory cues), and the postural constraints (i.e., balance control). We show how changes in reference frames are able to modify vestibular lesion-induced postural and locomotor deficits and propose that fast changes in reference frame may be considered as fast-adaptive processes after vestibular loss. Secondly, we review data dealing with the influence of vestibular loss on higher levels of internal representation sustaining spatial orientation and navigation. Particular emphasis is placed on spatial performance according to task complexity (i.e., the required level of spatial knowledge) and to the sensory cues available to define the position and orientation within the environment (i.e., real navigation in darkness or visual virtual navigation without any actual self-motion). We suggest that vestibular signals are necessary for other sensory cues to be properly integrated and that vestibular cues are involved in extrapersonal space representation. In this respect, vestibular-induced changes would be based on a dynamic mental representation of space that is continuously updated and that supports fast-adaptive processes.

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Résumé Le système vestibulaire participe à un grand nombre de fonctions allant des réflexes à la représentation spatiale. Dans cet article, nous passons en revue les données comportementales, perceptives et cognitives qui soulignent le rôle des changements de la représentation interne de l'espace sur le syndrome vestibulaire. Nous décrivons, en premier lieu, comment la perception visuelle de la verticale et l'orientation posturale dépendent de multiples cadres de référence et de l'intégration multisensorielle et comment les cadres de référence sont sélectionnés en fonction du statut du système vestibulaire périphérique (hyporéflexie unilatérale ou bilatérale), des contraintes environnementales (informations sensorielles) et posturales (contrôle de l'équilibre). Nous montrons comment les changements de cadres de référence sont en mesure de modifier les déficits posturaux et locomoteurs induits par la perte vestibulaire, et nous proposons que des changements rapides de cadres de référence peuvent être considérés comme des processus adaptatifs rapides consécutifs à la perte vestibulaire. Nous rapportons ensuite des données sur l'influence de la perte vestibulaire selon les niveaux de représentation interne qui sous-tendent l'orientation et la navigation spatiales. La performance spatiale est abordée en fonction de la complexité de la tâche (degré de connaissance spatiale) et des informations sensorielles disponibles permettant de définir la position et l'orientation dans l'environnement (navigation réelle à l'obscurité versus navigation visuelle virtuelle en l'absence de mouvement réel). Nous suggérons que les signaux vestibulaires sont nécessaires à l'intégration correcte des informations sensorielles et qu'ils participent à la représentation de l'espace extrapersonnel. Dans ce contexte, les changements consécutifs à la perte vestibulaire seraient basés sur une représentation dynamique de l'espace, continuellement mise à jour et qui soutiendrait des processus adaptatifs rapides.

Introduction

The vestibular system contributes to a wide range of functions, from postural and oculomotor reflexes to spatial representation and cognition. Vestibular organs, semicircular canals and otoliths, respectively measure head angular and linear accelerations, allowing the coding and the representation of head movements in space. Projections to ocular and spinal motoneurons enable the vestibular system to stabilize and orient gaze, head, and body in space. One of the specificities of the vestibular system is multimodal convergence of sensory cues, as soon as the first synapse in the brainstem and throughout the central vestibular pathways [4,101,174]. In addition, vestibular signals project to various cortical areas [10,23,53,106]. As a result, vestibular signals do not cause isolated conscious sensations as the other sensory systems do, but they take part in various high-level functions, among which internal spatial representation. Indeed, vestibular signals are involved in self- as well as extrapersonal perception, with sensations related to the whole-body position and motion in space and to the displacements of the environment relative to the individual. These features provide the basis for high-order adaptive changes after vestibular loss. In this review, we highlight the role of internal spatial representation changes in vestibular syndrome and in the subsequent vestibular compensation.

The peripheral vestibular syndrome involves different levels of damage, possibly additive from basic reflex to higher order deficits [37,39,50,54,93,98,124,149]. Patients with vestibular loss are primarily concerned with balance and gait problems [79]. Unilateral loss results in head [78] and trunk tilt towards the lesioned side [18], leg muscle tone asymmetry [2], weight shift to the side of the lesion [156], and impaired head stabilisation. Walking trajectory is deviated to the lesioned side, and locomotor pattern shows decreased step frequency and length [17,35,22,98]. After bilateral vestibular loss, patients often complain of balance disorders when standing or walking, but they may feel off-balance even when lying down or sitting. Oscillations of the head are increased during body rotations [72,65], walking, running, and hopping [66,136]. Increased instability has been reported when balance is compromised [8,124]. Unilateral ataxia is associated with oculomotor symptoms, including spontaneous nystagmus, ocular cyclotorsion, and oscillopsia related to impaired vestibulo-ocular reflex [76,105]. In addition, unilateral vestibular loss impairs gaze stabilisation via the dynamic properties of the optokinetic nystagmus, with asymmetry of the horizontal [34,133,170] and torsional [105] optokinetic responses. Bilateral vestibular-defective patients also show increased vestibular and visual oculomotor deficits [179]. Finally, patients with unilateral loss perceive the visual vertical as deviated towards the lesioned side [52,167]. Moreover, they often complain about spatial disorientation, which might be related to deficits in path integration and suggests changes at a high level of information processing [130,131]. These spectacular symptoms decrease with time in a process known as vestibular compensation [37,39,98,168]. However, some functions remain asymmetrical after a unilateral vestibular loss, especially during high frequency movements. Poor compensation has been mentioned for vestibulo-spinal reflex [1], posturo-locomotor function [17,18], horizontal vestibulo-ocular reflex [76], dynamic ocular counterrolling [41], and torsional optokinetic nystagmus [105]. Similarly, an asymmetrical pattern of vestibular functions lasting several years has been reported for perceptual responses, including:

- subjective postural vertical [5];
- roll tilt perception [77];
- and subjective visual vertical in static and dynamic visual conditions [167,110,107].

