Institute of Physiology and Anatomy German Sport University Cologne Head of Institute: Univ.-Prof. Dr. med. Otmar Bock

Effects of hypergravity on manual forces and displacements: causes and practical implications

Approved thesis submitted for the degree Doktor der Sportwissenschaften

by

Simon Guardiera from Troisdorf, Germany

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First referee: Second referee: Chair of the doctorate committee: Thesis defended on: Univ.-Prof. Dr. med. Otmar Bock PD Dr. Joachim Hermsdörfer Univ.-Prof. Dr. Ilse Hartmann-Tews Mai 19th, 2009

Affidavits following section 6 paragraph 2 No. 5 and 10 of the doctorate rules from the German Sport University Cologne, from September 29th 2004.

Hereby I declare: The work presented in this thesis is the original work of the author except where acknowledged in the text. This material has not been submitted either in whole or in part for a degree at this or any other institution. Those parts or single sentences, which have been taken verbatim from other sources, are identified as citations. I further declare that I complied with the actual "guidelines of qualified scientific work" of the German Sport University Cologne.

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Simon Guardiera

GENERAL COMMENTS

Due to my marriage in 2007 I changed my family name from Göbel to Guardiera. Therefore, the first manuscript used in this cumulative dissertation was published with my birth name, while the following manuscripts were published with my new name.

All publications used in this thesis were published in US-American Journals. To keep the work consistent throughout the whole text, the complete work was written in "American English".

Subjects in Studies 1-3 were exclusively male, since one of the major goals was to obtain results comparable to professional jet pilots of the German Air Force. In 2008 the first woman started to be a jet pilot flying the Tornado in Germany, with all colleagues being male. Therefore, it was not possible to investigate female professional jet pilots in the presented studies. I explicitly declare that our subject selection was only due to this scientific reason and was free of any discrimination against women.

When male and female subjects were tested, I limited the descriptions to the male form ("his") instead of specifying both genders ("his/ her"). I explicitly declare that this was done only for the sake of readability and was free of any discrimination against women.

ABBREVIATIONS

+Gz

In aviation physiology, +Gz is often used to indicate an acceleration in head-to-foot direction *higher* than normal earth's gravitational acceleration, sometimes also called **hypergravity**, **high-G**, **increased acceleration** or **sustained positive acceleration**.

Strictly speaking, +Gx, +Gy, +Gz present the direction of acceleration with respect to human's body. According to subject's body axis the letters x, y and z (sagittal, transversal and longitudinal) indicate the according axis, while the prefixed algebraic sign additionally indicates the direction along these axes. Thus, +Gx is an acceleration from chest-to-back, +Gy from left-to-right, and +Gz from head-to-foot. Negative accelerations are accordingly directed in the opposite directions. However, in accordance to the literature on aviation physiology this thesis uses +Gz exclusively as indicated above.

+1 Gz Normal earth's gravitational acceleration in head-to-foot direction.
For the sake of clearance and readability, the abbreviation "G" is used for the physical unit "g". Synonyms are 1 Gz or normal-G.

- +3 Gz Three times normal terrestrial gravitational acceleration in head-to-foot direction. In this situation the weight of every object is three times as high as under normal terrestrial condition. Occasionally, also 3 Gz is used as an abbreviation for three times terrestrial gravity.
- ACTH Adrenocorticotrope Hormone tropic hormone secreted by the hypophysis.
- **bpm** beats per minute physical unit for the heart rate.

DTC relative Dual Task Costs – calculation to quantify a dual task performance (i.e. two tasks at the same time) with respect to one of the single tasks. DTC are calculated as the difference of dual (D) and single (S) task performance, divided by the single task performance (DTC = (D-S) / S). For a detailed description see (51).

kn knots – physical unit of speed used in aviation (1 kn ~ 1.85 km/h).
 LBNP Lower Body Negative Pressure – a device to counteract astronauts' cardiovascular deconditioning. For further information see (42).

N Newton – physical unit of force. 1 N corresponds to the weight force of about 100 g on earth, i.e. a regular bar of chocolate.

RMSE Root Mean Square Error – calculation to quantify the (signadjusted) mean distance between two data series. In the 2dimensional case (i.e. x- and y-coordinates) presented in this thesis the RMSE is given by:

$$RMSE = \sqrt{\frac{\sum_{i=1}^{k} (\Delta X_i)^2 + \sum_{i=1}^{k} (\Delta Y_i)^2}{k}}$$

 ΔX_i and ΔY_i present the horizontal and vertical distances between both data series, while k presents the number of analyzed data points.

SWAT Subjective Workload Assessment Technique – psychological questionnaire to evaluate subjects' workload and stress. For further information see (77).

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1. INTRODUCTION AND OUTLINE

1.1 General introduction

Since the beginning of mankind, one of the major physical constants is the earth's gravitational acceleration. Every object on earth is pulled with 9.81 m/s² towards the earth's center of mass, called normal gravitational acceleration or +1 Gz. During their evolution, humans have adapted to this physical constant and almost every process, e.g. cardiovascular mechanisms or any human movement is adjusted to this terrestrial acceleration. Especially in the field of sports, humans are exposed to various accelerations beyond the normal gravity situation, e.g. during rotations on the high bar, while jumping on the trampoline or in motor sports like car racing. Due to the technical progress in transport facilities as cars or planes, such situations do occur more frequently even in every day life, e.g. during takeoff of planes or on a rollercoaster ride. Higher accelerations affect humans involved in space rocket takeoff or turns with modern high-speed jets, as can be seen in the following example: when a pilot of an F-16, a classical jet of the US Air Force, flies a turn with a 1000 m radius and a common speed of 350 kn, i.e. about 650 km/h, the pilot is exposed to about three times terrestrial gravitational acceleration (+3 Gz), thus, the pilot's weight is three times as high as under normal conditions. As one can imagine, such situations of increased terrestrial gravitational acceleration, called hypergravity or +Gz, can be very exhausting for the human body as several physiological changes, like a blood shift towards lower body parts, an increase in heart rate and blood pressure, or changes in the pulmonary gas exchange are observed (41). Also the pilot's motor control is massively challenged by phases of +Gz, e.g. when pushing a button or manually controlling the high performance jet plane. An accurate execution of these motor tasks is very important, as faulty or imprecise aircraft operation might impair the flight effectiveness or even the pilot's safety. In fact, most air disasters can be attributed to insufficient motor control of pilots (90), thus, the investigation of motor performance during phases of +Gz is particularly relevant. Additionally, such research is also interesting in the field of basic science, as an understanding of changes in motor performance in these extreme environments might also enhance the knowledge of basic principles of motor control under the normal gravitational condition on earth (e.g. in terms of dependence on gravity or adaptation processes).

Therefore, this thesis investigates selected questions of scientific interest in the field of motor performance in +Gz in order to enhance the current knowledge of applied as well as basic research topics in this field.

1.2 Human centrifuges

Scientific research on +Gz-related changes in motor performance is almost exclusively conducted in human centrifuges, which are also used as a training facility for pilots and astronauts. When compared to real jet flights, human centrifuges offer the advantage of a cost-limited, standardized and reproducible +Gz-stimulus. As an example, Fig. 1 shows the human centrifuge of the German Aerospace Center (DLR) in Cologne, Germany, which was used in the centrifuge studies presented in this thesis. The cabin of such a centrifuge is able to swing out during rotation so that centrifugal-, and earth's acceleration sum up to a resultant acceleration, which is directed vertically to the gondola's floor. Thus, a sitting subject experiences +Gz, since the acceleration is in line with his long body axis, and the magnitude of the acceleration is larger than +1 Gz. Depending on the arm length and the speed of the centrifuge, the acceleration can be modulated between +1 Gz (standing centrifuge) and, in the case of the DLR centrifuge, +10 Gz. In order to produce +3 Gz, as conducted in the experiments described in the present thesis, the cabin speed of this 5 m radius centrifuge needs to be about 42 km/h (35).

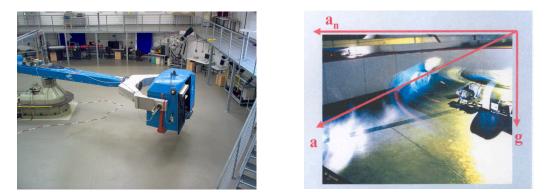


Fig. 1. Human centrifuge at the German Aerospace Center (DLR) in Cologne, Germany. The cabin of this 5 m radius centrifuge swings out during rotation so that the resultant (a) of earth's gravitational acceleration (g) and centrifugal acceleration (a_n) is in line with the long body axis in sitting subjects (+Gz acceleration). (Source: private picture and DLR-brochure)

1.3 Motor performance deficits in +Gz

During the last decades several scientific studies have examined motor performance in +Gz, mainly focusing on tracking tasks, pointing, and - in the last ten years isometric force production. Especially among research groups with an aviation background the examination of +Gz-related tracking task deficits has been very popular. This popularity has been largely caused by the application of tracking tasks to aviation, and hence by the possibility to use such tasks as a training method for pilots. Two types of tracking are described in literature, one of which is known as compensatory tracking, i.e. maintaining a cursor in a fixed position despite external disturbances. This is quite similar to maintaining level flight in an aircraft and to pilot-manipulated missile targeting radar. The second one is pursuit tracking, i.e. tracking the movement of a given target, which can be compared to pursuing an opponent's airplane. The performance in both types of tracking is usually measured by the Root-Mean-Square-Error (RMSE), which basically presents the (signadjusted) mean distance between subject's response and the target. Compensatory (37) as well as pursuit tracking (21, 30, 31) are well known to be impaired by phases of +Gz. Deficits already became apparent at a relatively low acceleration of +2 Gz, and further increased with ascending +Gz-level (37). On the one hand these deficits were dependent on specific task parameters, since in pursuit tracking the +Gz-related deficits became more obvious, when target oscillations had a higher frequency (79), and on the other hand they were also dependent on acceleration procedures, as the tracking error was considerably elevated during the onset of elevation (31). The latter aspect was attributed to subjects' vertigo produced by angular acceleration of the centrifuge (8, 9). Therefore, most subsequent studies did not investigate motor performance unless the final centrifuge speed was reached, and additionally they waited several seconds to allow transient vestibular responses to subside. One major problem in the examination of these close to reality tracking tasks is to specify the impairment, i.e. the motor-sensory or cognitive ability affected by +Gz, because of the complexity of this task (28). Therefore, tracking tasks are particularly relevant for aviation selection processes and training, but do not deliver enough information for basic research.

