Journal of Vestibular Research 20 (2010) 53–60
DOI 10.3233/VES-2010-0364
IOS Press

Effects of microgravity on cognition: The case of mental imagery

Luzia Grabherr* and Fred W. Mast
Department of Psychology, University of Bern, Bern, Switzerland

Received 15 February 2009
Accepted 17 March 2010

Abstract. Human cognitive performance is an important factor for the successful and safe outcome of commercial and non-commercial manned space missions. This article aims to provide a systematic review of studies investigating the effects of microgravity on the cognitive abilities of parabolic or space flight participants due to the absence of the gravito-inertial force. We will focus on mental imagery: one of the best studied cognitive functions. Mental imagery is closely connected to perception and motor behavior. It aids important processes such as perceptual anticipation, problem solving and motor simulation, all of which are critical for space travel. Thirteen studies were identified and classified into the following topics: spatial representations, mental image transformations and motor imagery. While research on spatial representation and mental image transformation continues to grow and specific differences in cognitive functioning between 1 g and 0 g have been observed, motor imagery has thus far received little attention.

Keywords: Vestibular, otoliths, cognitive performance, parabolic flight, human

1. Introduction

It is important to understand human cognitive functioning in microgravity to assure successful and safe manned space missions. Given the ambitious goal to accomplish manned space missions to Mars and the development of commercial space flights, knowledge of cognitive performance is crucial. This concerns also a more generic group of space travelers as opposed to carefully selected and highly trained astronauts. Cognitive performance can be impaired in microgravity, due to various factors such as stress, high workload, lack of sleep and physiological changes [5,18,29]. In this review we focus on the effects caused by the absence of the GIF (gravito-inertial force), which is no longer perceived as a sensory input. The otolithic organs process magnitude and direction of the GIF on Earth but their functioning is impaired in 0 g (e.g. [10,30,64]). However, until today, relatively few studies have investigated the consequences of absent gravity-related sensory information on cognitive functions. Vestibular-cognitive interactions are still not well understood, yet relevant literature is growing (for a review see [26,58]). This review aims to provide a systematic overview of how a weightless environment can influence mental imagery abilities and it will hopefully stimulate future research on cognitive functions in microgravity. Mental imagery has been investigated widely to infer about the cognitive processes that underlie our thoughts and subsequent actions. On the one hand, assessing mental imagery in microgravity can help to provide a more profound understanding of the underlying mechanisms. On the other hand, knowing more about how mental imagery can be affected in 0 g will help to better predict human behavior in microgravity. Moreover, mental imagery training could be developed to minimize the adverse effects of a 0 g environment.

*Corresponding author: Luzia Grabherr, Department of Psychology, University of Bern, Muesmattstrasse 45, CH-3009 Bern, Switzerland. Tel.: +41 31 631 4024; Fax: +41 31 631 8212; E-mail: luzia.grabherr@psy.unibe.ch.

ISSN 0957-4271/10/$27.50

2. Procedure

As an initial step, Web of Science was used as the main literature database. The keywords vestibular or otolith or gravity were used to identify articles with a focus on vestibular and/or gravitational influences, as opposed to other potential influences such as psychological factors (e.g., stress). We also requested the keywords microgravity or weightlessness or 0 g or parabolic flight to search specifically for studies performed in 0 g. Moreover, the keywords cognition or cognitive or mental or mind were used with regards to the content of this review. The terms animal or rats or fish were excluded, as we wanted to restrict ourselves to human cognitive functioning. A total of 42 articles were identified. From these 42 articles, 6 experimental studies were actually performed during (or in one case after) parabolic or space flights and investigated mental imagery processes. In addition to the experimental studies, we included one review article [34]. Other articles were excluded on the basis of different methodology (e.g., patient studies or ground-based simulation of a microgravity environment) or because they have only a loose connection to cognitive functions and mental imagery abilities. However, some of these studies are referred to in the discussion.

In a second step, more relevant literature was tracked by a backward literature search (references cited by these articles) and a forward literature search (articles which cite the identified articles). In addition to Web of Science, MEDLINE/PubMed and Scirus were also used as databases. A total of 13 relevant articles were identified. The studies were then categorized into the representational, transformational and motor-related aspects of mental imagery.