The objectives of this review are to assess to what extent the vestibular syndrome and its compensation are rooted in changes in internal spatial representation. The first part describes the basic level of internal spatial representation, namely how visual vertical perception is influenced by the environmental (i.e., sensory cues) and the postural (i.e., balance control) constraints. The second part deals with higher level of internal representation sustaining spatial orientation and navigation. Actually, the question here is to examine whether vestibular loss-induced changes depend on the different levels of spatial knowledge required by the navigational tasks. Finally, in the third part, we attempt to summarize the concepts developed on the basis of the above-mentioned experimental data and to propose our view of the vestibular syndrome, that is, the leading role of changes in internal spatial representation and body-space relationships.

Dynamics of reference frames after vestibular loss: adaptive processes rather than impairment

A basic level of internal spatial representation is the representation of the vertical, a fundamental reference given by the direction of gravity. By representing the vertical, the brain can organize a proper erect posture with respect to the ground. The representation of verticality is intimately linked to the available cues from the personal and extrapersonal spaces. In the following sections, we review how vertical perception and body orientation are related to multiple reference frames and multisensory integration. We highlight how reference frames for spatial orientation are selected and reweighed according to the status of the peripheral vestibular system, the environmental constraints, and the postural constraints.

Multiple reference frames for spatial orientation

Vertical perception and body orientation depend on how spatial information is encoded and how spatial reference frames are selected and weighted. Spatial information might be encoded with respect to external objects (allocentric reference frame), to the body (egocentric reference frame), or to gravity (geocentric reference frame) [3,11,95,128]. For the representation of verticality to be built, a first model puts forward the integration of visual, somatosensory, and vestibular cues [16,28,97,120]. In healthy humans, the respective contribution of the reference frames to the representation of the vertical has been investigated by the manipulation of different sensory cues.

Visual cues provide information about the orientation of objects in space and are the basis of the *allocentric frame of reference*. The role of the allocentric frame of reference in perception is commonly evidenced by manipulating static visual coordinates (i.e., oriented visual environments) and dynamic visual cues (i.e., optokinetic stimulation). In the so-called ''rod and frame test'', the tilt of a visual frame with respect to the true gravitational vertical is responsible for a deviation of the perceived vertical in the direction of the frame tilt [69,70,175]. With rotation of a visual background around the line of sight, the perceived vertical also deviates in the direction of the optokinetic stimulation [42,43,70]. Perceptual effects are concomitant with changes in the whole body posture, which also deviates in the direction of the optokinetic stimulation. The optokinetic-induced body tilt is generally interpreted as a realignment of the body with the subject's representation of the vertical [43].

Somatosensory cues provided by muscular, joint, and cutaneous receptors give kinaesthetic information about relative head, trunk and limb position in space and are the basis of the *egocentric frame of reference*. The role of the egocentric frame of reference has often been investigated by vibratory methods [80,96,146]. Muscle vibration is expected to induce an abnormal spindle afferent discharge. This could be interpreted as lengthening of the vibrated muscle, and it participates in postural orientation and modifies settings of the visual vertical orientation [118]. The existence of a proprioceptive chain from eyes to feet was reported in the organization of the whole-body posture [145]. Cutaneous receptors from the plantar sole also take an important part in sensing one's body orientation [91]. In addition, the abdominal viscera graviceptors contribute to the perception of the gravitational vertical [121,162,163].

Finally, the vestibular system, which detects linear and angular accelerations, provides an invariant frame of reference, given by the direction of gravity, which is the basis of the *geocentric frame of reference*. The predominant role of the static gravitational/otolithic inputs on the perceived verticality has been investigated mainly in roll-tilted subjects. Perceptual direction errors depend on the amount of body tilt [7,88,120,123]. Moreover, it has been shown that rotational and galvanic vestibular stimulations lead to a contralateral tilt of the perceived visual vertical [117,129,180].

Changes in reference frames after vestibular loss

Vestibular loss is a good model for evaluating how reference frames are selected and combined to elaborate an internal representation of the vertical. The influence of vestibular cues on visual vertical perception has been investigated by several studies conducted on patients with peripheral and central vestibular disorders, especially in those with a brainstem lesion involving the vestibular nuclei complex.

The geocentric frame of reference

There is a large body of clinical evidence that vestibular loss impairs spatial coding according to the gravity-based or geocentric reference frame. Indeed, the perceived orientation of the gravitational field is dramatically affected after damage along the graviceptive pathways from the peripheral-end organs to the vestibular nuclei, the thalamus, and the parieto-insular vestibular cortex. In patients with unilateral vestibular loss due to labyrinthectomy or vestibular neurotomy, the perceived visual vertical is typically tilted towards the lesioned side [14,38,52,143]. Perception of the static visual vertical regains the grav-

itational vertical around one year after vestibular loss [107,110,167]. The deviation is assumed to originate mainly from the imbalance in otolithic inputs from the healthy and lesioned vestibular end organs [16,52]. This observation is corroborated by the normal visual vertical perception of bilateral vestibular-defective patients [29,107]. In case of unilateral vestibular loss, the orientation of the whole-body posture fit that of the perceived visual vertical, though both deviations are not proportional.

