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# Multisensory integration in spatial orientation

Alain Berthoz and Isabelle Viaud-Delmon

Recent psychophysical studies on normal subjects, as well as brain imaging studies, have revised the concepts concerning the mechanisms underlying spatial orientation during navigation tasks. The emphasis has been put on internal models that allow the prediction of a planned trajectory and are essential in the steering of locomotion. Cognitive factors such as strategies and emotional parameters are now starting to be included in the research on spatial orientation. It is obvious that important individual and gender differences exist in the brain operations underlying spatial orientation in humans, which may help to understand the construction of a coherent perception and the organic neural disorders related to the internal representation of space.

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## Introduction

The control of spatial orientation during navigational tasks and locomotion requires a dynamic updating of the representation of the relations between the body and the environment. This depends upon central integration of current multisensory information but also on the comparison of sensory signals with planned trajectories, the body schema and past memories. Three main sensory modalities are involved in these processes: vision, the vestibular system and proprioception. In addition, efferent copies from motor signals also contribute to the updating of spatial representations during navigation. The brain mechanisms underlying spatial orientation have, in the past, mainly been studied in static conditions. We shall review here some recent studies concerning the brain mechanisms that are used to dynamically update, or memorise, routes or travelled paths. This review will also emphasise a neglected dimension in the study of spatial orientation: the role of emotion in the underlying processes. This role is examined by recent studies concerning the relationship between spatial orientation and anxiety disorders.

## Vestibular motion perception and memory during navigation

Despite a variety of models of sensory interaction [1,2,3,4], the neuronal mechanisms of high-level interaction between vestibular and other sources of information remains unclear. In addition, motion perception also depends heavily upon internal models and not only on input–output transformations, but there is no general theory

that can explain how the different afferent signals are combined in a unique coherent perception during navigation.

Recently, brain imaging techniques have improved the anatomical identification of the projection areas of vestibular, visual and kinaesthetic signals to the multimodal integration areas of the cerebral cortex involved in spatial orientation and memory in humans [5,6], and in the determination and perception of the mid-sagittal egocentric body reference [7]. These data, together with the data obtained in the primate cortex concerning the cortical systems dealing with head-in-space movement (see [8]), contribute to the knowledge of the neural structures involved in space perception but they provide little information concerning the neural processes involved. Novel psychophysical methods in humans, however, have allowed the study of both canal and otolith organs during tasks involving the perception and memory of bi-dimensional motion during navigation [9]. Mobile robots can be used to passively displace human subjects while visual stimuli can be provided by virtual reality techniques. Together, these recent developments have given rise to new tools for the study of visual—vestibular interactions during combined rotations and translations. They have also allowed the experimental testing of new hypotheses concerning the type of information that is stored in spatial memory during navigation. Such experiments have suggested that the brain stores dynamic patterns of motion, rather than just position on cartesian-like cognitive maps [10]. These, together with observations of deficits in vestibular memory in patients with cortical lesions, and positron emission tomography (PET) studies of the brain areas involved in the memory of travelled routes, have led to the formulation of the concept of ‘topokinetic memory’ [11], (i.e. the dynamic memory of the movements and associated landmarks and views during locomotion).

New methods of recording head and body movements during blind locomotion have also allowed the study of the spatial memory mechanisms underlying the steering of locomotion. In human subjects executing a locomotor turn — even in darkness — gaze direction leads the trunk and feet. This suggests that the steering is performed through predictive processes, probably involving complex interactions between kinesthetic information and internal models of the planned trajectory [12]. This predictive ability is not present in young infants and develops during the first few years [13]. It has also been proposed that there is a dissociation between the coding of distance and direction for the steering of locomotion [14].

## Spatial orientation and emotion

All the above results indicate that spatial orientation during navigation is dependent upon higher cognitive

processes involving the limbic and cortical areas related to spatial memory. However, another dimension has also recently been revealed to play a role in these mechanisms. There is a remarkable overlap between the brain structures involved in spatial orientation and spatial memory, and those involved in emotion (see [15,16]). Spatial disorientation is a complaint reported by many patients in psychiatry. Evidence of dysfunction of spatial orientation has been found in agoraphobics [17]. During navigation in a complex environment, panic-agoraphobic patients became lost more often and utilised fewer navigation points. Moreover, the maps drawn afterwards by these patients were inaccurate [18].