3. Mental imagery

Mental imagery is used in a variety of tasks, for example when contemplating a past event, daydreaming or mentally rehearsing a sequence of movements (e.g., a skier before a downhill race). Mental imagery relies on information stored in memory whereas perception depends on the presence of a sensory stimulus. Yet, mental imagery goes beyond simply recalling previous perception: information can be combined and transformed in multitudinous ways [22,31]. Therefore, mental imagery is involved in several important processes such as perceptual anticipation, problem solving (for example in mental transformation) and motor simulation [22]. Recent evidence has demonstrated improvement in perceptual learning by mental imagery training [59]. Prima facie mental imagery may not appear to be a cognitive function that is prone to be affected in a weightless environment. This judgment has been given precedence to certain motor processes [3,27,53,63] and visual perception [8,23,49,60,63]. However, neuroimaging studies have shown that there is a great degree of overlap in the brain regions active during movement execution and motor imagery [13], and during visual perception and visual mental imagery [31]. Thus, when we take into consideration that mental imagery draws on mechanisms involved in these processes [31], it is worthwhile to take a more detailed look.

3.1. Spatial representations in 0 g

How we represent space when the GIF is missing can be investigated by relying on observations from astronauts. Data from one astronaut lead to an early account of a potential cognitive change in mental representations [7]. Eyes closed, his task was to write his name horizontally and vertically on a notebook. Measurements were made from flight day 1 to 6 (except on flight day 4) and were compared to pre-flight measurements. Results showed that in microgravity word length decreased. Interestingly, this was especially true when the letters were aligned in the vertical direction. Moreover, the decrease in length was most notable during the first three days in space (see Fig. 4 in [7]). These efforts were continued in a follow-up study testing two astronauts during a 7-day spaceflight [33]. Instead of handwriting, they had to draw a series of Necker cubes (line drawings of cubes with ambiguous spatial orientation). Results were again compared to pre-flight measurements. A decrease of 9% in vertical height was observed in-flight compared to pre-flight measurements (in one astronaut) whereas no statistical difference was found for the horizontal length ratio. Furthermore, in 0 g, the astronauts performed the tasks either in a free-floating condition or seated and attached. No statistical difference was found between these two conditions and thus, this finding is likely due to the absence of otolithic cues.

A few years earlier than the above mentioned study [33], Gurfinkel and colleagues [25] studied spatial orientation in 0 g. Two cosmonauts had to draw ellipses in the air without visual feedback, either parallel or perpendicular to their longitudinal body axis. They found no overall impairment in 0 g. Lathan, Wang and Clément [33] revisited these results and report a specific decrease in the vertical length for both types of ellipses of again roughly 9%, while there were only marginal changes in horizontal length.

More recent experiments have been conducted during parabolic flight [9]. Nine participants were tested free-floating aboard the A300 Zero-G aircraft and results were compared to pre-flight performance. Blindfolded participants were required to write and to draw different types of simple geometric shapes (squares, circles, lines). Preliminary results indicate a significant decrease of 21% in word length but no significant difference in the ratio of the length for horizontal vs. vertical lines in 0 g compared to 1 g. The authors indicate (although without providing statistical values) that only the space in between the letters was reduced whereas the size of the letters remained the same. The results are not yet conclusive regarding the underlying mechanisms. On the one hand it is possible that the results represent a change in the metric representation of perceptual space [9]. On the other hand changes in proprioception and/or motor effects cannot be ruled out completely. Sensorimotor changes in 0 g have been reported frequently (for a review see [2,32]) and the absence of the GIF could affect movements in the vertical direction more than in the horizontal direction. Moreover, the authors reported that the drawings were performed faster in 0 g compared to 1 g, but attributed this to participants stress [9] and not to a potential facilitation caused by the absence of gravitational constraints. Future research has to be carried out in order to clarify the question concerning the underlying mechanisms.

It is conceivable that the internal representation of space changes over time and manifests itself more clearly with longer durations in 0 g [9]. However, results from one astronaut do not support this assumption as the decrease in word length was most pronounced during the first days in space [7]. Further experiments in space are planned to clarify questions of the duration of exposure to 0 g [9]. Comparisons to post-flight measurements could also help to investigate adaptation processes.

Clément and colleagues suggested that "we represent the height of our body and the space around us as a function of the gravitational information" [9, p. 680]. To our knowledge, no study has investigated, quantitatively, whether the size of the mental representation of our own body changes in microgravity. This would certainly be interesting to assess. In fact, the results of a study, which is discussed in more detail in the next section, suggest that participants were impaired in mentally transforming their own body representation when the GIF was absent [24].