The allocentric frame of reference

In a series of experiments with Menière's disease patients, we investigated the weight and selection of the allocentric reference frame during visual vertical judgment and posturo-locomotor tasks (Fig. 1). Concerning visual vertical judgment, we showed that, when vertical and horizontal static visual references are available in the surrounding (such as the edge of the walls and doors), tilt of the perceived vertical towards the lesioned side is reduced, even though a significant deviation remains with respect to the gravitational vertical. Simultaneously, when visual coordinates are present, the head and centre of foot pressure are directed towards the opposite (intact) side [19]. We propose that this postural reversal is related to modifications in reference frames patients base themselves on. Since a true vertical visual reference is perceived as tilted towards the intact side, the head tilt in the same direction may result from an alignment of patients' heads with respect to the distorted visual reference frame they perceive. This last assumption is verified by requiring the patients to align themselves with a vertical bar (unpublished data). That visual vertical and horizontal references are responsible for such reversal of posture is evidenced by the opposite deviations, towards the lesioned side, recorded in light without vertical and horizontal coordinates (pseudo-random dot visual pattern) as well as in darkness. Such a complete postural inversion has also been observed for unilateral vestibular-defective patients tested in a dynamic task of knee-bends [18]. Opposite deviations both for head and trunk have been reported in the roll and yaw planes, when vision is available and in darkness. Finally, visual references are also capable of reversing the vestibular lesion-induced deviation of walking trajectory [17] (Fig. 1). These results argue for high-level adaptive mechanisms, which would explain the immediate and labile postural changes. Therefore, maintaining a simple, quiet standing posture requires more than basic reflexes from various sensory systems. These opposite patterns of postural disturbances in the presence of visual references disappear one month after unilateral vestibular loss. To our knowledge, only Marchand et al. [113] have drawn attention to the decreased head tilt in hemilabyrinthectomized kittens, which sometimes even overshoot the vertical when vision is available. Based on distorted vestibular cues, changes in postural pattern deviation may constitute a transitory perceptual-adaptive process allowing the patients to shift from an external (allocentric) to a bodily (egocentric or gravitational) reference frame to orient the body in space.

Considering these data, one can expect great perceptive changes in the presence of tilted static visual references. When tested with the rod and frame test, unilateral vestibular-defective patients exhibited greater visual vertical deviation when the frame was tilted towards the lesioned ear than towards the healthy ear [74,110]. These authors postulated that unilateral vestibular-defective patients process static visual references asymmetrically. In other respects, it is well established that healthy subjects greatly differ according to their frame effect, often referred to as visual field dependence—independence. Some individuals exhibit strong frame effect (visual field dependent subjects), while others report weak frame effect (visual field independent subjects) [69,84,125,175]. These two distinct subpopulations have also been found for patients suffering from Menière's disease [110]. However, the frame effect is strongly increased for visual field dependent patients. Such enhanced visual field dependence may be based on the increased weight of allocentric references and could represent a strategy to compensate for the fluctuating vestibular function owing to Menière's disease. We showed that unilateral vestibular neurotomy does not change the visual field dependence—independence defined preoperatively. Nevertheless, the frame effect becomes asymmetrical for both patients groups, with reduced or even abolished contralesional visual field dependence and unaffected ipsilesional visual field dependence. The asymmetry remains three months post-lesion [110].

Similarly, the effect of dynamic visual cues (rotation of a visual background around the line of sight) induces an asymmetrical perception of the vertical. Such asymmetry has been evidenced for unilateral vestibular-defective patients operated on for vestibular schwannoma [64], Menière's disease [107], and for patients with vestibular brainstem lesions [24]. Again, unusual perceptive responses have been found in the early stage after vestibular loss since rotation of the visual field induces a tilt of the perceived vertical towards the lesioned side, whatever the direction of the optokinetic stimulation [107]. Actually, this striking result is supposed to be the sum of two distinct perceptive phenomena: a static visual vertical tilted to the lesioned side (vertical recorded in a static visual condition) and a dynamic visual vertical (optokinetic-induced tilt of the vertical) asymmetrically organized around the new static visual vertical. The asymmetry comes from a decreased sensitivity to contralesional optokinetic stimulations while the amplitude of the optokinetic-induced tilt remains unchanged for ipsilesional stimulations. Interestingly, the asymmetry reported here is similar to that reported with the rod and frame test and remains one year after neurotomy. The decrease in visual vertical deviation for contralesional stimulations to visual stimuli may correlate with the decreased sensitivity to roll-tilt stimuli directed towards the lesioned side [40]. The way we consider these results leads to another unusual conclusion: the effect of dynamic visual cues on the perception of the vertical reveals no increase in visual field dependence after unilateral vestibular loss. For bilateral vestibular-defective patients, on the contrary, studies performed with rotating backgrounds show a symmetrical increase in visual field dependence evidenced by the increased magnitude of the perceived vertical tilt symmetrically organized around an unmodified static vertical aligned with the gravitational reference [29,70,107]. Taken together, these data suggest that the perceptive effects of bilateral vestibular loss cannot be described as the sum of the effects of two unilateral vestibular losses. The adaptive mechanisms involve an increased