Other scientists investigated pointing movements to offer an insight into +Gz-related changes of motor performance. In these studies subjects were asked to point at

visually presented targets without vision of their arm, in order to prevent corrections based on visual feedback during the movement. The majority of studies found that subjects exceeded the desired distance and pointed too far in +Gz (13, 14, 16, 26), even on a relatively low level of +1.8 Gz during parabolic flights (22). This increase in pointing amplitude was constant across the range of target amplitudes (13). Only a few studies evaluating pointing movements immediately after the onset of +Gz reported too short pointing (26, 87). As mentioned above, in this early part of +Gz-phases subject's vertigo may influence the results. Additionally, it is proposed that compared to the other studies this discrepancy results from differences in the movement speed: the latter studies (26, 87) required very high speeds, while most of the other studies (13, 14, 16) demanded only moderate speed, which might have allowed more corrections during the movements due to proprioceptive feedback (14).

Another group of studies dealt with the production of isometric forces in +Gz. This task offers the advantage that only minimal arm and hand movements are necessary, e.g. when squeezing the tissue while producing a force. Thus, mechanical aspects of +Gz affecting the movement are probably of minor influence. As in pointing movements, no visual feedback about success is provided to subjects, in order to prevent visually based online corrections. Results were not always consistent. Grip forces, i.e. isometric finger forces necessary to hold a moving object, were increased only in very early phases of +1.8 Gz, namely the first one or two +Gz phases of a parabolic flight lasting 18 s each. Thereafter, subjects almost perfectly matched their grip force to the changed weight, i.e. to the load force of an object in +Gz (6, 45). This is surprising, as considerable deficits were shown for the mass estimation of a moving object in +Gz (78). Bock and Cheung investigated isometric force production upon verbal instruction using the pinch grip, and showed that subjects produced substantially increased forces in +Gz. In contrast to the studies cited above, the +Gz-related force exaggeration did not show any decline over a duration of about $2 \min (15)$. This different outcome might be due to methodological differences: the measurement device in the first study was actively held and prevented from falling by the subject. Consequently, more proprioceptive cues were provided than through the fixed pinch grip device in the latter study (which presumably led to limited proprioception). Results of the pinch grip were confirmed and extended by subsequent studies using an isometric joystick, which was manipulated by the power

grip (40, 80). Subjects' task was to reproduce visually prescribed forces of different directions and magnitudes while exposed to +3 Gz for about 7 min. A noticeable exaggeration in peak forces, i.e. the highest produced force during each response, without any decline over time was observed. Since similar results were obtained for the pinch (15) and the power grip (40, 80), the +Gz-related force exaggeration is most likely to be independent of the grip type, at least when the measurement device is fixed (see above). As shown in Fig. 2, the +Gz-related force increase was visible in all directions, regardless whether the stick was mounted horizontally (80) or vertically (40). Thus, the effect is valid in all directions of three-dimensional space. The force overshoot increased with increasing +Gz-level for about 2 N in +1.5 Gz and about 10 N in +3 Gz, but was constant for different magnitudes presented, i.e. the overshoot of 10 N in +3 Gz applies to small and large magnitudes presented to the subjects (40).

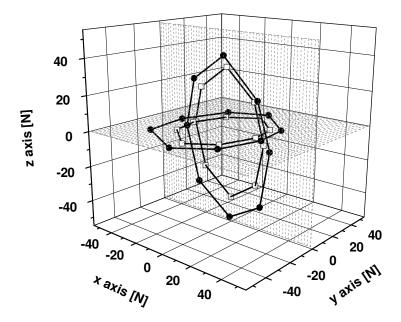


Fig. 2. Subjects' mean peak force production upon visually presented targets of different amplitudes and directions using an isometric joystick in the horizontal and the frontal plane (n = 12 each plane). Force production in +3 Gz (solid circles) was exaggerated in all directions of three-dimensional space when compared to the according +1 Gz data (open squares). (Source: (40))

The investigation of isometric force production in +Gz is of special interest for the working life of professional jet pilots, since many modern jet planes like the F-16 of the US Air Force are controlled by an isometric stick called force-field stick. These

pilots are frequently exposed to accelerations of +2 Gz and more during turns or loops and still have to be able to control their jet plane accurately (73). The observed force exaggeration in +Gz described above could impair the desired flight path, probably forcing pilots to conduct corrections requiring additional attention, which might in turn enhance their workload and stress. Such effects could compromise the success of pilots' flight missions or even lead to a potential safety problem. Consequently, the detailed investigation of isometric forces in +Gz seems to be particularly relevant. It remains questionable e.g. whether a prolonged task practice might reduce this effect, or whether +Gz-experienced pilots show the same force exaggeration. Nevertheless, scientific studies examining effects of +Gz on isometric force production – apart from the studies mentioned above – are rare. Therefore, one major goal of this thesis was the continuous investigation of isometric force production in +Gz. Additionally, other topics related to flight operations like the comparison of isometric and displacement sticks are evaluated (see 1.5).

1.4 Causes for +Gz-related deficits in motor performance

The preceding paragraph revealed that motor performance is massively degraded in phases of +Gz, but the various attempts to explain the observed deficits have been left unnamed so far. Obviously, the presented studies cover a broad spectrum of different tasks, with several methodological differences and various specific circumstances that influence each presented result. It is therefore not possible (and not desirable) to reassess the explanatory statement of each of these studies in detail. Instead, the present thesis mainly focuses on the production of isometric forces for two reasons, one of which is the relevance of isometric force production for jet pilots already stated above. The second one is the fact that detailed research on the origin of +Gz-related deficits is most promising in this task, since the mechanical impact of +Gz is of minor relevance only in the isometric force production. Thus, it seems worth reviewing the major explanatory statements provided in literature for their relevance for this specific task. Improved comprehension of the causes for the observed force exaggeration might in turn be valuable for other types of motor performance, as it is also possible that identified mechanisms can – at least partly – also explain deficits in other motor tasks, as proposed by various authors (15, 40). This seems reasonable because of the similarity of the presented findings, e.g. the increased isometric force production corresponds to the increased pointing amplitude

in +Gz, and both tasks similarly showed a constant impairment at different target amplitudes (see 1.3). The following causes might be responsible for the observed isometric force exaggeration in +Gz as proposed in literature.

a) Mechanical aspects (14, 26, 40)

It is well established that learning a motor task, e.g. pointing, results in the creation of motor programs, which can be recalled and adjusted when needed (81). In +Gz, such motor programs have to be adjusted to the new force environment. An inadequate use of unadjusted or misadjusted motor programs would therefore - at least in the first few movements in +Gz – result in changes in motor performance, e.g. an upward pointing movement would be deviated downwards due to the extra mechanical load (the so called "muscle-loading effect" (87)). However, except for one group (26, 87), all other studies described too high instead of too low pointing (13, 14, 16, 22, 26). One could argue that downward deviations are overcompensated with proceeding responses due to proprioceptive information, but Bock et al. did not find any support for this view in their very detailed analysis of movement kinematics (13). A transfer of this argument on isometric force production is not valid, since only minimal movements are necessary during the production of isometric forces, and consequently no adjustment of motor programs to changed gravitational acceleration is required (40). Moreover, force exaggeration was observed in all directions of three-dimensional space. Thus, the effect seems to be independent with respect to the G-vector, which is inconsistent to the argument above. Therefore, mechanical aspects of +Gz do not seem to be responsible for the observed force exaggeration in +Gz. (40).

b) Disturbed vision (8, 27, 41, 74, 88)

It was frequently described that luminous visual objects appear to be elevated above their true physical position in +Gz (27, 74, 82, 88). This effect, called "elevator illusion", is attributed to changes in oculomotor control caused by the increased stimulation of the otolith organs in +Gz. If subjects misperceive a target position as being too high with respect to their body position, an overshooting response for upwardly directed pointing would be the result, as in fact confirmed by many studies (13, 14, 16, 22, 26). Additionally, +Gz is known to result in diffuse vision or lack of colors due to blood pooling in the lower extremities and reduced oxygenated blood

flow in the head (41). Such degraded vision could massively impair motor performance, e.g. in tracking tasks, when a clear vision is necessary to observe the target. However, especially at lower +Gz-levels the cardiovascular system is able to compensate for such effects, as first restrictions in sitting subjects occur at about +4.1 +/- 0.7 Gz (mean +/- standard deviation) (41). Investigation of isometric forces was conducted at +3 Gz, thus, below this threshold. Moreover, force exaggeration in +Gz was observed upon verbal instructions without any visual component at all (15), as well as in tasks, when subjects only reproduced targets representing either a small, medium or large force. In this latter case the precise position had no relevance (40, 80). In consequence, both, the elevator illusion and a diffuse vision, do not seem to be the origin for the observed force exaggeration in +Gz.

c) Proprioceptive deficits (16, 19, 32, 57)

It is assumed that +Gz is likely to increase the activity of muscle stretch receptors in antigravity muscles and to reduce this activity in their antagonists, thus, perceived arm position could be underestimated (57). Consequently, a pointing too high would be the result, as indeed found in many studies (13, 14, 16, 22, 26). This hypothesis is not fully convincing, as Bock et al. found changes of velocity profiles with proceeding responses in their detailed analysis of movement kinematics during pointing movements, which could not be explained by proprioceptive deficits (13). Moreover, at least in phases of simulated +Gz there was no incorrect localization of the arm reported for the passive position sense (11). It was also argued that the increase of force production in +Gz might be the consequence of deficient signals of mechanoreceptors in the skin (7). However, isometric forces are already increased 100 ms after response onset (40), when no proprioceptive feedback can be effective (23, 49). Thus, subjects' responses are impaired from the early onset, instead of being altered due to faulty proprioception during the response. Therefore, also proprioceptive deficits affecting the ongoing response are most likely not to be a cause for the observed force exaggeration in +Gz (40).

d) Reinterpretation hypothesis (13, 16)

Recent studies proposed that the increase in gravitational force is registered by proprioceptive signals and reinterpreted as increased arm weight. This seems conceivable since +Gz and increased arm weight (e.g. when wearing a heavy coat)

are mechanically equivalent as long as the arm remains stationary. When the arm is moved, however, the inertia is different in both situations. A reinterpretation of +Gzas increased arm weight would therefore result in an overestimation of arm's inertia, and hence in too large pointing movements (14, 16). Compared to the theories presented above, this seems to be most convincing. Therefore, the latest papers on this topic favored this hypothesis to explain the deficits in pointing (13, 14). This hypothesis might also hold for isometric forces (40, 80), since subjects might have issued stronger efferent commands in order to move the seemingly higher mass. This reinterpretation hypothesis has neither been found to be confirmed nor rejected as a possible cause for the observed force exaggeration in +Gz, so far. However, this argument seems very unlikely, as no movements are required for isometric force production.