3.2. Mental image transformations in 0 g

Mental image transformations involve a representation of an object[1] plus an additional 'transformational' process such as a mental rotation (imagined rotation of an object either in two or three-dimensional space), a mental translation (all points of an object are imagined to shift with equal distance in the same direction) or any other transformational process (e.g., mental deformation, diminution or magnification). We make use of spatial image transformations in numerous everyday contexts, for example when giving directions, furnishing a flat or playing videogames such as Tetris. Since Shepard and Metzler [57] have put forward a distinct paradigm to study mental image transformation, it became a widely investigated higher cognitive function. Even in microgravity, a considerable amount of studies have looked at mental transformation performance. An early observation in one astronaut suggested that mental rotation is facilitated when gravitational constraints are absent [7]. Different types of stimuli have since been used in 0 g: geometrical figures such as abstract 3D objects (Shepard and Metzler cubes) [35,36, 43], matrices [16], bodies [16,24], body-parts [24] and faces [12]. Some of these studies have been described in a review article by Leone in 1998 [34].

Depending on the stimuli and the task (e.g., same-different vs. left-right judgments) different strategies can be evoked which involve, at least partly, distinct cortical activations [66]. At least two types of mental image transformations can be distinguished: egocentric mental transformation tasks whereby a mental representation of one's own body or body part is imagined to be moving relative to the environment and object based mental transformations during which an external object is transformed with respect to the participant and the environment. Overall, no differences in an object-based mental transformation task were observed between in-flight measures of 8 cosmonauts compared to a control group tested on the ground [35,36]. In contrast, performance in an egocentric mental transformation task was impaired in microgravity. 5 participants tested during parabolic flight produced both higher error rates (ERs) as well as higher response times (RTs) in 0 g compared to horizontal flight (1 g) [24]. A follow-up case study with two new participants is in line with these findings, at least concerning the error

[1] Please note that this object can also be a mental representation of one's own body, body part or a non-existent, purely imagined object.

rates. Moreover, these two participants showed no impairment during the 0 g phases of parabolic flight in an object-based mental transformation task [24]. The absence of an effect in different g-levels on the object-based mental transformation task suggests that this task can be solved by the means of purely visual-spatial processes, which are not influenced by the absence of vestibular input. Indeed, an earlier study using another visual-spatial task revealed that astronauts were still able to perform the task by relying on a head-retinal reference frame [19]. The egocentric mental transformation task, however, differs in this respect from the object-based mental transformation task. The presence of a gravitational frame of reference seems to facilitate the mapping of mental own body and body-part representations onto spatial coordinate positions.

3.3. *Imagined movements in 0 g*

Imagined movements, also referred to as motor imagery, involve the conscious mental rehearsal of a motor act without actually performing it, that is, without producing any overt movements. [2] It has been put forward that motor imagery corresponds to a subliminal activation of the motor system [28] and it has been repeatedly shown that motor imagery is, in many critical aspects, closely related to action [40]. There are, for example, common neurological and physiological aspects of motor function and motor imagery. They appear to share underlying neural substrates and their autonomic responses (e.g., heart rate, respiration) correlate [13]. Interestingly, corresponding eye movements between imagery and action have also been found [61]. Another line of evidence supporting a link between imagined and executed actions comes from studies revealing consistencies in the time it takes to imagine performing a particular movement (e.g., tying a shoe) and the time it takes to actually execute the movement [14,51]. However, different response time patterns were observed when participants carried additional weights. One study revealed increased response times in the imagery condition compared to the execution condition when participants carried additional weights [14], whereas another study found no difference between the two conditions [51]. To our knowledge, no study has yet been designed to investigate motor imagery in microgravity and thus many questions remain still open. For example, do imagined movements mimic the timing of slowed arm movements observed from tracking tasks in 0 g (e.g. [53])? Papaxanthis and colleagues [50] tested 5 cosmonauts once before and twice after a long-term spaceflight. The task was to perform and to imagine a locomotor task – stepping onto a platform, jumping from it and walking straight for 4 meters. Results revealed that on the second day post-flight, execution time was significantly increased compared to pre-flight measurements. On the sixth day post-flight, execution time converged to pre-flight measurements. Interestingly, response times in the imagery condition were always identical to the response times in the corresponding execution condition. These results suggest that motor imagery processes accurately reflect the re-adaptation processes to normal gravity. Moreover, these results give reason to hypothesize that imagined movements would accurately mimic motor execution in microgravity. Furthermore, the results of a ball catching experiment tested among astronauts suggest that the observed motor performance was impaired because the participants applied an internal model of gravity, which no longer accurately predicts the ball's trajectory in microgravity [44]. We hypothesize that this internal model would also be applied in the mental prediction of ball trajectories and thus no differences in response times would be observed between the overt motor execution and the mental act in 0 g.