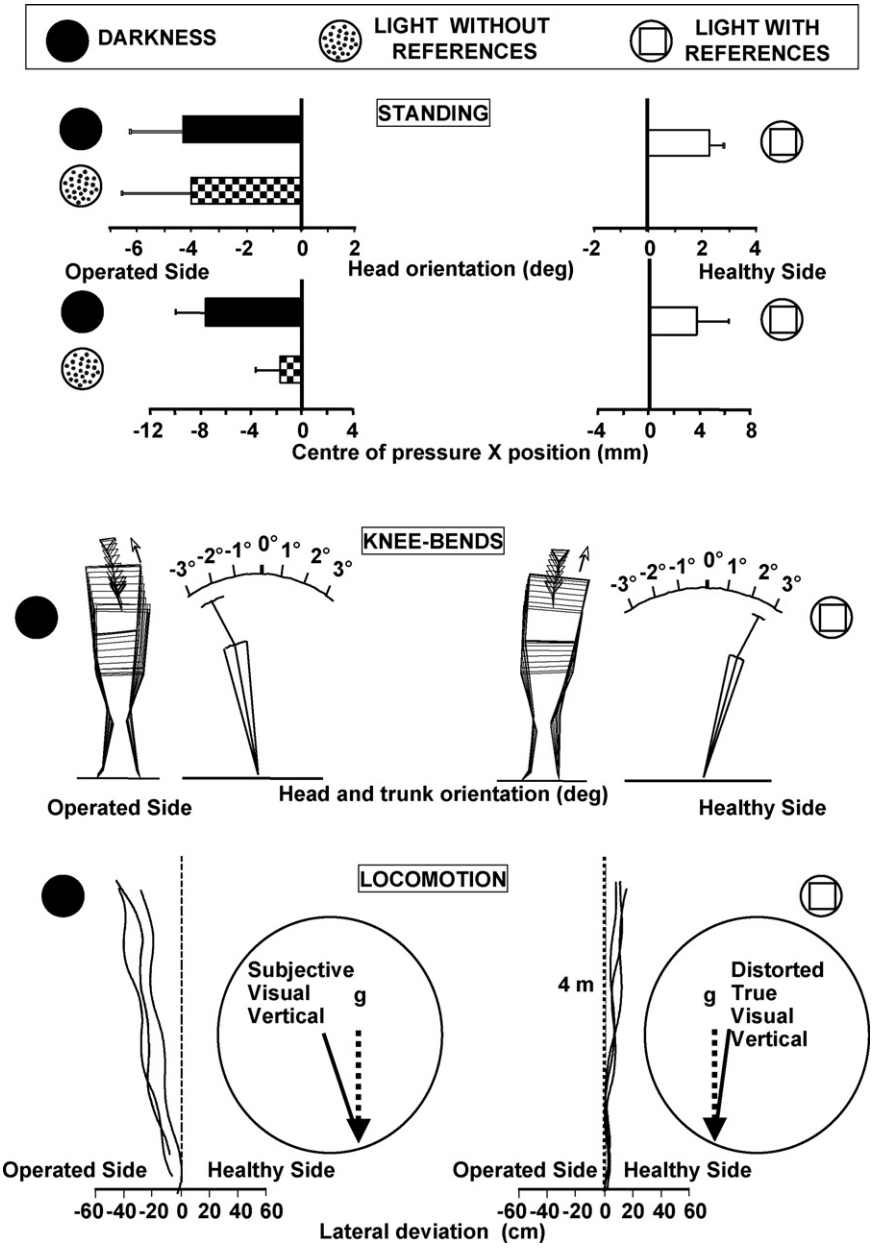

Fig. 1 Changes in reference frames after vestibular loss. Postural orientation and locomotor trajectory for Menière's patients tested one week after unilateral vestibular neurotomy under different visual conditions: darkness, light without vertical and horizontal references, and light with vertical and horizontal references. Top: head orientation in the frontal plane and lateral position of the centre of foot pressure for patients standing on a static force-plate. Middle: example of stick diagram and mean angular head and trunk orientation in the frontal plane during a dynamic task of knee-bends. Bottom: raw walking trajectories during normal speed locomotion. Note that all postural and locomotor parameters are deviated to the lesioned side in darkness and that these vestibular-lesion induced deviations are reversed in visual conditions providing vertical and horizontal coordinates [17,18,19].

weight of the dynamic visual cues to compensate for the lack of vestibular information only when vestibular loss is bilateral.

The egocentric frame of reference

The contribution of somatosensory cues to the representation of the vertical is of particular importance after vestibular loss. In healthy participants, prolonged roll body tilt deviates the subjective visual vertical [7,69,123,165]. Patients without vestibular function show an enhanced deviation of the subjective visual vertical during lateral body tilt. These findings indicate that this perception is likely to be mediated by somatosensory cues [28]. Evidence for the role of somatosensory cues in the egocentric internal representation of orthogonal coordinates also comes from findings in patients with unilateral vestibular deficits, who show an increased tonic shift of the subjective visual horizontal during vibration applied to the mastoid bones [89]. Enhanced contribution of neck muscle proprioception is corroborated by the unilateral increase in somatosensory

weight, restricted to the affected side, while measuring the subjective visual straight ahead [155]. These data indicate a substituting role of proprioceptive cues for missing vestibular inputs. It seems that there is a clear dissociation between the subjective visual vertical and the subjective visual postural. Actually, despite their loss in sensitivity for perception of body verticality, bilateral-defective patients are as accurate as healthy subjects in determining their body position in space (subjective postural vertical) during roll [14] and pitch [27] body tilts. These data suggest that somatosensory cues alone may suffice to reasonably estimate uprightness but that reliable vestibular input increases sensitivity [14].

The ecological approach of orientation

Another model of orientation perception is based on two principles of the ecological approach to perception promulgated by Gibson [58,59]: the mutual link between the organism and its environment and the indivisibility of perception and action. On this basis, Stoffregen and Riccio [153] and Riccio et al. [138] have postulated that vertical perception is determined primarily by balance dynamics generated by balance control. In other words, the major reference for the upright comes from the direction of the unstable equilibrium (the so-called ''direction of balance''). This hypothesis gained further support from recent data in healthy participants. Bray et al. [26] have compared subjects' abilities to set a rod alone or to set a rod within a tilted frame in different postural contexts: sitting, standing, and balancing on a beam. They have shown that the perceived visual vertical is more accurate during unbalanced postures (on the beam) and have concluded that ''we are most aware of our place in the world when about to fall''.