e) Computational stress (12)

It is assumed that the unusual environment of +Gz causes a huge amount of sensory and emotional input, which needs to be computed centrally. Such cognitive processes are supplementary to the processes needed for the conduction of a motor task. Following the view of Kahneman, the resources of such sensory-motor processing are shareable, but limited (51, 72). If the computational demand of the motor task and the computational demand of the additional sensory input of +Gz together exceed these resources, performance in one or both computational processes deteriorates. As a consequence, observed deficits in motor performance, e.g. too high pointing, could be a sign of computational stress in the nervous system (12). In higher +Gz levels, i.e. more than +4 Gz, reduced cortical blood flow might degrade cognitive abilities even more (41), and - in terms of Kahneman's model - again reduce the total amount of cognitive resources, thus worsening the situation. Similar thoughts, although not substantiated by an according theory or scientific data, were discussed for deficits in tracking performance (28), and the argument might also apply for isometric force production in +Gz. However, well-founded experimental support is missing. An established method to test this hypothesis is the dual task approach combining the motor performance task as the primary task with a secondary task (e.g. another motor or cognitive task). Following the theory of Kahneman, this secondary task increases the computational demand. Hence, if the task is sufficiently demanding, performance in the primary and /or the secondary task

should deteriorate, since the limit of attentional resources is reached. Any additional computational stress, e.g. a third task or an unusual environment, should then result in a further decrease in performance. Thus, if +Gz represents an additional cognitive demand, dual task performance in +Gz should be more strongly impaired than dual task performance in +1 Gz, each of the dual tasks compared to the according single task performance. This can be quantified by relative dual task costs (DTC), calculated as the difference of dual (D) and single (S) task performance, divided by the single task performance (as a formula: DTC = (D-S) / S). Therefore, positive DTC present a dual task deficit, while negative DTC demonstrate a performance increase in the dual task condition. However, earlier studies using tracking tasks in combination with different motor performance and cognitive tasks (20, 28) solely used the performance of the primary task in +1 Gz as a comparison value for the dual task performance in +Gz, instead of the according dual task performance in +1 Gz. Therefore, in these studies it is not possible to differentiate between the computational stress induced by the secondary task, and the computational stress induced by the +Gz environment, so that reliable data to confirm or reject this view of computational stress are missing.

f) Vestibulo-spinal influences (40, 80)

The main sense in humans detecting acceleration is the vestibular organ located in the inner ear. The +Gz acceleration along subjects' long body axis causes a deflection of the hair cells in the saccule, one of the otolithic organs responsible for vertical linear acceleration in an upright human. This deflection results in an increased activity in afferent nervous pathways (vestibular nerve) ending in the vestibule nuclei, which are connected to various areas, e.g. the cerebellum (tractus vestibulocerebellaris) and the spinal cord (tractus vestibulo-spinalis). It has been proposed that the +Gz-related increase in the activity of descending vestibulo-spinal pathways (55) excites spinal motoneuron pools (70), and thus modifies central commands. Such modified central commands could be responsible for the observed increase in muscle tone during +Gz (55) and could well be a causal factor for the observed exaggeration of force: an increased muscular tone might modify the proprioceptive input to the Central Nervous System (CNS), which in turn might interact with descending voluntary motor commands. This argument would also explain the observed initial force increase 100 ms after response onset (40), since subjects responses would then be affected by modified central commands from their early onset on. One of the major problems with proving or rejecting this hypothesis at least in humans is the measurement of activity in these pathways or in the according motoneuron pools in the spinal cord. Studies in monkeys revealed an additional activity in vestibular nerves due to +Gz (36), however, additional activity does not necessarily entail changed motor commands or impaired motor performance, since e.g. such changes could be corrected through proprioception. Therefore, reliable experimental results supporting this view are missing. Because of the various other aspects influencing motor performance in +Gz (see above and below), an experimental setup exclusively activating vestibulo-spinal pathways without using +Gz would be desirable to verify whether vestibulo-spinal influences are a cause for the observed isometric force exaggeration.

g) Stress or arousal (2)

It is obvious that riding a centrifuge with a multiple of normal earth's gravitational acceleration is a stressful situation to inexperienced subjects. Indeed, previous studies described psycho-physiological changes attributable to stress. Some scientists investigated stress hormone concentrations in subjects' blood directly after acceleration to +Gz, and found an increase in the concentration of catecholamines (69) as well as cortisol, which is one of the most popular stress hormones (68, 76). Both, catecholamines and cortisol are excreted by the adrenal gland. The authors attribute these increases to larger emotional stress and strenuous physical activities in +Gz. Other studies used electroencephalogram (EEG) to measure changes in cortical activity attributable to the stressful environment of +Gz. Consistently, these studies described an increase in theta band activity (i.e. EEG oscillations with a frequency between 4 and 7 Hz) in phases of +Gz, which is typically associated with emotional arousal and high level of alertness (1, 10). Psychological results on effects of +Gz obtained by questionnaires are rare. Albery and colleagues used the Subjective Workload Assessment Technique (SWAT) and reported that subjective workload increased in +Gz (2, 21). However, this technique does not differentiate between mental and physical workload, hence, conclusions on +Gz as a stressful environment must be drawn carefully. To sum up, there seems to be scientific evidence (although not in all cases convincing as shown for psychological parameters) that +Gz is indeed a stressful environment, but studies combining several stress measurements in

the same subjects, e.g. endocrinological and psychological methods, are missing. Furthermore, the influence of this stressful environment on motor performance remains unclear, since the studies mentioned above investigated psychophysiological parameters or motor performance, but not both. To my knowledge, only one study combined the investigation of motor performance and psychophysiological parameters: Albery has shown that tracking performance deteriorates in +3.75 Gz, while SWAT scores, heart rate and total eye blinks increased (2). However, since the increase in heart rate and total eye blinks could also be due to the physiological changes evoked by +Gz (41), and the increase in SWAT scores could not be exclusively related to a higher level of mental stress or arousal, but rather to the physical workload (see above), this study does not provide convincing evidence for a correlation between an increased level of stress and deficits in motor performance. Nevertheless, a relation between +Gz as a stressful environment on the one hand, and a deterioration of motor performance on the other hand seems well imaginable, since similar correlations are described for other stressful situations like the elevation to weightlessness during spaceflight (59, 60, 62, 63). Despite these theoretical arguments, valuable studies in +Gz are missing, and to date stress can neither be assumed nor dismissed as a relevant factor on +Gz-related changes in motor performance in general, or in isometric force production in particular.

h) Physical activation (41)

As already mentioned above, +Gz results in several cardiovascular responses like a blood shift towards the lower extremities, an increase in blood pressure or an increase in heart rate (41). However, less is known about the impact of such +Gz-induced cardiovascular activation on the execution of fine motor tasks. In sports science, a few studies investigated subjects' performance during or after physical exercise, which has at least some similar cardiovascular consequences like +Gz (e.g. the increase in heart rate and blood pressure). Several studies reported a facilitation of *cognitive* performance after moderate and short exercise, e.g. in simple and choice reaction time (18, 25, 33, 71), visual discrimination (3, 65) or decision making (66, 85). In contrast, *motor* performance in complex tasks typical for sports (38, 43, 50) was found to be impaired after exercise, whereas corresponding data on simple motor tasks are still rare. It seems arguable that these tasks are impaired by physical exercise, since previous work using transcranial magnetic stimulation (TMS) found

an initial facilitation followed by a depression of motor evoked potentials (MEP) immediately after moderate exercise (17, 39). Although cardiovascular activity during physical exercise is not completely comparable to +Gz induced changes, these results support the assumption that the physical activation induced by +Gz might indeed affect isometric force production in +Gz. But further research is needed to support this view.

To sum up, several arguments supposed to explain the observed +Gz-related changes in motor performance were proposed in the last decades. As presented, some of these arguments do probably not have the ability to explain the force exaggeration in +Gz (a-d), while others might in fact be a potential cause for the increase in isometric forces in +Gz (e-h). Therefore, a second major goal of this thesis is to further scrutinize these latter possibilities, and hence to increase the knowledge on the mechanisms responsible for the exaggerated isometric force production in +Gz (see 1.5).

1.5 Research objective

The preceding paragraphs 1.3 and 1.4 provided a review of changes in motor performance in +Gz and of possible explanations for these effects with a focus on isometric force production. As already mentioned above, this thesis deals with two mayor goals: first, the investigation of research questions on motor performance related to flight operations, and second, the investigation of research questions on possible causes for +Gz-induced deficits in motor performance. Divided into these two categories the following scientific questions were the basis for seven manuscripts forming the present thesis.

Research questions on motor performance related to flight operations

The investigation of isometric force production in +Gz is of special interest for professional jet pilots, since the observed force exaggeration might affect the pilot's effectiveness or even safety. However, several relevant questions are still unclear in the context of isometric force production in +Gz. It might be arguable that the observed force exaggeration is of minor relevance, since pilots are exposed to phases of +Gz several times during each flight, and might therefore adapt their motor performance to the +Gz environment quickly and effectively. Such motor adaptation

is well known for other external force fields (56, 75, 84) and might therefore be reasonable for the +Gz environment, too. Moreover, it is still questionable, if a training conducted in +1 Gz might also have enhancing effects on force exaggeration, as it is assumed for the +Gz training. Since pilots constantly perform simulated aircraft control in ground-based flight simulators (i.e. +1 Gz), this might be of high significance for pilots' training schedules. From a scientific view it seems conceivable that such training could at least improve the utilization of feedback processes. Therefore, the present thesis investigates whether the observed force exaggeration in +Gz is affected by a training period performed in +Gz, and a training period performed in +1 Gz, respectively.

To date, studies evaluating isometric force production in +Gz have used +Gzinexperienced subjects who had never been involved in a centrifuge study or a jet flight before (15, 40, 45, 80). Therefore, it remains open whether +Gz-experienced jet pilots show similar effects. As these pilots are routinely exposed to +Gz during several flights per week, they might have adapted to these circumstances and therefore might not show the same force exaggeration as observed in non-pilot subjects. Such a long-term adaptation seems plausible since similar processes have been observed for other physiological parameters such as blood pressure (29), muscle activity measured by electromyography (EMG) (46, 47, 48), and mental performance (61) before. The assumption of such effects would be further supported by work of Augurelle et al. (6), who found that grip forces produced in +Gz during parabolic flights were only impaired in +Gz-inexperienced subjects. Hence, the present work investigates whether professional jet pilots produce exaggerated isometric forces in +Gz as well.