4. Summary and future directions

Please refer to Table 1 for an overview of the studies that were discussed. Taken together, the reviewed studies suggest that mental imagery per se is not affected in microgravity, instead specific tasks reveal to be affected by the absence of the GIF. Spatial representations of words and geometrical figures decrease in vertical but not horizontal length. In the case of mental image transformations, participants' performance was impaired when they needed to spatially update a mental representation of their own body or body-part, but showed no impairment for the spatial rotation of external objects. Finally, imagined movements adequately mimicked the actual motor performance after a long exposure to 0 g. However, no actual data have been recorded in microgravity.

[2] Although covert motor processes play a part in mental image transformations [62,65] and may also play a role in the detrimental performance found in mental own body and body-part transformations in 0 g [24], they are not discussed in this section because participants are often unaware of these underlying motor processes. In other words, there is often no conscious act of imagining a movement during mental transformations.

Table 1
Overview of the studies. The table summarizes the mental imagery studies that were performed in microgravity or after a long exposure to microgravity

Study	Task	0 g condition	Control condition	Participants	Main finding in 0 g
Spatial representations					
Clement et al., 1987	Writing with eyes closed	Space flight	Pre-flight	1 man	Decrease in vertical word length
Gurfinkel et al., 1993 (after Lathan et al., 2000, p. 39)	Drawing ellipses in the air with eyes closed	Space flight*	Pre-flight (and post-flight)	2 men	Decrease in vertical length
Lathan et al., 2000	Drawing Necker cubes with eyes closed	Space flight*°	Pre-flight	2 participants	Decrease in vertical dimension
Clement et al., 2009	Writing and drawing with eyes closed	Parabolic flight°	Pre-flight	6 men, 3 women	Decrease in length
Mental image transformations					
Clement et al., 1987	Body tilt estimation	Space flight°	–	1 man	Increasing tilt angle with flight duration
Matsakis et al., 1993	Same-different judgments of abstract objects (ERs, RTs)	Space flight*	Pre-flight and post-flight, control group	3 participants	Tendency for performance improvement
Leone et al., 1995; Leone et al., 1995	Same-different judgments of abstract objects (ERs, RTs)	Space flight*	Pre-flight and post-flight, control group	8 men	No overall differences
De Schonen et al., 1998	Learning and recognition of faces (ERs, RTs)	Space flight*	Pre-flight (and post-flight)	3 participants	Impaired recognition of faces learned in 0 g
Eddy et al., 1998	Same-different judgments of matrices, task switching between mathematical and left-right judgments of bodies (ERs, RTs)	Space flight	Pre-flight and post-flight	4 men	No overall differences
Grabherr et al., 2007 (main study; case study)	Left-right judgments of body stimuli; Left-right and same-different judgments of bodies (ERs, RTs)	Parabolic flight°; Parabolic flight*	1 g during flight; 1.8 g during flight	5 men; 1 man, 1 woman	Impaired performance in left-right judgments
Imagined movements					
Papaxanthis et al., 2003	Motor execution and motor imagery	–	Pre-flight and post-flight	5 men	Congruency of motor execution and imagery

*Participants were fixated during the experiment, °Participants were tested in free-floating condition.

This review focused on the influence the absence of the GIF has on cognitive functions. Knowing more about cognitive functions and in particular about mental imagery is important because these functions can be trained to eventually overcome adverse effects experienced in microgravity. This is suggested by reports of astronauts who were able to voluntarily assign a spatial reference frame to their environment. These astronauts have reported to choose a wall as the spacecraft floor and another as the ceiling. If they enter less well-known modules they can suddenly become disoriented [48]. Mental imagery might be a promising tool to train astronauts prior to spaceflight to consistently assign frames of reference and to prevent motion sickness. On the ground, it has been shown that reference frames can be cognitively modulated by using imagery [39,41,42] and small effects of cognitive training against the adverse effects induced by an artificial gravity environment have been observed [40,45]. Moreover, motor tasks that are known to degrade in 0 g might benefit from motor imagery training during spaceflight. For example, crucial tasks, such as extravehicular activities are extensively trained on Earth but changes in motor performance due to the absence of gravity cannot be fully simulated beforehand. Thus, a step-by-step mental rehearsal of the planned task in 0 g might accurately prepare the astronaut for the task. The use of motor imagery training and its efficiency has been demonstrated successfully in sports psychology and rehabilitation training [15].