Given the multiple effects of vestibular loss on vertical perception and postural stabilisation, it is of particular interest to analyse the relationship between body balance requirement (postural constraints) and the perceived visual vertical in vestibular-defective patients. The ameliorating effect of balancing has been demonstrated for Menière's patients tested after unilateral vestibular neurotomy while standing, sitting, and lying supine [109]. Indeed, the ipsilesional bias in visual vertical judgment in darkness increases when changing from an unbalanced upright posture to a fully stable lying supine position. This suggests that postural balance control makes a key contribution to the perception of the vertical. However, the beneficial effect of standing upright on perceiving the vertical disappears from the second postoperative month onwards. This may be due to the more precarious balance control in the early postoperative stage [100]. However, one cannot exclude the role of an increased weighting of the somatosensory cues allowing the patients to align the perceived visual vertical with their body axis while standing.

Conclusion

To conclude, we suggest that perceptive changes reported after vestibular loss should not be considered only as an impairment — with perceptive values expected to regain preoperative ones as a sign of good compensation — but rather as a variety of adaptive processes. This hypothesis is supported by two sets of experimental data:

- postural reversal resulting from changes in reference frames;
- and the ameliorating effect of higher postural constraints on vertical perception.

Some of the perceptive changes last only a few weeks, in the very first postlesion period, and others seem to constitute permanent changes. Concerning the neural mechanisms behind these perceptive changes, we propose that on-line and fast selection and reweighing of reference frames are possible due to overlapping neural substrates for egocentric, allocentric, and geocentric reference frames. Neuroimaging studies in healthy humans indicate that egocentric and allocentric reference frames may rely on neural activity in a large fronto-parietal network including the premotor cortex, inferior parietal lobule, posterior parietal cortex, insula, and the temporo-parietal junction [21,36,51,55,164,178]. Interestingly, this network overlaps with regions that code for the geocentric reference frame and that receive gravitational vestibular inputs, such as the temporo-parietal junction, insula, inferior parietal lobule, and posterior parietal cortex [23,45,83,106,108]. The adaptive mechanisms described above could also rely on reciprocal inhibitory interactions between cortical regions coding one's body motion on the basis of egocentric/geocentric (vestibular) and allocentric (visual) information. In addition, it is known from electrophysiological and computational studies that, to occur, integration does not need sensory signals to be expressed in a common reference frame (head centered or eye centered); rather it involves a mixture or a continuum of reference frames [4,135].

Changes in spatial representation (spatial orientation and navigation) after vestibular loss

Varieties of spatial navigation

Due to its properties of early multisensory integration, the vestibular system contributes critically to spatial navigation taken in its broad sense, that is, including spatial orientation (or wayfinding) and displacement. Navigation involves different processes, such as sensing the environment, building up an internal spatial representation, and using it [103]. During navigation, the position and orientation of the individual within the environment is provided and updated on the basis of information stemming from the external world (mainly visual cues, in humans) and/or on the basis of information generated by self-movements through the environment (somatosensory and vestibular cues) [56,140]. The respective roles of information from extrapersonal versus personal space have been documented by a large body of empirical data and theoretical developments [128,142]. Mutually consistent sensory and movement information informs individuals that they are moving within a stable environment; that is, the visually changing appearance results from the displacement (locomotor activity) and not from a modification of the environment itself. Visual cues are reported to play a predominant role [172]; the optic flow provides direction and distance components of the pattern of trajec-

tories [92]. However, movement-related information alone can lead to spatial knowledge in the absence of vision, even if this information seems better suited for rotations than for translations [12,33,131,139]. Since vision ordinarily provides information about both the navigator's motion and the layout of near and far space [154], blind people should be disadvantaged in the development of normal spatial ability. Studies conducted to assess the calibrating role of vision for the integration of sensory information compared the performances of congenitally blind, adventitiously blind, and blindfolded sighted participants in various navigation tasks [57,103,141,159]. Spatial performance is generally impaired in congenitally blind people, especially on tasks requiring a high level of spatial knowledge, which reveals the fundamental importance of visual experience. In addition, group differences are observed in terms of navigational strategies. In this part of the review, we address the question of the calibrating role of vestibular cues for the integration of sensory information.

Moreover, internal spatial representations sustaining navigation may be based on distinct memory processes. One of these is route knowledge [62,127,150]. A person can form associations between successive perceptual images along a route or can store a route as a succession of segment lengths and turns. This route knowledge is sufficient for repeating travel along the same path on subsequent occasions but by itself does not permit the computation of never-experienced paths, such as shortcuts and detours. Another process is known as path integration [13,48,56,61]. Expressed in the most general terms, path integration is the process of updating one's current location on the basis of sensed displacements and turns [104] and is likely to involve an azimuthal reference (like the sun or a mountain range), vestibular inputs, and proprioception, possibly aided by optic flow and local features of the environment [33,95]. Path integration involves minimal storage of information in memory: used in connection with perceptual images of the environment, the position and orientation information obtained from path integration can be used to gradually develop a representation of the spatial arrangement of components of the environment, a representation functionally equivalent to the common conception of ''cognitive map'' [56,158]. Finally, people may use landmark knowledge: a person exploring or navigating through novel territory can use bearing and distance information obtained from more distant landmarks, available from different parts of an environment, as a means of integrating distinctive locations within the environment into a coherent global (survey-type) representation that, again, is functionally equivalent to the common notion of cognitive map.

Different levels of spatial knowledge may be required according to the navigation task to be performed. Simple tasks, like path-reproduction, require only keeping in memory orientation and distance information along the orientation path and involve mainly route knowledge. Most complex tasks such as shortcutting or selecting a new route require the integration of spatial parameters and are thought to involve survey knowledge [49,62,103,150]. Path integration may be adequate for navigation in small- or medium-scale environments but not for large-scale environments.