Many high-performance aircrafts are equipped with regular (displacement) control sticks (e.g. the Eurofighter), rather than using isometric sticks. A further purpose of this thesis was to determine whether hand displacements are affected in a similar way like force production. Such a comparison between displacement and isometric sticks could be helpful to determine, which type of stick might be more appropriate for the operation of high-performance aircrafts. +Gz-related changes in displacement movements with a joystick seem conceivable due to the similarity to pointing movements, which showed a strong impairment in +Gz, as described above (13, 14,

16, 26). However, small displacements conducted with a joystick might also be differently affected by +Gz when compared to large pointing movements, since e.g. different forces are required and other, smaller muscle groups are involved.

Changing conditions of e.g. weather or wind during jet flights might force pilots to adapt their motor performance to new and unknown circumstances. If this so called motor learning¹ is slow or ineffective during phases of +Gz, pilots' ability to control the aircraft sufficiently might be compromised, which in turn might affect the mission's effectiveness or even the pilots' safety. To my knowledge, motor learning processes in +Gz have never been investigated in scientific studies. This seems surprising, since besides its relevance for jet pilots, motor learning is supposed to be very susceptible to the effects of stress. Thus, the investigation of motor learning in the stressful environment of +Gz (see 1.4 g) might help to extend the knowledge of the correlation of stress and a motor task. Therefore, this thesis also investigates the impact of +Gz on a motor learning task.

As already mentioned in the early beginning of this work, especially studies on tracking tasks, which are mostly used as a training or selection device, revealed a deficit in specifying the +Gz-related impairment. Several aspects may influence such complex tasks, e.g., a decreased tracking performance could be caused by an impaired timing (i.e. subject's response is always ahead or behind the stimulus), or by an impaired movement quality (i.e. subject's response does not reflect the stimulus' movement pattern). Moreover, each of these two aspects could also simply rely on the mechanical impact of +Gz (14, 26, 40). Since the RMSE only describes general deficits without specifying any details, it seems necessary to further scrutinize the effects of +Gz on tracking performance with respect to timing, movement quality and the mechanical impact of +Gz. Therefore, an additional part of this thesis deals with the evaluation of such tracking deficits.

¹ Strictly speaking, the ability to adapt motor performance to new and unknown circumstances is called sensori-motor adaptation. Such processes are characterized by *relearning* established movement patterns. Sensori-motor adaptation only forms a subgroup of motor learning processes, which also include *new-learning* unknown movements without reverting to existing patterns. However, since the term "motor learning" is used more often in daily life, the present thesis uses this general term.

Research questions on possible causes for +Gz-induced deficits in motor performance

The review in paragraph 1.4 revealed that different theories were proposed to explain the observed deficits in motor performance. Some possible explanations are probably not sufficient to originate the observed force exaggeration, as was explained for mechanical aspects, disturbed vision, proprioceptive deficits or the reinterpretation hypothesis (1.4 a-d). Other hypotheses mentioned might indeed explain this effect, but valuable scientific data supporting these theories are missing. The present thesis therefore investigates whether computational stress (1.4 e), vestibulo-spinal activity (1.4 f), or physical activation (1.4 h) – each considered separately – might explain the observed impairment in isometric force production. Since pointing movements are as well known to be affected by +Gz and since it is assumed that deficits in different motor tasks in +Gz have a common origin as explained in 1.4, we also investigate displacement movements with respect to the hypotheses 1.4 e, f and h. Since it was demonstrated that comprehensive studies on +Gz as a stressful environment are missing, we further try to extend this view by combining endocrinological and psychological methods in the same subjects (1.4 g).

Research questions on motor performance related to	flight operations
Is the observed force exaggeration in +Gz reduced by a training conducted in +Gz?	Study 1
Is the observed force exaggeration in +Gz reduced by a training conducted in +1 Gz?	Study 2
Do +Gz-experienced pilots show the same force exaggeration in +Gz like +Gz-inexperienced subjects?	Study 3
Are displacements with a joystick affected by +Gz?	Study 2
Does +Gz have an impact on motor learning processes?	Study 4
Is a decreased tracking performance in +Gz related to mechanical effects or to an impairment in timing or accuracy?	Study 4

Research questions on possible causes for +Gz-induced deficits in motor performance		
Is the observed force exaggeration in +Gz caused by computational stress?	Study 1	
Is the observed force exaggeration in +Gz caused by vestibulo-spinal activity?	Study 6	
Are displacements with a joystick affected by vestibulo-spinal activity?	Study 6	
Is the observed force exaggeration in +Gz caused by +Gz-induced physical activation?	Study 7	
Are displacements with a joystick affected by physical activation?	Study 7	
Does +Gz effect an increase in endocrinological and psychological stress parameters?	Study 5	

 Table I. Summary of the main research questions covered in the present thesis including the according study number.

1.6 Outline

Study 1 investigated whether the observed exaggeration in isometric force production might be reduced by prolonged practice in +Gz, and whether +Gz impairs the dual task performance of force production combined with a secondary task, as an indication for computational stress (see 1.4 e). To this end, collegiate subjects used an isometric joystick with their dominant hand to produce forces of prescribed directions and magnitudes. In practice trials, subjects received continuous visual feedback about their performance, whereas in test trials they did not. Additionally, subjects used their other hand for a four-choice reaction-time task. In test trials both tasks were performed separately and concurrently to allow calculation of cognitive dual task costs (see 1.4 e). An experimental group (n=12) performed these test trials three times: in +1 Gz, in +3 Gz short time after the beginning of +Gz, and again in +3 Gz after 10 min of practice trials. A control group (n=12) performed the same test design, but remained in +1 Gz only. During early +3 Gz-responses in the experimental group, initial force (i.e. 100 ms after response onset) increased abruptly by about 140%, and peak force (i.e. the highest produced force during each response) by 35%. Both values decreased again after prolonged practice in +3 Gz, with a complete recovery for peak force, but only a partial recovery for initial force, both with respect to the according values in the control group. Dual-task interference was observed, which did not vary with +Gz-level or practice. In conclusion, this study confirmed the exaggeration of isometric force production in naïve subjects (40), and additionally revealed that a practice performed in +Gz compensates for these detrimental effects of +Gz by partial adaptive reprogramming (see amelioration in initial forces), and by additional feedback-based corrections (see difference between complete recovery in peak, but incomplete recovery in initial forces). Potential effects of force exaggeration on aircraft control could therefore probably be reduced by prolonged practice in +Gz. Moreover, this study showed that force production is cognitively demanding, since dual task interference was observed, but given that cognitive dual task costs did not vary with +Gz-level or practice, computational stress seems unlikely as an underlying reason for the observed force exaggeration in +3 Gz.

Study 2 was designed to scrutinize whether task practice is also effective if performed in +1 Gz instead of +3 Gz. Additionally, this study investigated whether

subjects exposed to +3 Gz produce both, exaggerated forces and exaggerated hand displacements. To answer these questions, one group of subjects (pre-trained isometric group, n=6) performed the same task like in Study 1, but subjects were accelerated to +3 Gz for the first time after an extensive practice of the isometric force production task with visual feedback, lasting about 25 min. Other subjects reproduced visually prescribed directions and magnitudes using a displacement instead of an isometric joystick. After an introduction these latter subjects were divided into a test group (n=12) performing their task without visual feedback in +1 Gz and in +3 Gz, and a control group (n=12) performing the same task in +1 Gz only, to control time effects. Pre-trained subjects produced the same force exaggeration in peak and initial force as observed for subjects in Study 1, who only performed a short task practice before acceleration to +Gz. In contrast, hand displacements were not found to be impaired by +Gz. These results demonstrate that the exaggerated force production in +3 Gz is not overcome by task practice in +1 Gz, as opposed to task practice in +3 Gz (see Study 1). Thus, we did not find any support for the assumption that a practice in +1 Gz might at least improve utilization of feedback processes (see 1.5). In order to avoid motor deficits during flight maneuvers inducing +Gz, the data suggest that pilot training containing extended phases of +Gz should be preferred to simulation practice conducted in +1 Gz only. This study further revealed that the control of isometric and regular sticks seems to be based on partly distinct neural mechanisms with different +Gz-dependence. This different outcome for displacements and isometric forces is in accordance with the view that displacement and force control rely on separate mechanisms (24) residing in distinct brain areas (54). Thus, +Gz-related processes, e.g. descending vestibulospinal activity, may enhance spinal excitability (70) in circuits related to force control, but not in those related to displacement control. In conclusion, displacement sticks might be preferred over isometric sticks in high-performance aircrafts – at least in terms of motor performance during +Gz.

Study 3 investigated whether +Gz-experienced professional jet pilots show a similar isometric force exaggeration like +Gz-inexperienced subjects. Fortunately, we had the unique possibility to investigate seven professional PA-200 Tornado pilots of the German Air Force with a test design similar to the one used in Study 1. Subjects again produced visually prescribed forces of specific direction and magnitude using

an isometric joystick. Test trials without visual feedback about success were performed with the centrifuge stationary (+1 Gz) or rotating (+3 Gz). The study revealed that peak forces during test trials were significantly higher in +3 Gz than in +1 Gz, although this increase of about 25% referring to the +1 Gz value was somewhat smaller in pilots than in non-pilot controls, as observed in Study 1 (increase of about 35%). We therefore conclude that a frequent exposure to varying +Gz levels through regular practice flights several times a week is not sufficient for a profound adaptation of force-producing mechanisms to +3 Gz. In consequence, pilots' performance of isometric tasks could be compromised during flight maneuvers in +Gz, especially in the very early minutes of their flight, before short term adaptation processes as observed in Study 1 become effective.

Study 4 dealt with subjects' tracking performance and investigated to what extend the decrease in performance in +Gz might be due to the mechanical impact of +Gz, or to timing or accuracy deficits. Additionally, the study scrutinized, whether +Gz also impairs subjects' ability of motor learning, i.e. the ability of adapting motor performance to new and unknown circumstances. To investigate motor performance, a Test Group (n=10) manually tracked a sinusoidal moving target in either +1 Gz or +3 Gz. To evaluate motor learning, the cursor feedback was then left-right inversed and subjects had to adapt their performance to this disturbance while remaining in +3 Gz. A Control Group (n=10) performed the same paradigm in +1 Gz only, a Weight Group (n=12) also remained in +1 Gz, but with additional arm load simulating the +3 Gz phases. In contrast to earlier studies, tracking performance was not only evaluated by the RMSE, but also by a cross-correlation analysis to detect the specific deficit in timing and accuracy. Results confirmed that tracking performance measured by the RMSE decreased by about 50% in +3 Gz compared to +1 Gz values. A comparison of the Test and the Weight Group revealed that this deficit was not fully due to the mechanical impact of +3 Gz, since performance in the Weight Group only decreased by about 25%. The cross correlation analysis showed that tracking accuracy but not tracking timing was impaired in +3 Gz. Left-right inversion resulted in a typical motor learning in all subjects, however, +3 Gz did not have any positive or negative influence. In conclusion, this study demonstrated that +Gz-related deficits in tracking tasks are not fully due to the mechanical impact of +Gz, but rather to deficits in performance accuracy. Hence, it seems arguable that deficits in tracking tasks might

be partly due to the same processes as proposed for other motor performance tasks, e.g. vestibulospinal activity or the effects of stress. However, such processes do not impair motor learning, since we did not observe any learning deficits in +Gz. Therefore, we did not find any support for the assumption that pilots' ability to adapt their motor performance to new situations might be degraded in phases of +Gz.