Cognitive functions other than mental imagery have also been tested in microgravity such as mathematical and grammatical reasoning, (spatial) memory, attention, time perception and dual-task performance. In most cases performance in cognitive tasks was not, or only slightly, impaired during exposure to microgravity with the exception of dual-tasks (for a review see [5, 10,18,38]). Only studies performed in or after exposure to microgravity were discussed in this review, and we did not include any ground-based simulation studies such as bed-rest studies. A common limitation of space studies, as well as parabolic flight studies, is the small sample size. But these methods also have different strengths and weaknesses. Space studies allow (so far) only the investigation of astronauts, a particular sample size of mostly male, highly trained and motivated persons, what makes it difficult to generalize results. Moreover, within-subject tests have to be measured before and after space missions. This makes it difficult to control for several factors such as learning effects, workload, intake of medication, and other psychological and physiological factors. The clear advantage of space studies is their duration, allowing for testing complex and time consuming experiments and to assess long-term adaptation effects. Parabolic flights have the advantage that testing can be completed during one flight (0 g and 1 g), on the same day with roughly the same mental state (e.g., fatigue, medication). The downside of parabolic flight is that the free fall phase is limited to about 20 seconds per parabola, thus limiting the length and complexity of the experiment. Because space missions differ in several aspects from parabolic flights, one-to-one comparisons of experimental results of human cognitive performance should be made with care. Yet, testing the same tasks in both conditions allows for balancing their inherent disadvantages.

How can vestibular influences be separated from physiological and/or psychological influences? Often, it remains unclear whether altered vestibular information or other physiological factors such as increased volume of fluids in the upper body, or psychological influences (e.g., stress, high workload) account for the changes in performance. For example, recent studies by Schneider and colleagues [54–56] emphasize that effects found in microgravity are rather due to secondary psychological effects, especially stress, than primary physiological effects. Interestingly, however, a non-specific stress factor such as anxiety may not be totally independent from the influence of altered vestibular input. On Earth, several studies have linked vestibular processing to anxiety, especially in persons suffering from panic attacks, acrophobia and agoraphobia (e.g. [4,20,21]). Neuroanatomical correlates of anxiety and vestibular processing are associated with a network of the parabrachial nucleus [1] and/or the insular cortex [47]. Ground-based complimentary research (e.g., body tilt and/or patients studies) can help to better investigate the causal links between vestibular processing and anxiety. Initial findings demonstrate, however, that altered vestibular input can have consequences, which go far beyond what was commonly believed to be the impact of vestibular information.

Most findings reported in this article are based on behavioral measures such as response times. As much as behavioral measures have helped to establish valuable insights into human cognitive functioning in 0 g, the advent of cognitive neuroscience has brought along a new inventory of powerful and novel research techniques, especially in the domain of neuroimaging. So far, space or parabolic flight studies could not exploit the progress. Safety, weight and space restrictions make it difficult to use otherwise well established techniques like fMRI, PET, or MEG. Yet, some of these techniques are promising and feasible tools for further investigation of cognitive-vestibular interactions in microgravity. For instance, TMS has been used to study motor performance in 0 g [11] but could also be used to study higher cognitive processes in 0 g. The studies by Schneider and colleagues [54,56] are also interesting in this light to promote future research using EEG in microgravity. So far, only few studies have measured electrical cortical activity in microgravity [6,17, 52,54,56] but were successful in data collection. Moreover, clinical studies (patient studies) during parabolic flight [37] could help to gain valuable insights into underlying (neural) processes, but also to promote medical innovation on Earth [46]. Future research will be needed to promote the use of these techniques in microgravity. But their use will help to gain further insights into cognitive functioning in different g levels and to complement the results of growing behavioral studies.

Acknowledgements

We would like to thank Caroline Falconer and two anonymous reviewers for helpful suggestions on the manuscript. This article was funded by a Sinergia grant from the Swiss National Science Foundation.

References

[1] C.D. Balaban and J.F. Thayer, Neurological bases for balance-anxiety links, *J Anxiety Disord* **15** (2001), 53–79.
[2] O. Bock, Problems of sensorimotor coordination in weightlessness, *Brain Res Rev* **28** (1998), 155–160.
[3] O. Bock, B. Fowler, D. Comfort and S. Jüngling, Visual-motor coordination during spaceflight, in: *The Neurolab Spacelab Mission: Neuroscience Research in Space*, (Vol NASA SP-2003-535), J.C. Buckey and J.L. Homick, eds, NASA, Houston, TX, 2003, pp. 83–89.