The experience of vertigo and dizziness is a common symptom in several psychiatric disorders. Dizziness is also one of the key symptoms of panic. Because vestibular system dysfunction leads to dizziness and disorientation, it has been hypothesised that a peripheral vestibular abnormality could explain the presence of certain symptoms related to space perception in anxiety disorders [19]. Despite a strong association between dizziness and anxiety [20\*], however, it is difficult to demonstrate a cause-and-effect relationship between pathological anxiety and vestibular system dysfunction. There is a growing literature on vestibular abnormalities in anxiety disorders, in particular agoraphobia and panic disorder (see [21\*,22\*] for reviews). Numerous studies have investigated a potential link between anxiety and the vestibular system, but few of them have addressed the specific topic of spatial representation. In particular, the problem of the construction of a coherent perception of space has not been addressed in these studies.

Dizziness is characterised by a marked distortion of self-world relations and reflects a discrepancy between internal sensation and external reality. Spatial disorientation, as well as dizziness, can be due to a peripheral problem in any of the sensory modalities; or, it may be due to a central problem, involving not one particular sensory modality but rather the integration and weighting of the different modalities and their relation with memory. Complaints concerning spatial disorientation in psychiatry have seldom been considered as a possible manifestation of a distorted multisensory integrative ability. Several kinds of sensory mismatches are encountered in everyday life but despite this, the central nervous system usually manages to update the internal representation of the body in the surrounding space. Such sensory conflicts may occur between any of the vestibular, visual or somatosensory systems. For example, passive transports generate sensorimotor mismatch because of the absence of motor feedback. In some cases, a mismatch among simultaneous sensory information may elicit an erroneous perception of the body in space, resulting in a vertigo syndrome. Vertigo may thus be induced by physiological external stimulation. However, when no physical explanation is found to explain the symptom of vertigo, it is common to label it as 'psychogenic'. We think it is necessary

to go beyond such a dichotomy between 'physiological' and 'psychogenic' vertigo in order to reach a better comprehension of the mechanisms of spatial orientation.

### **Space phobia**

A number of phobias that are acquired by dizziness-prone patients have been described. They often involve avoidance of stimulus situations having certain visual characteristics.

Space phobia [23] is characterised by fear of the absence of visual orienting cues and fear of falling, which is unlike the fear of public places found in agoraphobia. Space and motion discomfort [24] occurs in situations characterised by inadequate visual or kinaesthetic information for normal spatial orientation, and may contribute to promoting agoraphobic avoidance in patients with vestibular dysfunction. Postural phobic vertigo [25] refers to dizziness and subjective disturbance of balance while standing or walking despite normal clinical balance tests. Perceptual stimuli such as a bridge, a staircase, an empty room, a street or a social situation (e.g. a crowd, restaurant or concert) are provoking factors. The Motorist Disorientation Syndrome [26] refers to a difficulty when driving over the crests of hills and on open, featureless roads.

In all these syndromes, a false sense of orientation arises either from inappropriate signals from distorted vestibular canal and otolith organs, in the case of a vestibular dysfunction, or from a disordered central interpretation of sensory information. Symptoms of dizziness are mainly precipitated by certain visual surroundings. Some vestibular patients are sensitive to particular visual environments (e.g. supermarket aisle, crest of a hill when driving). Idiosyncratic visual and vestibular factors may play a part in the outcome of any peripheral or central lesion that causes loss of balance and spatial orientation, underlining the necessity to study the variation of the tolerance to visual and vestibular stimuli among normal people. Bronstein [27] proposed that visual vertigo may occur specifically in patients with balance disorders who show high reliance on visual channels for postural control and spatial orientation.

Agoraphobic patients demonstrate an abnormal destabilisation when maintaining upright posture under sensory conflicting conditions [28,29]. It has been hypothesised that dizziness symptomatology could be linked to a strategy for maintaining balance or orientation that relies on a dominant contribution of vision. Even though a recent study [30] attributed a stronger role of proprioceptive cues in the maintenance of balance in agoraphobic patients, the results of this study illustrated once more the possible role of a higher process involving multisensory integration in anxiety disorders. It is indeed striking to note that an altered visual-vestibular interaction has often been observed in anxious patients. In addition, we have recently obtained evidence in anxious subjects of a lack of anticipatory oculomotor behaviour during passive rotations in darkness, which may reveal a physiological manifestation of

a differing orientation strategy [31] in these persons compared with nonanxious subjects.