Finally, much work has dealt with the neural basis of navigation. A new era of investigation has been opened by the discovery of place cells in the rodent hippocampus [126,127], of head-direction cells in the post-subiculum [157], and more recently grid cells in the entorhinal cortex [75,137,148]. The respective roles of such brain structures in spatial memory and navigation are still under debate, in particular with respect to the precise role of the hippocampus in the processes of cognitive mapping and path integration. In humans, neuroimaging and neuropsychological studies have evidenced neural bases of navigation in the medial and right inferior parietal cortex, the posterior cingulate cortex, parts of the basal ganglia, the left prefrontal cortex, the bilateral medial temporal region (including the parahippocampal gyrus), and the hippocampus proper [30,46,47,134]. Many of these studies have stressed the importance of vestibular information during spatial navigation.

Spatial navigation after vestibular loss

In an elegant series of studies performed with animals without labyrinths and with labyrinthine-defective children, Beritoff [9] first evidenced the contribution of the vestibular system to spatial orientation. Since then, a lot of studies focused on detection and estimation of displacements in darkness, based mainly on vestibular information. These studies will be presented here according to two lines. First, those which pay particular attention to simple tasks and analyse the differential role of canal and otolithic receptors by using passive or active displacements. Second, studies dealing with more complex tasks and more global internal spatial representation such as navigation in real-world environment or without any actual self-motion in a visual (virtual) world.

Simple navigation tasks

In simple tasks, healthy subjects are able to precisely estimate their body angular displacements during passive whole body rotations [15,68]. Additionally, detection and memory of linear displacements by the otolithic receptors allow one to estimate passive body translation [13,20,85] and active walking [116,122,160]. When visual references are lacking, loss of vestibular inputs induces an erroneous perception of self-motion and of computation of the subject's position with respect to memorized targets. Indeed, defective gaze stabilization on a memorized target has been reported for bilabyrinthectomized patients asked to estimate head trajectory during linear self-motion [85]. Impaired orientation has also been reported for passive body rotations [119]. Unilateral vestibular loss induces an asymmetrical perception of self-orientation in space for patients seated on a rotating chair in darkness, with hypometric responses when rotated towards the lesioned side and normometric responses to the intact side [171]. The authors suggested that such asymmetrical perceptual responses are due to the inability of the remaining labyrinth to signal off direction. The walking trajectory deviation towards the lesioned side reported for unilateral vestibular-defective patients tested eyes closed could involve the same mechanisms. Deviation from a linear trajectory has been observed in patients during the acute stage after unilateral vestibular neurotomy [17,131], after

resection of acoustic neuromas, and in chronic vestibulopathy [35]. In addition, vestibular loss-induced deviations from the walking direction depended on the locomotion speed. Lateral deviation towards the lesioned side is higher for normal locomotion speed. Increased walking speed improves the direction of the walking trajectory [17,22]. These data corroborate the task-dependent locomotion strategies described in unilateral vestibular-neurectomized cats for preserving their dynamic equilibrium: an adaptive increase in locomotion speed reduces their balance and gait problems in a rotating beam task [102]. Walking trajectory deviations have also been reported for circular locomotion tasks pointing out vestibulospinal asymmetries [86]. In the same line, patients with vestibular deficits fail to accurately turn corners when walking along a triangular path [60]. By contrast, bilateral labyrinthine-defective patients required to perform a goal-directed linear locomotion perform as well as normal subjects in terms of the distance error in reaching the target [61]. However, larger lateral errors, modifications of gait parameters, and instability are reported when patients walk without vision. Those authors question the role of the vestibular system in estimating distance. This function could be more independent of the vestibular cues. An alternative explanation would be that, in such a simple task, proprioceptive cues may compensate for vestibular loss to properly estimate the distance of the trajectory. Such a vestibular—somatosensory/motor rearrangement is put forward to explain the adaptive plasticity in the control of a locomotor trajectory in healthy subjects exposed to two hours of walking on the perimeter of a horizontally rotating disc and asked thereafter to walk blindfolded straight ahead on firm ground [63]. Subjects generate curved walking trajectories although they perceive themselves as walking linearly. These data point to the prominent role of the vestibular system for passive whole-body displacements, but they raise the question of the functional role of vestibular inputs during active and more complex displacements. The above studies, however, used simple tasks (walking straight ahead or path-reproduction) in which subjects had to acquire spatial knowledge during passive transport or during active walking through an environment.

Complex navigation tasks

Few studies have analysed whether vestibular loss influences more complex navigation tasks including several direction and distance components. Yet, tasks involving spatial inference processes are highly appropriate to revealing spatial skills since they require previously memorized information to be reorganized [25,130,131]. These studies tackle spatial performance according to task complexity and/or according to the sensory cues available. In the initial work of Beritoff [9], labyrinthine-defective children were unable to actively reconstruct the route along which they had been passively carried in the absence of visual cues. One can argue that in more natural conditions, self-motion feedback information coming from locomotor activity could compensate impaired navigation. However, patients with peripheral vestibular damage often complain of spatial disorientation and of distance estimation, especially in driving conditions such as parking. To investigate the effects of unilateral vestibular loss on the ability to perform navigation in humans, Péruch et al. [131] analysed simple versus complex navigation tasks in Menière's patients with various available sensory cues: proprioceptive, vestibular, or visual (virtual) conditions (Fig. 2). After exploring two legs of a triangle, participants are required either to reproduce the exploration path (simple task), to follow the reverse path, or to take a shortcut to the starting point of the path (complex tasks). Patients' performances were recorded before unilateral vestibular neurotomy and during the time-course of recovery (one week and one month) and were compared to those of matched control subjects tested at similar time intervals. The data confirm that unilateral vestibular loss impairs the orientation component (estimation of the angular displacements) of navigation. The distance component (estimation of the linear displacements) of the spatial representation is also impaired, although to a lesser extent. Interestingly, deficits depend on the required level of spatial knowledge since they are restricted to the complex tasks (reversing and shortcutting). Path-reproduction leads to the same performance for patients and controls, while path-reversing and shortcutting induce higher errors for patients than for controls. In addition, spatial representation is differentially impaired according to the available sensory cues: deficits are not significant in the active locomotor blindfolded condition, while they become significant in conditions involving visual and vestibular information (one week after unilateral vestibular neurotomy), and they are maximal when visual cues alone are available (during the whole tested period: before neurotomy up to one month). That route-reversing and shortcutting are responsible for lower performances than in the processing of already explored paths had been described by Péruch et al. [132] during