[4] C.C. Boffino, C.S. de Sá, C. Gorenstein, R.G. Brown, L.F. Basile and R.T. Ramos, Fear of heights: cognitive performance and postural control, *Eur Arch Psychiatry Clin Neurosci* **259** (2009), 114–119.

[5] J.G. Casler and J.R. Cook, Cognitive performance in space and analogous environments, *Int J Cogn Ergon* **3** (1999), 351–372.

[6] G. Cheron, A. Leroy, C. De Saedeleer, A. Bengoetxea, M. Lipshits, A. Cebolla, L. Servais, B. Dan, A. Berthoz and J. McIntyre, Effect of gravity on human spontaneous 10-Hz electroencephalographic oscillations during the arrest reaction, *Brain Res* **1121** (2006), 104–116.

[7] G. Clement, A. Berthoz and F. Lestienne, Adaptive changes in perception of body orientation and mental image rotation in microgravity, *Aviat Space Environ Med* **58** (1987), A159–A163.

[8] G. Clement and A. Bukley, Mach's square-or-diamond phenomenon in microgravity during parabolic flight, *Neurosci Lett* **447** (2008), 179–182.

[9] G. Clement, C. Lathan, A. Lockerd and A. Bukley, Mental representation of spatial cues in microgravity: Writing and drawing tests, *Acta Astronaut* **64** (2009), 678–681.

[10] G. Clément and M.F. Reschke, *Neuroscience in Space*, Springer, New York, 2008.

[11] N.J. Davey, S.R. Rawlinson, A.V. Nowicky, A.H. McGregor, K. Dubois, P.H. Strutton and R.C. Schroter, Human corticospinal excitability in microgravity and hypergravity during parabolic flight, *Aviat Space Environ Med* **75** (2004), 359–363.

[12] S. de Schonen, G. Leone and M. Lipshits, The face inversion effect in microgravity: is gravity used as a spatial reference for complex object recognition? *Acta Astronaut* **42** (1998), 287–301.

[13] J. Decety, The neurophysiological basis of motor imagery, *Behav Brain Res* **77** (1996), 45–52.

[14] J. Decety, M. Jeannerod and C. Prablanc, The timing of mentally represented actions, *Behav Brain Res* **34** (1989), 35–42.

[15] R. Dickstein and J.E. Deutsch, Motor imagery in physical therapist practice, *Phys Ther* **87** (2007), 942–953.

[16] D.R. Eddy, S.G. Schiflett, R.E. Schlegel and R.L. Shehab, Cognitive performance aboard the life and microgravity spacelab, *Acta Astronaut* **43** (1998), 193–210.

[17] A.R. Elliott, S.A. Shea, D.J. Dijk, J.K. Wyatt, E. Riel, D.F. Neri, C.A. Czeisler, J.B. West and G.K. Prisk, Microgravity reduces sleep-disordered breathing in humans, *Am J Respir Crit Care Med* **164** (2001), 478–485.

[18] B. Fowler, D. Comfort and O. Bock, A review of cognitive and perceptual-motor performance in space, *Aviat Space Environ Med* **71** (2000), A66–A68.

[19] A.D. Friederici and W.J. Levelt, Spatial reference in weightlessness: perceptual factors and mental representations, *Percept Psychophys* **47** (1990), 253–266.

[20] J.M. Furman, R.G. Jacob and M.S. Redfern, Clinical evidence that the vestibular system participates in autonomic control, *J Vestib Res* **8** (1998), 27–34.

[21] J.M. Furman, M.S. Redfern and R.G. Jacob, Vestibulo-ocular function in anxiety disorders, *J Vestib Res* **16** (2006), 209–215.

[22] G. Ganis, W.L. Thompson, F. Mast and S.M. Kosslyn, The brain's mind's images: the cognitive neuroscience of mental imagery, in: *The Cognitive Neurosciences III*, M.S. Gazzaniga, ed., MIT Press, Cambridge, MA, 2004, pp. 931–941.

[23] S. Glasauer and H. Mittelstaedt, Perception of spatial orientation in different g-levels, *J Gravit Physiol* **4** (1997), P5–P8.

[24] L. Grabherr, F. Karmali, S. Bach, K. Indermaur, S. Metzler and F.W. Mast, Mental own-body and body-part transformations in microgravity, *J Vestib Res* **17** (2007), 279–287.

[25] V.S. Gurfinkel, F. Lestienne, S. Levik Yu, K.E. Popov and L. Lefort, Egocentric references and human spatial orientation in microgravity. II. Body-centred coordinates in the task of drawing ellipses with prescribed orientation, *Exp Brain Res* **95** (1993), 343–348.