Study 5 combined neuroendocrinological (stress hormone concentration) and psychological (questionnaire) methods in the same subjects in order to examine the relevance of +Gz as a stressful environment. A test group of 11 participants underwent a 15 min acceleration to +3 Gz in a human centrifuge. Before and immediately after this centrifuge run we collected blood samples taken through a permanent venous catheter providing the stress hormone concentration of cortisol, adrenocorticotrope hormone (ACTH), prolactin, epinephrine and norepinephrine. Additionally, the perceived physical and mental state were recorded using the MoodMeter[®] developed by Kleinert (53). A control group of another 11 participants underwent the same protocol in +1 Gz to control time effects. In the test group serum cortisol concentration during exposure to +Gz increased by 70%, plasma ACTH tripled, prolactin doubled, epinephrine increased by 70% and norepinephrine by 45%, while no changes could be observed in the control group. All psychological parameters revealed an overall deterioration in +3 Gz, however, only one parameter, i.e. perceived physical health, reached significance. These findings demonstrate that +Gz induces a comprehensive increase in various stress hormone concentrations, which go along with a decrease in perceived physical and mental state. It therefore seems assumable that psycho-physiological changes have to be regarded as a relevant factor for changes in central and peripheral neural processing during phases of +Gz.

Study 6 evaluated whether the observed force exaggeration in +Gz might be due to vestibulospinal activity. It is well known that the perception of moving visual scenes increases the activity of vestibular nuclei in animals and humans (5, 58), and thus induces reflexive eye movements (34), postural adjustments (89), and illusory self-motion perception even in the absence of actual body movement (4, 44, 92, 91). In this study we used such visual stimuli instead of +Gz to stimulate the vestibular system, in order to avoid the various implications of +Gz, e.g. cardiovascular or endocrinological effects (see 1.4). Subjects either observed a stationary visual field

as a reference, or an upward- or downward moving visual field to induce vestibular activity. At the same time, subjects either produced pre-trained manual isometric forces (Exp. A; 12 subjects) or displacements (Exp. B; another 12 subjects), each of specific direction and magnitude comparable to Study 1. As a control, a third group of 12 subjects did not produce any motor responses, but their arm Electromyography (EMG) was registered (Exp. C). The data revealed that isometric force production was substantially higher with the moving than with the stationary field, irrespective of field direction. Similar results were obtained for the EMG, while displacements were not at all affected by visual stimulation. Therefore, we can conclude that vestibular stimulation has detrimental effects on motor performance, which are similar to those observed in +3 Gz. This suggests that vestibular effects contribute to the exaggerated force production in +Gz, maybe mediated by an increased muscle activity. The effect on motor performance seems to be independent of the polarity of vestibular stimulation, since the effect was similar for upward- and downward visual stimulation. Additionally, we found different effects on manual forces and displacements as already observed in +Gz, hence, forces and displacements seem to be controlled by pathways which interact differently with the vestibular system.

Study 7 evaluated the effects of acute bouts of physical exercise on isometric force production and displacement movements. As in Studies 1-3, subjects' task was to reproduce targets of a given magnitude and direction using an isometric (Isometric Group, n=10) or a displacement joystick (Displacement Group, n=10). After an introduction with visual feedback about success, subjects conducted this task before (Pre) and after (Post) a bicycling phase of five minutes with a mean heart rate of 130 bpm without visual feedback. To control time effects, a third group also using the isometric joystick performed the same paradigm but rested for five minutes (Control Group, n=10). Later on, we calculated subject's peak- and initial amplitude (100 ms after response onset) of each response. As intended by the experimental design subjects' heart rate in the Isometric- and the Displacement Group increased to about 130 bpm in the early Post phase and then gradually decreased again towards Pre values, while the heart rate in the Control Group remained unchanged. Peak forces in the Isometric Group showed similar results: from a stable Pre level, forces increased by about 25% in the beginning of the Post phase before decreasing again. In contrast, initial forces remained unchanged in the Isometric Group. In both, the Displacement-

and the Control Group neither peak- nor initial amplitudes changed after exercise and rest, respectively. This study could reveal that moderate and short exercise - which is known to facilitate cognitive performance – can impair motor performance. This is neither due to serial-order effects such as fatigue or the mere passage in time, since the effect was absent in the Control Group, nor to central processes, since it emerged only during later parts of responses (cf. differential outcome on initial and peak amplitude). Instead, altered proprioceptive feedback might have impaired performance corrections resulting in the observed increase in peak force. Therefore, excessive force production during centrifugation and after physical exercise seems to have different causes (see Study 6). However, motor performance deficits in +Gz during subjects' responses could be caused by vestibulo-spinal activity, but might have further deteriorated by faulty proprioceptive feedback induced by physical activation in +Gz. Moreover, this study again supports the view that forces and displacements are controlled by different neuronal pathways. The outcome of this study could also be relevant for the design of training protocols for athletes in various types of sport, since forces and displacements are integral components of every sports skill.

2. FIRST STUDY:

Practice ameliorates deficits of isometric force production in +3 Gz

Simon Göbel¹, Otmar Bock¹, Hans Pongratz², and Wolfgang Krause²

¹ Institute of Physiology and Anatomy, German Sport University Cologne, Germany ² Surgeon General, German Air Force, Siegburg, Germany

Reference

Göbel S, Bock O, Pongratz H, Krause W. Practice ameliorates deficits of isometric force production in +3 Gz. Aviat Space Environ Med 2006;77(6):586-91.

2.1 Abstract

Background: Our earlier work has shown that human subjects produce exaggerated isometric forces when exposed to three times terrestrial gravity (+3 Gz). The present work investigates whether prolonged practice under +3 Gz reduces this deficit, and whether it affects the cognitive costs of force production.

Methods: 24 young male student volunteers produced forces without visual feedback of prescribed directions and magnitudes with their dominant hand, and used their other hand for a four-choice reaction-time task. Both tasks were performed separately and concurrently, in normal terrestrial gravity (normal-G), 30s after the beginning of +3 Gz, and after practice in +3 Gz.

Results: During early +3 Gz responses, initial force (100 ms into the response) increased abruptly by about 140%, and peak produced force by 30%. Both values decreased again after prolonged practice; this recovery was complete for peak force, but only partial for initial force. Dual-task interference was observed, which didn't vary with +Gz-level or practice.

Discussion: The detrimental effects of +3 Gz on force production are compensated by adaptive reprogramming (see initial force) and by additional feedback-based corrections (see difference between peak and initial force). Force production is cognitively demanding, but cognitive costs don't seem to vary with +Gz-level or practice.

3. SECOND STUDY:

Acceleration effects on manual performance with isometric and displacement joysticks

Simon Guardiera¹, Otmar Bock¹, Hans Pongratz², and Wolfgang Krause²

¹ Institute of Physiology and Anatomy, German Sport University Cologne, Germany ² Surgeon General, German Air Force, Siegburg, Germany

Reference

Guardiera S, Bock O, Pongratz H, Krause W. Acceleration effects on manual performance with isometric and displacement joysticks. Aviat Space Environ Med 2007;78(10):990-4.

3.1 Abstract

Background: We have shown before that novice human subjects produce exaggerated isometric forces when exposed to 3 times normal terrestrial acceleration (+3 Gz), and that this deficit is compensated by intensive training in +3 Gz. We now investigate whether training in normal terrestrial gravity (normal-G) is also effective. We further examine whether subjects in +3 Gz produce not only exaggerated forces, but also exaggerated hand displacements.

Methods: Experiments were conducted in the stationary (normal-G) or rotating (+3 Gz) gondola of a man-rated centrifuge. With their dominant hand, subjects produced either forces using an isometric joystick, or hand displacements using a regular joystick. Response directions and magnitudes were prescribed visually. In practice trials, subjects received continuous visual feedback about their performance, while in test trials they didn't.

Results: Subjects produced exaggerated forces in +3 Gz, whether or not they previously practiced the task in normal-G. In contrast, subjects did not produce exaggerated hand displacements in +3 Gz.

Discussion: Exaggerated force production in +3 Gz is not overcome by task practice in normal-G, as opposed to task practice in +3 Gz. This might be an indication, that pilot training should contain extended practice of force production during phases of increased gravity (+Gz) to avoid motor deficits during flight maneuvers inducing +Gz. Furthermore, the control of isometric and regular joysticks seems to be based on partly distinct neural mechanisms, with different +Gz-dependence. Thus, against the background of motor performance during +Gz, regular sticks might be favorably compared to isometric sticks in high-performance aircrafts.

4. THIRD STUDY:

Isometric force production in experienced fighter pilots during +3 Gz centrifuge acceleration

Simon Guardiera¹, Otmar Bock¹, Hans Pongratz², and Wolfgang Krause²

¹ Institute of Physiology and Anatomy, German Sport University Cologne, Germany ² Surgeon General, German Air Force, Siegburg, Germany

Reference

Guardiera S, Bock O, Pongratz H, Krause W. Isometric force production in experienced fighter pilots during +3 Gz centrifuge acceleration. Aviat Space Environ Med 2007;78(11):1072-4.

4.1 Abstract

Background: We have shown earlier that naïve subjects produce exaggerated isometric forces when exposed to increased acceleration (+Gz) for the first time. The present study investigates, whether +Gz-experienced PA-200 Tornado pilots show similar deficits.

Methods: Experiments were conducted in the stationary (+1 Gz) or rotating (+3 Gz) gondola of a man-rated centrifuge. With their dominant hand, seven pilots produced visually prescribed forces of specific direction and magnitude using an isometric joystick. In practice trials, subjects received continuous visual feedback about their performance, while in test trials they did not.

Results: Peak forces during test trials were significantly higher in +3 Gz than in +1 Gz, although this increase of about 25% referring to the +1 Gz value was somewhat smaller in pilots than in non-pilot controls (increase of about 36%).