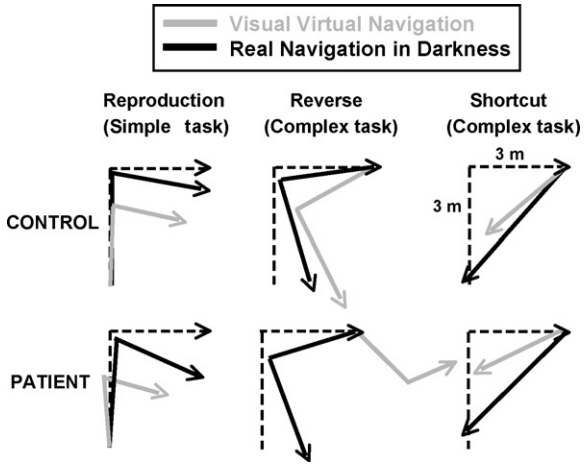

Fig. 2 Changes in spatial navigation after vestibular loss. Representative trajectories of one control (top) and one patient (bottom) tested one week after unilateral vestibular neurotomy in two sensory conditions: visual virtual navigation (without actual body displacement) and real navigation in darkness. The trajectories show turn and distance errors with respect to the exploration path (dotted line with arrows). Note that in real navigation in darkness the patient's trajectories are close to those of the control whereas drastic changes appear in visual virtual navigation, in particular for the complex tasks (path-reversing and shortcutting) [131].

navigation in a visually simulated (virtual) environment in healthy subjects. Performance is impaired even further for the patients.

The impairment of the patients' performance in the visual (virtual) tasks seems to be at variance with the literature dealing with visual substitution processes in vestibular compensation [44,99,151]. The results argue against a visual substitution process in vestibular compensation when applied to the case of cognitive processing. Accordingly, one might have expected either a normal spatial performance or even an improved performance in a purely visual navigation task because patients would have compensated defective vestibular information on the basis of visual information. How can such a discrepancy be explained? It is well known that the same perceptual, motor, and neurophysiological effects can be induced either by self-motion or by visual surround motion in the opposite direction. Such a visual-vestibular convergence has been described in structures involved in postural control such as the vestibular nuclei [177], vestibular area 2v [31] and the parieto-insular vestibular cortex [67]. Moreover, these data suggest that peripheral vestibular information is necessary to the cortical and hippocampal processes involved in mental map navigation [71]. In support of the studies of Péruch et al. [130,131], Brandt et al. [25] demonstrated that patients with acquired chronic bilateral vestibular loss tested with a virtual variant of the Morris watermaze exhibit significant navigation deficits. Clearly, these spatial deficits are not associated with general memory deficits. The matching of spatial memory and navigation deficits, on one hand, and of the pattern of hippocampal atrophy, on the other hand, is a strong demonstration that navigation depends highly on vestibular functions. The influence of vestibular signals on hippocampal formation has also been further evidenced by neuroimaging studies of caloric vestibular stimulation [169] and imagined locomotion [87]. Numerous electrophysiological investigations in animals have stressed the role of the hippocampus in spatial processing in normal [173] and vestibular-defective animals, which results in place cell dysfunction [147,152]. Path integration involves other different areas in the central nervous system that take part in the elaboration and use of a mental spatial representation. Among them, parietal, prefrontal, and occipital areas are involved at different stages.

Conclusion

In summary, it seems that vestibular information is necessary to maintain proper cognitive functions such as internal representation of the body position and motion in space. This suggests that all the sensory cues are necessary to build up an accurate mental representation. That vestibular information is necessary to elaborate an accurate internal spatial representation is highlighted by the higher spatial deficits in navigation tasks requiring the highest level of spatial knowledge. Put differently, when one sensory cue is impaired, the environment may be experienced in a different way, and a different mental representation may be constructed. An intriguing finding is that, paradoxically, the disturbance of spatial memory after such a vestibular lesion is not directly linked to the activation of vestibular inputs since deficits are maximal with visual cues alone (visual navigation), even when subjects are stationary. Apparently, vestibular information is necessary for a proper global spatial perception. So, even without any self-motion, having no labyrinth on one or on both sides is not the same thing perceptually as holding a cue constant (by holding the head stationary in healthy participants). This highlights the importance, in healthy individuals, of vestibular information signalling the head is stationary. Clinical data support the idea that vestibular cues are involved not only in body representation in space but also in extrapersonal space representation. A second finding is that the more complex the task, the higher the weight of vestibular cues in building up an accurate internal spatial representation. We conclude that vestibular information participates in spatial knowledge at a high sensory integration level. In the same line, vestibular stimulations can help correct the spatial references of brain-damaged patients with a high level of spatial impairment, as shown for patients with spatial neglect [32,144].