[26] D.A. Hanes and G. McCollum, Cognitive-vestibular interactions: a review of patient difficulties and possible mechanisms, *J Vestib Res* **16** (2006), 75–91.

[27] H. Heuer, D. Manzey, B. Lorenz and J. Sangals, Impairments of manual tracking performance during spaceflight are associated with specific effects of microgravity on visuomotor transformations, *Ergonomics* **46** (2003), 920–934.

[28] M. Jeannerod and V. Frak, Mental imaging of motor activity in humans, *Curr Opin Neurobiol* **9** (1999), 735–739.

[29] N. Kanas, G. Sandal, J.E. Boyd, V.I. Gushin, D. Manzey, R. North, G.R. Leon, P. Suedfeld, S. Bishop, E.R. Fiedler, N. Inoue, B. Johannes, D.J. Kealey, N. Kraft, I. Matsuzaki, D. Musson, L.A. Palinkas, V.P. Salnitskiy, W. Sipes, J. Stuster and J. Wang, Psychology and culture during long-duration space missions, *Acta Astronaut* **65** (2009), 659–677.

[30] F. Karmali and M. Shelhamer, The dynamics of parabolic flight: Flight characteristics and passenger percepts, *Acta Astronautica* **63** (2008), 594–602.

[31] S.M. Kosslyn, G. Ganis and W.L. Thompson, Neural foundations of imagery, *Nat Rev Neurosci* **2** (2001), 635–642.

[32] J.R. Lackner and P. DiZio, Human orientation and movement control in weightless and artificial gravity environments, *Exp Brain Res* **130** (2000), 2–26.

[33] C. Lathan, Z. Wang and G. Clement, Changes in the vertical size of a three-dimensional object drawn in weightlessness by astronauts, *Neurosci Lett* **295** (2000), 37–40.

[34] G. Leone, The effect of gravity on human recognition of disoriented objects, *Brain Res Rev* **28** (1998), 203–214.

[35] G. Leone, M. Lipshits, V. Gurfinkel and A. Berthoz, Influence of graviceptives cues at different level of visual information processing: the effect of prolonged weightlessness, *Acta Astronaut* **36** (1995), 743–751.

[36] G. Leone, M. Lipshits, V. Gurfinkel and A. Berthoz, Is there an effect of weightlessness on mental rotation of three-dimensional objects? *Cogn Brain Res* **2** (1995), 255–267.

[37] I. Mackenzie, E. Viirre, J.M. Vanderploeg and E.R. Chilvers, Zero G in a patient with advanced amyotrophic lateral sclerosis, *Lancet* **370** (2007), 566.

[38] D. Manzey and B. Lorenz, Mental performance during short-term and long-term spaceflight, *Brain Res Rev* **28** (1998), 215–221.

[39] F. Mast, S.M. Kosslyn and A. Berthoz, Visual mental imagery interferes with allocentric orientation judgements, *Neuroreport* **10** (1999), 3549–3553.

[40] F.W. Mast, L. Bamert and N. Newby, Mind over Matter? Imagined body movements and their neuronal correlates, in: *Spatial Processing in Navigation, Imagery and Perception*, F.W. Mast and L. Jäncke, eds, Springer, 2007, pp. 353–368.

[41] F.W. Mast, A. Berthoz and S.M. Kosslyn, Mental imagery of visual motion modifies the perception of roll-vection stimulation, *Perception* **30** (2001), 945–957.

[42] F.W. Mast and C.M. Oman, Top-down processing and visual reorientation illusions in a virtual reality environment, *Swiss Journal of Psychology* **63** (2004), 143–149.

[43] Y. Matsakis, M. Lipshits, V. Gurfinkel and A. Berthoz, Effects of prolonged weightlessness on mental rotation of three-dimensional objects, *Exp Brain Res* **94** (1993), 152–162.

[44] J. McIntyre, M. Zago, A. Berthoz and F. Lacquaniti, Does the brain model Newton's laws? *Nat Neurosci* **4** (2001), 693–694.

[45] P. Meliga, H. Hecht, L.R. Young and F.W. Mast, Artificial gravity–head movements during short-radius centrifugation: influence of cognitive effects, *Acta Astronaut* **56** (2005), 859–866.

[46] A.J. Mortimer, M.E. DeBakey, R. Gerzer, R. Hansen, J. Sutton and S.N. Neiman, Life science research in space brings health on Earth, *Acta Astronaut* **54** (2004), 805–812.

[47] M. Nagai, K. Kishi and S. Kato, Insular cortex and neuropsychiatric disorders: a review of recent literature, *Eur Psychiatry* **22** (2007), 387–394.