Discussion: Since pilots' responses were exaggerated in +3 Gz, it seems that frequent exposure to varying +Gz levels is not sufficient for a profound adaptation of forceproducing mechanisms to +3 Gz. In consequence, pilots' performance on isometric tasks could be compromised during flight maneuvers in +Gz.

5. FOURTH STUDY:

Motor performance and motor learning in sustained +3 Gz acceleration

Simon Guardiera¹, Stefan Schneider², Alexandra Noppe¹, and Heiko K. Strüder²

¹ Institute of Physiology and Anatomy, German Sport University Cologne, Germany

² Institute of Motor Control and Movement Technique, Dept. of Exercise

Neuroscience, German Sport University Cologne, Germany

Reference

Guardiera S, Schneider S, Noppe A, Struder HK. Motor performance and motor learning in sustained +3 Gz acceleration. Aviat Space Environ Med 2008;79(9):852-9.

5.1 Abstract

Introduction: Previous studies have shown that increased head-to-foot acceleration (+Gz) like that experienced in maneuvering aircraft impairs motor performance. However, there are few studies of motor performance providing detailed descriptions of specific deficits (e.g., mechanical function, timing, or loss of accuracy), and almost none investigating motor learning processes. Therefore, the present study evaluated whether these parameters may explain tracking deficits during +Gz, and whether +Gz also affects motor learning.

Methods: To investigate motor performance, a Test Group (n = 10) manually tracked a sinusoidal moving target either in normal earth gravity (+1 Gz) or during steadystate acceleration (+3 Gz). Cursor feedback was then left-right reversed, and subjects had to adapt their performance to this disturbance while remaining in the same acceleration environment. A Control Group (n = 10) performed the same paradigm in +1 Gz; a Weight Group (n = 12) also remained at +1 Gz with additional arm weighting to simulate the +3 Gz load.

Results: Tracking performance in +3 Gz was impaired by about 50% compared to +1 Gz values. The deficit was not entirely due to the mechanical effect of +3 Gz, since performance in the Weight Group decreased by only about 25%. Moreover, tracking accuracy but not tracking timing was impaired at +3 Gz. Left-right switching resulted in typical motor learning in all subjects. Exposure to +3 Gz had no influence on motor learning.

Discussion: Deficits in tracking performance are probably not due to mechanical impairment or timing deficits, but rather reflect effects on accuracy due to vestibulospinal influences or the stressful environment at +3 Gz However, these effects do not impair motor learning.

6. FIFTH STUDY:

Centrifugal acceleration to 3 Gz is related to increased release of stress hormones and decreased mood in men and women

Stefan Schneider¹, Simon Guardiera², Jens Kleinert³, Anja Steinbacher³, Thomas Abel¹, Heather Carnahan⁴, and Heiko K. Strüder¹

¹ Institute of Motor Control and Movement Technique, Dept. of Exercise

Neuroscience, German Sport University Cologne, Germany

² Institute of Physiology and Anatomy, German Sport University Cologne, Germany

³ Institute of Psychology, German Sport University Cologne, Germany

⁴ Dept. of Surgery, University of Toronto, Canada

Reference

Schneider S, Guardiera S, Kleinert J, Steinbacher A, Abel T, Carnahan H, Strüder HK. Centrifugal acceleration to 3 Gz is related to increased release of stress hormones and decreased mood in man and women. Stress 2008;11(5):339-47.

6.1 Abstract

Introduction: It has been suggested that the central and peripheral neural processes (CPNP) are affected by gravitational changes. Based on the previous experiments during parabolic flights, central and peripheral changes may not only be due to the changed gravitational forces but also due to neuroendocrine reactions related to the psycho-physiological consequences of gravitational changes. The present study focuses on the interaction of neuroendocrine changes and the physical and mental states after acceleration to three-time terrestrial gravity (3 Gz).

Methods: Eleven participants (29.4 +/- 5.1 [SD] years (male (n = 8): 30 +/- 5.1 years; female (n = 3): 27.7 +/- 2.1 years) underwent a 15 min acceleration to 3 Gz in a human centrifuge. Before and after the acceleration to 3 Gz circulating stress hormone concentrations (cortisol, adrenocorticotropic hormone (ACTH), prolactin, epinephrine, norepinephrine) and perceived physical and mental states were recorded. A second control group of 11 participants underwent the same testing procedure in a laboratory session.

Results: Serum cortisol concentration during exposure to the centrifugal acceleration increased by 70%, plasma concentration of ACTH increased threefold, prolactin twofold, epinephrine by 70% and norepinephrine by 45%, whereas the perceived physical well-being decreased.

Discussion: These findings demonstrate that psycho-physiological changes have to be regarded as a relevant factor for the changes in CPNP during phases of hypergravity exposure.

7. SIXTH STUDY:

Effects of vestibular stimulation on the production of manual forces and displacements

Marc Dalecki¹, Otmar Bock¹, and Simon Guardiera¹

¹Institute of Physiology and Anatomy, German Sport University Cologne, Germany

Reference

Dalecki M, Bock O, Guardiera S. Effects of vestibular stimulation on the production of manual forces and displacements. Aviat Space Environ Med 2008;under revision.

7.1 Abstract

Background: We have shown before that subjects produce exaggerated arm forces when exposed to three times the normal gravitational acceleration (+3 Gz), and that this deficit is not related to direct mechanical effects, faulty proprioception, or increased cognitive load. Here we investigate whether it is related to vestibular stimulation.

Methods: Novice subjects observed a stationary, upward- or downward moving visual field while producing pre trained arm forces (Exp. A) or displacements (Exp. B); a control group produced no motor responses, and their arm EMG was registered (Exp. C).

Results: Produced forces and EMG were higher with the moving than with the stationary field, irrespective of field direction. Displacements were comparable with the moving and stationary field.

Discussion: Vestibular stimulation has detrimental effects on motor performance which are similar to those of +3 Gz, thus suggesting that it contributes towards exaggerated force production in phases of increased acceleration. The effects on motor performance seem to be independent of the polarity of vestibular stimulation. Manual forces and displacements seem to be controlled by pathways which interact differently with the vestibular system.

8. SEVENTH STUDY:

Acute bouts of exercise affect manual forces and displacements differently

Simon Guardiera¹, Otmar Bock¹, and Steffen Hoeppener¹

¹Institute of Physiology and Anatomy, German Sport University Cologne, Germany

Reference

Guardiera S, Bock O, Hoeppener, S. Acute bouts of exercise affect manual forces and displacements differently. Med Sci Sports Exerc. 2008;submitted.

8.1 Abstract

Introduction: Several studies investigated the effects of acute bouts of physical exercise on cognitive, as well as on complex motor performance tasks. Less is known about simpler motor tasks, such as targeted movements and forces. The present study therefore investigates these tasks before and after a moderate bicycling exercise.

Methods: The subjects' task was to reproduce targets of given magnitude and direction using an isometric (Isometric Group, n=10) or a displacement joystick (Displacement Group, n=10), without visual feedback. They conducted this task before (Pre) and after (Post) a bicycling phase of five minutes with a mean heart rate of 130 bpm. We calculated subjects' peak- and initial- (i.e. 100 ms after onset) response amplitude.

Results: Heart rate increased from the Pre to the early Post phase in both groups, and then gradually decreased again towards Pre values. Peak forces in the Isometric Group showed similar results: from a stable Pre level, forces increased by about 25% before decreasing again. In contrast, initial amplitudes in the Isometric Group and initial- as well as peak amplitudes in the Displacement Group showed no changes.

Conclusions: The present study reveals that moderate exercise - which is known to *facilitate* cognitive performance - can *impair* motor performance. This is probably not due to central processes since it emerged only during later parts of responses (cf. differential outcome on initial and peak amplitude), but rather to altered proprioceptive feedback. The differential effects on forces and displacements support earlier findings that both are controlled by distinct neural pathways. This outcome might be relevant for the design of training protocols for athletes since forces and displacements are integral components of every natural behavior.

9. MAIN FINDINGS AND CONCLUSIONS

Research questions on motor performance related to flight operations

To revise, the present thesis covered two main goals in the field of motor performance in sustained acceleration to a multiple of normal earth's gravity (+Gz). A first goal was to proceed the investigation of motor performance in +Gz (see 1.3). Most of the aspects investigated are applicable to the occupational field of jet flying, since pilots of such modern high-speed jets frequently are exposed to +Gz and still have to be able to manipulate the control devices accurately. We could show that the previously observed isometric force exaggeration in +Gz (40) can be partly compensated by a prolonged task practice with visual feedback in +Gz. This rapid compensation is based on partial adaptive reprogramming as well as additional corrections predicated on proprioceptive feedback (Study 1). In contrast, an equivalent practice conducted in +1 Gz adequate to simulation training on the ground was ineffective (Study 2). Furthermore, long term adaptation to the +Gz environment could not be observed, since professional jet pilots, who are frequently exposed to +Gz during practice flights, only showed a slightly smaller deficit in isometric force production than +Gz-inexperienced subjects (Study 3). In consequence, our results suggest that pilots' ability to control their aircraft might especially be compromised in +Gz phases during the very early minutes of a flight, i.e. before short term adaptation processes become effective. This does not mean, however, that practice flights can be abolished, as pilots showed no long term adaptation to the observed motor deficits during +Gz maneuvers. One has to bear in mind that an impairment in motor performance is only one aspect related to +Gz, while other aspects, e.g. blood pressure (29), mental performance (61) and object comprehension (45), indeed showed adaptation processes on repeated exposure to a changed gravitational environment. In terms of stick control in high-performance jets, this thesis further revealed that regular sticks might be favorable compared to isometric sticks, since there were no +Gz-related deficits found in displacement movements conducted by a regular stick in contrast to isometric force production (Study 2).

We additionally investigated the +Gz-related deficits in tracking tasks, and found that the observed impairment is not due to timing deficits, but partly to the

mechanical aspects of +Gz and to deficits in performance accuracy (Study 4). The latter observation of decreased accuracy might present similar processes as assumed for exaggerated force production (see below), because a decrease in accuracy might well be due to an overshoot in tracking responses as a consequence of increased force production. The same study revealed that such effects do not affect motor learning, thus, again referring to jet pilots, we did not find any support that the ability to adapt motor performance to new situations is degraded in phases of +Gz.

The results and conclusions mentioned above present a significant contribution to basic research enhancing the knowledge of motor performance in +Gz. This knowledge might, as also shown above, be valuable for pilots' operations in high-performance aircrafts. However, the limitations to such a generalization need to be mentioned as well. Most studies were conducted with eleven or twelve subjects, while two studies were only performed with 6 and 7 subjects respectively (see Studies 2 and 3), thus, the number of subjects was relatively small. Moreover, the motor tasks examined only represent specific task components of pilots' day-to-day business, e.g. the unidirectional force component in the very complex task of operating a high-performance aircraft. Therefore, precise conclusions on piloting or manufacturing jet planes must be drawn carefully, unless continuous research is conducted in a more realistic environment, e.g. using interactive flight simulators inducing +Gz. Such simulation studies would afford the advantage of combining controlled conditions of basic research with realistic flight maneuvers.