### Gender and sensory integration

There are several sources of individual differences in space orientation, the most recognised of which is gender. Differences in space orientation between males and females have often been approached in terms of differing spatial abilities, but some studies indicate that gender differences in sensory integration could also exist.

Evidence for gender differences in circularvection (i.e. the illusion of self-motion when viewing moving visual surrounds) exists [32], and could be related to the greater susceptibility of females to motion sickness [33]. The 'mal de débarquement' syndrome (the sensation of rocking and swaying that persists after sea travel) also appears to be more common among females. The etiology of this syndrome is unknown, but it has been thought to result from an inability of the brain to integrate and adjust to new spatial surroundings [34]. In an experiment on sensory adaptation, female subjects were found to recalibrate their vestibular perception to a lesser extent after exposure to conflicting visual-vestibular stimuli [35]. All these findings consistently suggest gender differences in the central processes dealing with visual-vestibular interaction and internal strategies of spatial orientation and spatial memory.

We cannot exclude the idea that the observed differences in sensory integration in males and females are related to the differences observed in the ability to maintain a sense of self-position in relation to the global shape of the environment. Several studies have demonstrated that females use distal cues for spatial orientation in a different way to males (see [36]). While it has already been proposed that gender differences in the structure of the hippocampus, caused by the effects of sex hormones [37], could represent a neural correlate of the difference in spatial ability, the neural substrates of the difference in sensory integration are unknown. Further research using magnetic and metabolic brain imagery methods will be necessary if we are to understand the underlying differences between human males and females in the processing of spatial information.

### Conclusions and future directions

It is now necessary to obtain more information concerning the neural basis of these higher cognitive processes. Brain imaging will certainly be useful, but we believe that recording of neurones in freely-moving monkeys during navigation tasks will also be absolutely necessary. The recent discoveries of Rolls *et al.* [38] concerning the mechanisms by which the monkey hippocampus may code the relationship between the animal and its surrounding space are examples of the new approaches that may be followed fruitfully. It will also be important in the future to study the individual strategies that are used by subjects of the same, and of differing sexes, to solve spatial problems. For example, the simple measurement of eye movements during a

rotation memory test suggests that different subjects can use either allocentric or egocentric strategies [39]. Moreover, during a locomotor task the brain can either update the location and orientation of objects in a continuous manner or delay the updating until the end of the locomotion, performing only an egocentric path integration during the travelled route [40].

More investigations are needed to analyse different aspects of multisensory integration in anxious patients in tasks implying perception as well as motor control. In particular, the roles of the hippocampus, parietal cortex and frontal cortex in the mechanisms that allow steering of locomotion during navigation tasks should be investigated. More generally, it is necessary to design brain imaging experiments in humans using paradigms in which subjects recall actual, actively-performed navigation tasks. Some attempts in this direction have been made [41] and should be continued.

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- One of the most important unsolved questions concerning spatial orientation is the mechanism by which the brain separates the acceleration of gravity and the linear acceleration of the head during translations. Several authors have suggested that this is performed by a separation of the inertial and the gravitational components of head movements through a neural mechanism of filtering in the brain stem. Low pass filtering would yield the component due to gravity and high pass filtering to linear acceleration. This paper reports experiments on human subjects submitted to a tilt after having been rotated around an earth-vertical axis. Eye movement recordings provide evidence that, contrary to the above hypothesis, the brain solves the problem through an internal model of the difference between gravity and acceleration.
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The brain areas involved in the processing of the egocentric body midline were studied by functional magnetic resonance imaging in human subjects. Subjects were asked to indicate with a button when a visual target moving on a screen was either passing through the mid-sagittal plane of the body or through the two extremities of a linear horizontal trajectory. A parieto-frontal system was found to characterise the specific processing of the mid-sagittal plane. The location of the two areas is akin to the right posterior-inferior parietal cortex, in which lesions induce the neurological syndrome known as neglect.
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This paper summarises several studies concerning the steering of locomotion. Subjects were asked to walk blindfolded around previously-seen circles or triangular paths. The experiments were performed both with normal subjects and patients with bilateral or unilateral vestibular lesions. Head movement was measured with computerised video techniques. The results suggest that there is a dissociation between the control of distance and direction. A similar hypothesis has been proposed for arm movements by others. The possible role of a newly-discovered head-direction cell system in the coding of direction is discussed.
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