[48] C.M. Oman, Spatial orientation and navigation in microgravity, in: *Spatial Processing in Navigation, Imagery and Perception*, F.W. Mast and L. Jäncke, eds, Springer, 2007, pp. 369–387.

[49] C.M. Oman, I.P. Howard, T. Smith, A.C. Beall, A. Natapoff, J.E. Zacher and H.L. Jenkin, The role of visual cues in microgravity spatial orientation, in: *The Neurolab Spacelab Mission: Neuroscience Research in Space*, (Vol NASA SP-2003-535), J.C. Buckey and J.L. Homick, eds, NASA, Houston, TX, 2003, pp. 69–81.

[50] C. Papaxanthis, T. Pozzo, R. Kasprinski and A. Berthoz, Comparison of actual and imagined execution of whole-body movements after a long exposure to microgravity, *Neurosci Lett* **339** (2003), 41–44.

[51] C. Papaxanthis, M. Schieppati, R. Gentili and T. Pozzo, Imagined and actual arm movements have similar durations when performed under different conditions of direction and mass, *Exp Brain Res* **143** (2002), 447–452.

[52] V. Pletser and O. Quadens, Degraded EEG response of the human brain in function of gravity levels by the method of chaotic attractor, *Acta Astronaut* **52** (2003), 581–589.

[53] J. Sangals, H. Heuer, D. Manzey and B. Lorenz, Changed visuomotor transformations during and after prolonged microgravity, *Exp Brain Res* **129** (1999), 378–390.

[54] S. Schneider, V. Brummer, H. Carnahan, A. Dubrowski, C.D. Askew and H.K. Struder, What happens to the brain in weightlessness? A first approach by EEG tomography, *Neuroimage* **42** (2008), 1316–1323.

[55] S. Schneider, V. Brummer, S. Gobel, H. Carnahan, A. Dubrowski and H.K. Struder, Parabolic flight experience is related to increased release of stress hormones, *Eur J Appl Physiol* **100** (2007), 301–308.

[56] S. Schneider, V. Brummer, A. Mierau, H. Carnahan, A. Dubrowski and H.K. Struder, Increased brain cortical activity during parabolic flights has no influence on a motor tracking task, *Exp Brain Res* **185** (2008), 571–579.

[57] R.N. Shepard and J. Metzler, Mental rotation of three-dimensional objects, *Science* **171** (1971), 701–703.

[58] P.F. Smith, Y. Zheng, A. Horii and C.L. Darlington, Does vestibular damage cause cognitive dysfunction in humans? *J Vestib Res* **15** (2005), 1–9.

[59] E.M. Tartaglia, L. Bamert, F.W. Mast and M.H. Herzog, Human Perceptual Learning by Mental Imagery, *Curr Biol* (2009).

[60] E. Villard, F.T. Garcia-Moreno, N. Peter and G. Clement, Geometric visual illusions in microgravity during parabolic flight, *Neuroreport* **16** (2005), 1395–1398.

[61] J. Wagner, T. Stephan, R. Kalla, H. Bruckmann, M. Strupp, T. Brandt and K. Jahn, Mind the bend: cerebral activations associated with mental imagery of walking along a curved path, *Exp Brain Res* **191** (2008), 247–255.

[62] M. Wexler, S.M. Kosslyn and A. Berthoz, Motor processes in mental rotation, *Cognition* **68** (1998), 77–94.

[63] L.R. Young, C.M. Oman, D. Merfeld, D. Watt, S. Roy, C. DeLuca, D. Balkwill, J. Christie, N. Groleau, D.K. Jackson and et al., Spatial orientation and posture during and following weightlessness: human experiments on Spacelab Life Sciences 1, *J Vestib Res* **3** (1993), 231–239.

[64] L.R. Young, C.M. Oman, D.G. Watt, K.E. Money, B.K. Lichtenberg, R.V. Kenyon and A.P. Arrott, M.I.T./Canadian vestibular experiments on the Spacelab-1 mission: 1. Sensory adaptation to weightlessness and readaptation to one-g: an overview, *Exp Brain Res* **64** (1986), 291–298.

[65] J.M. Zacks, Neuroimaging studies of mental rotation: a meta-analysis and review, *J Cogn Neurosci* **20** (2008), 1–19.

[66] J.M. Zacks, J.M. Ollinger, M.A. Sheridan and B. Tversky, A parametric study of mental spatial transformations of bodies, *Neuroimage* **16** (2002), 857–872.