Research questions on possible causes for +Gz-induced deficits in motor performance

The second major goal of this thesis was to evaluate possible causes for the observed exaggeration of isometric forces in +Gz. As presented in the Introduction, several arguments were proposed to explain +Gz-related deficits in motor performance. Previous work has already shown that the observed force exaggeration is probably not due to mechanical aspects (40), disturbed vision (15), or proprioceptive deficits (40). Also the reinterpretation hypothesis appears to be implausible (although it cannot be ruled out completely), since there is no movement required for the production of isometric forces. For this reason a misinterpreted inertia is of minor consequence.

The present thesis therefore investigated whether computational stress (1.4 e), vestibulo-spinal activity (1.4 f), and physical activation (1.4 h) might explain the observed impairment in isometric force production. We could show that also computational stress seems unlikely as an underlying reason for force increase in +Gz, since the cognitive demand investigated by the dual task approach did not vary with the +Gz-level (Study 1). In contrast, the present thesis provides data supporting the assumption that increased vestibulo-spinal activity might be a cause for the observed force exaggeration in +Gz (Study 6). Subjects produced larger isometric forces while viewing an upward- or downward moving visual scene, which is known to increase the activity of vestibular nuclei in animals and humans (5, 58). Given that subjects in this study remained stationary in a +1 Gz environment, other aspects of +Gz, which might affect motor performance, e.g. physical activation or stress reactions, can be excluded as a relevant factor for the observed force increase in this study. Hence, we can conclude that vestibular stimulation has detrimental effects on motor performance similar to those observed in +3 Gz, but slightly smaller in size. This latter aspect could be due to the fact that the visual stimulation used in this study did not match +3 Gz, as it was rather too small. Otherwise, the observed force exaggeration in +Gz might also be a cumulative effect of changed vestibulo-spinal activity and other aspects, like cardiovascular activation or stress (see below). Other work conducted during phases of varying gravitational force in parabolic flights (including +1.8 Gz) suggest that vestibulo-spinal influences act at a suprasegmental instead of a spinal level (67). These influences probably result in an increased muscle tone – as it was also observed during the visual stimulation in Study 6 – which in turn affects voluntary motor commands (see 1.4).

This thesis further shows that also other effects of +Gz have to be taken into account when discussing causes for increased force production in +Gz. By investigating subjects' force production after 5 min of bicycling, we could demonstrate that physical exercise could impair isometric force production (Study 7). This impairment was different to the one observed in +Gz, since only peak, but not initial forces 100 ms after response onset were affected by physical exercise. Thus, excessive force production after bicycling and during centrifugation seems to have different causes, i.e. vestibulo-spinal influences during centrifugation and deficient proprioceptive feedback after physical exercise. However, it seems arguable that performance

deficits during subjects' responses caused by vestibulo-spinal influences might be further deteriorated by faulty proprioception. For example, +3 Gz results in a physical activation with an increase of heart rate by about 40 bpm, which corresponds to an increase in force production of about 20% (see Study 7). The observed exaggeration of peak forces of about 35% in +3 Gz (see Study 1) could well be a cumulative effect of vestibulo-spinal and inaccurate correction processes caused by physical activity. However, one has to bear in mind that physical exercise and +Gz-induced cardiovascular effects are not equivalent and conclusions must be drawn carefully. Further research using e.g. Lower Body Negative Pressure Equipment (LBNP²) could enhance the knowledge of the interrelation between cardiovascular activity and changed motor performance in +Gz.

+Gz-related psycho-physiological changes might also be a relevant factor, as we could show that +Gz induces a comprehensive increase in various stress hormone concentrations, which goes along with a decrease in perceived physical and mental state (Study 5). These results expand the knowledge of +Gz as a stressful environment by combining psychological and endocrinological methods, but a clear interaction with specific motor performance deficits cannot be shown. However, this proof is necessary as stress is known to either facilitate or decrease humans' motor performance, depending on the level of stress following the inverted-U hypothesis by Yerkes and Dodson (64, 86, 93). To evaluate a possible correlation between motor performance deficits and psycho-physiological parameters, Studies 4 and 5 were actually carried out with the same subjects, although published in two manuscripts. Hence, it is possible to perform a multiple regression analysis. To this end we calculated the difference between +3 Gz and +1 Gz for the RMSE of the tracking task, and for stress hormone concentrations (Cortisol, Prolactin, Epinephrine, Norepinephrine), as well as for the psychological rating (motivational and physical state, psychological strain). We used the motor performance deficit induced by +Gzas the dependent variable, and the +Gz induced change in the various stress

² LBNP devices were originally developed to prevent astronauts from cardiovascular deconditioning resulting in orthostatic hypotension, i.e. syncope or fainting, when returning back to earth after prolonged spaceflight. In such devices a specific negative air pressure is applied to the enclosed lower body part of the weightless astronaut, resulting in the same blood shift as induced by gravity while standing on the surface of the earth. Similarly, +Gz induced blood shifts could be simulated even on earth using LBNP, by increasing the level of negative body pressure in a resting subject.

Method	Parameter	df	F-value	R ²	p-value
	Overall model	(7;12)	4.54	0.73	0.0109
Stress hormone concentration	Cortisol	(1;12)	11.43	0.49	0.0055
	Prolactin	(1;12)	0.62	0.05	0.4450
	Epinephrin	(1;12)	0.02	0.00	0.8913
	Norepinephrin	(1;12)	0.00	0.00	0.9827
Psychological rating	motivational state	(1;12)	16.21	0.57	0.0017
	physical state	(1;12)	1.81	0.13	0.2028
	psychological strain	(1;12)	11.60	0.49	0.0052

parameters as the predictors. As Table II presents, the significant overall model of this multiple regression analysis reveals that the modulation is sufficient.

Table II. Statistical results (Degrees of Freedom (df), F- and p-value of the according F-tests, and partial correlation coefficient R^2) of the multiple regression analysis evaluating the partial correlation of the motor performance deficit induced by +Gz and the various stress parameters. Significant results are marked in **bold**.

The partial correlations show that the increase in cortisol concentration and in perceived psychological strain as well as the decrease in perceived motivational state, significantly correlate with +Gz-related deficits in motor performance. This outcome indicates that subjects performed more badly, when they were stressed, thus, +Gz-related deficits in motor performance go along with an impairment of psycho-physiological parameters. However, it also has to be pointed out that this is an explorative analysis and conclusions must be drawn carefully, since the number of subjects was very low in relation to the number of parameters. Hence, more research combining motor performance and psycho-physiological parameters in +Gz with a larger number of subjects is necessary. Moreover, the impact of stress needs to be quantified for isometric force production as well, to enlarge the knowledge of possible causes for the observed force increase in +Gz. Control experiments using other stressors than +Gz might also be valuable to separate stress reactions from cardiovascular or vestibular effects during phases of +Gz. Experiments investigating professional jet pilots, who are probably less stressed by centrifugation, would

further increase the knowledge of the interrelation between effects of stress and motor performance in +Gz.

The previous paragraphs revealed that the observed exaggeration of isometric force production in +Gz probably has a multi-causal origin with vestibulo-spinal activity playing a dominant role. As displacements are neither affected by +Gz, vestibular stimulation nor physical activity, these underlying mechanisms seem to affect only forces, and do not apply for displacements. This is in accordance with the view that displacement and force control are mediated through distinct neuronal pathways, as shown in humans (24, 54) and monkeys (83). Vestibulo-spinal influences as well as physical activity might therefore change signal transduction in neuronal pathways related to force control instead of movement control.

To sum up, the presented data support the following hypothesis for the observed force exaggeration in +Gz: additional vestibulo-spinal activity modifies motor commands at a supraspinal level where a strong connection between vestibulespinal- and motor pathways is well known (52, 55) resulting in an increased muscle tone, which in turn affects voluntary motor performance (see Study 6). These mechanisms result in a highly exaggerated initial force production of about 140% in the early beginning of response in +Gz (see Study 1). Later on, peak forces are only increased by about 35%, thus, force exaggeration is probably recognized by proprioception and corrected. However, corrections remain incomplete due to the cumulative effects of vestibulo-spinal influences and physical activity, as both aspects caused an increase in peak force production when investigated separately (see Studies 6 and 7). As a latter aspect stress is likely to affect these mechanisms, but the precise impact still needs to be evaluated (see Study 5). After all, it seems likely that this hypothesis outlined so far is only valid for the observed force exaggeration and is not representative for other types of motor performance, as displacements were not affected. Therefore, the present thesis suggests that different motor tasks like pointing or tracking have to be evaluated separately with respect to the various causes proposed in the Introduction. In this way, the knowledge of mechanisms underlying the observed changes in motor performance in +Gz will further increase.

10. REFERENCES

- Adey WR. Neurophysiological Estimates of Human Performance Capabilities in Aerospace Systems. Final Report, No. AFOSRTR-75-0170, for Project AF-6813; 1975.
- Albery WB. The effect of sustained acceleration and noise on workload in human operators. Aviat Space Environ Med 1989;60(10 Pt 1):943-8.
- 3. Allard F, Brawley L, Deakin J, Elliot F. The effect of exercise on visual attention performance. Human Performance 1989;2:131-45.
- Allison RS, Howard IP, Zacher JE. Effect of field size, head motion, and rotational velocity on roll vection and illusory self-tilt in a tumbling room. Perception 1999;28(3):299-306.
- 5. Allum JH, Graf W, Dichgans J, Schmidt CL. Visual-vestibular interactions in the vestibular nuclei of the goldfish. Exp Brain Res 1976;26(5):463-85.
- 6. Augurelle AS, Penta M, White O, Thonnard JL. The effects of a change in gravity on the dynamics of prehension. Exp Brain Res 2003;148(4):533-40.
- Augurelle AS, Smith AM, Lejeune T, Thonnard JL. Importance of cutaneous feedback in maintaining a secure grip during manipulation of hand-held objects. J Neurophysiol 2003;89(2):665-71.
- Benson AJ. Chapter 32: Spatial disorientation common illusions. In: Ernsting J, Nicholson AN, Rainford DJ, editors. Aviation Medicine. Oxford; 1999. p. 437-454.
- Benson AJ. Chapter 31: Spatial disorientation general aspects. In: Ernsting J, Nicholson AN, Rainford DJ, editors. Aviation Medicine. Third ed. Oxford; 1999. p. 419-436.
- Berkhout J, O'Donnel RD, Leverett S. Changes in Electroencephalogram Spectra during Repeated Exposure to +Gz Acceleration. Final Report, No. AMRLTR-72-123, for Project AF-7184; 1973.
- Bock O. Joint position sense in simulated changed-gravity environments. Aviat Space Environ Med 1994;65(7):621-6.
- Bock O. Grasping of virtual objects in changed gravity. Aviat Space Environ Med 1996;67(12):1185-9.