Towards a model of internal spatial representation changes in vestibular syndrome

The above-mentioned studies emphasize the importance of changes in the internal spatial representation after vestibular damage, and we suggest that these changes have functional consequences on the induced postural and locomotor syndrome. Internal spatial representation is based on integration within cortical areas of all the available sensory cues and is elaborated from interactions between the subjects and their environment. This representation therefore incorporates the sensorimotor memory of past experiences, which is permanently updated by the new sensorimotor knowledge resulting from actual experiences and environmental constraints. Permanent swaps between automated sensorimotor patterns and cortical representation allow these patterns to be reconfigured and to significantly influence postural control [128,161]. Vestibular damage constitutes a drastic change in body-space relationship, and our view is that changes in internal spatial representation have a leading role in the vestibular syndrome and its subsequent recovery. We base our assumption on two elements. The first one postulates that internal spatial representation changes participate in fast-adaptive sensorimotor processes. The second one assumes that vestibular signals are necessary for other sensory cues to be properly integrated.

Changes in internal spatial representation: a fast adaptive process

In the present approach, we suggest that internal spatial representation is a dynamic mental function, permanently built up, which remains stable, that is, constant, as long as sensory condition, postural context, and higher cognitive processes remain unchanged. Any change in any of these aspects can modify the perception of space. After vestibular loss, reversal of postural orientation as a function of the sensory context, posture-related perceptive changes,

and switching strategies are strong arguments in favour of changes in internal spatial representation.

Our model of internal spatial representation changes in vestibular syndrome lies first on changes in spatial reference frames. A simple transition from darkness to light, that is, from an egocentric to an allocentric frame of reference, induces immediate and labile postural changes. Shifting from one reference to another induces the reversal of the direction of the vestibular-induced postural and locomotor symptoms. These modifications cannot rely on structural or cellular mechanisms contributing to the recovery process, like those involved in the restoration of spontaneous activity in the deafferented vestibular nuclei. Such plasticity mechanisms need time and, once established, act permanently. In contrast, changes in internal spatial representation come into play so fast and are so remarkably flexible that they evoke a brain selection of a new reference frame among the existing ones. Marendaz and Ohlmann have emphasized that the selection of reference frames depends on several factors such as interindividual differences, vicarious processes, and environmental constraints [84,112,114,115,125]. Here, we suggest that other factors also contribute to the weighing of the spatial reference frames and to their context-dependent selection. One is the status of the vestibular system. In bilateral vestibular-defective patients, judgment of verticality and body orientation in space strongly depends on the allocentric reference frame. In contrast, patients with unilateral vestibular loss select either allocentric or egocentric cues, depending on their perceptive style and their ability to switch from one reference to another according to environmental and postural constraints. Postlesion stage (acute versus chronic) and postlesion experience (rehabilitation or not) are supplementary factors involved in reweighing and selecting reference frames for vestibular patients.

Postlesion switching strategies supporting internal fast-adaptive processes have been observed as soon as one week and up to one year in Menière's patients submitted to a curative unilateral vestibular neurectomy [100]. There is also evidence of changes in motor strategies, often aimed at stabilizing head and eye in both animal models [73] and humans [94]. To avoid oscillopsia, some vestibular-defective patients exhibit a head on trunk stabilization rather than a head in space stabilization, which is a motor strategy observed in the ontogenesis of head stabilization in the young child [6]. Shifting from ankle strategy to hip strategy has also been described with ageing [176] in healthy subjects submitted to threatening postural tasks [81], and in vestibular-defective patients [82].

Switching from one motor plan to another is generally well adapted to the environmental constraints or the pathological state, but maladaptive strategies have been reported. For instance, ankle stiffness may be inappropriate for dynamic postural control. Similarly, poor compensation in highly visuo-dependent patients could result from their inability to switch from one reference frame to another according to the sensory context.

Finally, it is clear that internal spatial representation changes induce fast-adaptive postural changes, and that postural constraints are also able to modify perception. Such a reciprocal link, previously described in healthy subjects, seems to be reinforced after vestibular loss. For vestibular-defective patients, the role of postural constraints in perception of orientation is probably greater because of their greater need for balance control.

Vestibular signals are necessary for other sensory cues to be properly integrated

We suggest that vestibular cues are necessary for other non-vestibular cues to be properly integrated and, consequently, for an accurate spatial representation to be built. Indeed, striking data from navigation experiments have shown that spatial representation is impaired even when vestibular cues are not required for the task. The fewer the sensory cues, the more impaired the spatial representation. When only visual cues remain, maximum changes are reported. Therefore, it seems that vestibular loss changes the way sensory cues are integrated. That vestibular signals are able to enhance perception from other sensory cues has been reported for patients with spatial neglect since clinical signs were compensated under vestibular stimulation [90,111].

Conclusion

Subjects balance, orient themselves, and navigate in a space mentally built and, as already suggested by Van Nechel [166], external space perception is a mental construction organising the sensory cues to model the body-space relationship. Here, we suggest that vestibular signals are involved not only in building body representation in space but also in extrapersonal space representation. To summarize our view of the vestibular syndrome and the leading role of internal spatial representation, we suggest that vestibular-induced changes are based on a dynamic mental representation of space, permanently built up, and that supports fast-adaptive processes. Internal spatial representation is unstable and depends on the nature of the available sensory cues and on postural constraints. Finally, mental representation probably depends as well on higher cognitive processes, including attention and emotion, which modulate the way we sense information. This could explain, at least partly, why the vestibular syndrome and the subsequent vestibular compensation differ among patients and why impairments described by the patients are not always at the same scale as those measured by the classical analysis methods. Future studies will be useful in further testing these assumptions.

Conflict of interest

None.

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