- Bock O, Arnold KE, Cheung BS. Performance of a simple aiming task in hypergravity: II. detailed response characteristics. Aviat Space Environ Med 1996;67(2):133-8.
- Bock O, Arnold KE, Cheung BS. Performance of a simple aiming task in hypergravity: I. overall accuracy. Aviat Space Environ Med 1996;67(2):127-32.
- 15. Bock O, Cheung BS. Control of isometric force in hypergravity. Aviat Space Environ Med 1998;69(1):27-31.
- Bock O, Howard IP, Money KE, Arnold KE. Accuracy of aimed arm movements in changed gravity. Aviat Space Environ Med 1992;63(11):994-8.
- Bonato C, Zanette G, Manganotti P, Tinazzi M, Bongiovanni G, Polo A, et al.
 'Direct' and 'crossed' modulation of human motor cortex excitability following exercise. Neurosci Lett 1996;216(2):97-100.
- Brisswalter J, Durand M, Delignieres D, Legros P. Optimal and non-optimal demand in a dual-task of pedaling and simple reaction time: Effects on energy expenditure and cognitive performance. Journal of Human Movement Studies 1995;29:15-34.
- Canfield AA. The Influence of Increased Positive g on Reaching Movements. The Journal of Applied Psychology 1953;37(3):230-236.
- Chambers RM, Hitchcock L. The effects of acceleration on pilot performance. Johnsville, Pa.: U.S.Naval Air Development Center; 1963. Report No.: NADC-MA-6219.
- Chelette TL, Albery WB, Goodyear CD. Human task performance throughout prolonged high g exposure. Final Report: Armstrong Laboratory, Wright-Patterson AFB OH; 1996. Report No.: AL/CF-TR-1996-0135.
- 22. Chen Y, Mori S, Koga K, Ohta Y, Wada Y, Tanaka M. Shift in arm-pointing movements during gravity changes produced by aircraft parabolic flight. Biol Sci Space 1999;13(2):77-81.
- 23. Chernikoff R, Taylor FV. Reaction time to kinesthetic stimulation resulting from sudden arm displacement. J Exp Psychol 1952;43(1):1-8.
- 24. Chib V, Mussa-Ivaldi FA. The central nervous system independently controls motions and forces. Annual Meeting of the Society for Neuroscience (http://web.sfn.org), Atlanta, GA, USA 2006;Abstract No: 742.7(Retrieved

07.25.2008, from the World Wide Web: http://www.abstractsonline.com/viewer/viewAbstractPrintFriendly.asp?CKey ={AEA40E8C-052E-4D28-A443-5883B8B7BCD6}&SKey={0017447F-C07E-4102-A989-ED19D586AEDD}&MKey={D1974E76-28AF-4C1C-8AE8-4F73B56247A7}&AKey={3A7DC0B9-D787-44AA-BD08-FA7BB2FE9004}).

- Chmura J, Nazar K, Kaciuba-Uscilko H. Choice reaction time during graded exercise in relation to blood lactate and plasma catecholamine thresholds. Int J Sports Med 1994;15(4):172-6.
- 26. Cohen MM. Hand-eye coordination in altered gravitational fields. Aerosp Med 1970;41(6):647-9.
- 27. Cohen MM. Elevator illusion: Influences of otholith organ activity and neck proprioception. Percept Psychophys 1973;14:401-06.
- Collyer SC. Testing psychomotor performance during sustained acceleration.
 Final Report: School of Aerospace Medicine; 1973. Report No.: SAM-TR-73-52.
- 29. Convertino VA. High sustained +Gz acceleration: physiological adaptation to high-G tolerance. J Gravit Physiol 1998;5(1):P51-4.
- Creer BY, Smedal HA, Wingrove RC. Centrifuge study of pilot tolerance to acceleration and the effects of acceleration on pilot performance. Washington, D.C.: Sci./Techn. Info. Div., NASA; 1960. Report No.: NASA TN-D-337.
- 31. Creer BY, Stewart JD, Douvillier JG, Jr. Influence of sustained accelerations on certain pilot-performance capabilities. Aerosp Med 1962;33:1086-93.
- 32. Darwood JJ, Repperger DW, Goodyear CD. Mass discrimination under Gz acceleration. Aviat Space Environ Med 1991;62(4):319-24.
- Davranche K, Audiffren M. Facilitating effects of exercise on information processing. J Sports Sci 2004;22(5):419-28.
- 34. de Graaf B, Bos JE, Wich S, Bles W. Arthrokinetic and vestibular information enhance smooth ocular tracking during linear (self-)motion. Exp Brain Res 1994;101(1):147-52.
- DLR. Humanzentrifuge. Deutsches Zentrum f
 ür Luft- und Raumfahrt 2008(Retrieved 09.25.2008, from the World Wide Web: http://www.dlr.de/me/desktopdefault.aspx/tabid-2011/2949_read-4539/).

- Fernandez C, Goldberg JM. Physiology of peripheral neurons innervating otolith organs of the squirrel monkey. I. Response to static tilts and to longduration centrifugal force. J Neurophysiol 1976;39(5):970-84.
- 37. Fletcher DE, Collins CC, Brown JL. Effects of positive acceleration upon the performance of an air-to-air tracking task. J Aviat Med 1958;29(12):891-7.
- 38. Forestier N, Nougier V. The effects of muscular fatigue on the coordination of a multijoint movement in human. Neurosci Lett 1998;252(3):187-90.
- Fulton RC, Strutton PH, McGregor AH, Davey NJ. Fatigue-induced change in corticospinal drive to back muscles in elite rowers. Exp Physiol 2002;87(5):593-600.
- Girgenrath M, Gobel S, Bock O, Pongratz H. Isometric force production in high Gz: mechanical effects, proprioception, and central motor commands. Aviat Space Environ Med 2005;76(4):339-43.
- Glaister DH, Prior RJ. The effects of long duration acceleration. In: Ernsting J, Nicholson AN, Rainford DJ, editors. Aviation Medicine 3rd edition. Oxford, England: Butterworth Heinemann; 1999. p. pp. 128-47.
- 42. Graveline D. Lower Body Negative Pressure Device. spacedoc.net (Retrieved 11.21.2008, from the World Wide Web: http://www.spacedoc.net/lower_body_negative_pressure.html).
- 43. Grebot C, Groslambert A, Pernin JN, Burtheret A, Rouillon JD. Effects of exercise on perceptual estimation and short-term recall of shooting performance in a biathlon. Percept Mot Skills 2003;97(3 Pt 2):1107-14.
- Groen EL, Bles W. How to use body tilt for the simulation of linear self motion. J Vestib Res 2004;14(5):375-85.
- Hermsdorfer J, Marquardt C, Philipp J, Zierdt A, Nowak D, Glasauer S, et al. Grip forces exerted against stationary held objects during gravity changes. Exp Brain Res 1999;126(2):205-14.
- Hewson DJ, McNair PJ, Marshall RN. Aircraft control forces and EMG activity: comparison of pilots before and after flying training. Aviat Space Environ Med 2001;72(5):437-42.
- 47. Hewson DJ, McNair PJ, Marshall RN. Aircraft control forces and EMG activity: comparison of novice and experienced pilots during simulated takeoff and landing. Aviat Space Environ Med 1999;70(8):745-51.

- Hewson DJ, McNair PJ, Marshall RN. Aircraft control forces and EMG activity: comparison of novice and experienced pilots during simulated rolls, loops and turns. Aviat Space Environ Med 2000;71(8):798-805.
- 49. Higgins JR, Angel RW. Correction of tracking errors without sensory feedback. J Exp Psychol 1970;84(3):412-6.
- 50. Hoffman MD, Gilson PM, Westenburg TM, Spencer WA. Biathlon shooting performance after exercise of different intensities. Int J Sports Med 1992;13(3):270-3.
- 51. Kahneman D. In: Attention and Effort. Englewood Cliffs, New Jersey: Prentice-Hall Inc.; 1973. p. 1-27, 178-202.
- 52. Kennedy PM, Cresswell AG, Chua R, Inglis JT. Vestibulospinal influences on lower limb motoneurons. Can J Physiol Pharmacol 2004;82(8-9):675-81.
- 53. Kleinert J. Adjektivliste zur Erfassung der wahrgenommenen körperlichen Verfassung (WKV): Skalenkonstruktion und erste psychometrische Befunde. [Adjective list for assessing Perceived Physical State (PEPS). Scale construction and psychometric results]. Zeitschrift für Sportpsychologie 2006;13:156-164.
- 54. Krutky M, Chib V, Mussa-Ivaldi FA. Differential interference of motion and force control in the central nervous system. Annual Meeting of the Society for Neuroscience (http://web.sfn.org), Atlanta, GA, USA 2006;Abstract No: 742.23(Retrieved 07.25.2008, from the World Wide Web: http://www.abstractsonline.com/viewer/viewAbstractPrintFriendly.asp?CKey ={66F49EAF-8AEA-4EF4-B33C-F8A9D6F6CA0C}&SKey={0017447F-C07E-4102-A989-ED19D586AEDD}&MKey={D1974E76-28AF-4C1C-8AE8-4F73B56247A7}&AKey={3A7DC0B9-D787-44AA-BD08-FA7BB2FE9004}.).
- 55. Lackner JR, DiZio P. Gravitoinertial force level affects the appreciation of limb position during muscle vibration. Brain Res 1992;592(1-2):175-80.
- 56. Lackner JR, Dizio P. Rapid adaptation to Coriolis force perturbations of arm trajectory. J Neurophysiol 1994;72(1):299-313.
- 57. Lackner JR, Graybiel A. Illusions of postural, visual, and aircraft motion elicited by deep knee in the increased gravitoinertial force phase of parabolic flight. Evidence for dynamic sensory-motor calibration to earth gravity force levels. Exp Brain Res 1981;44(3):312-6.

55

- Lacour M, Vidal PP, Xerri C. Visual influences on vestibulospinal reflexes during vertical linear motion in normal and hemilabyrinthectomized monkeys. Exp Brain Res 1981;43(3-4):383-94.
- 59. Manzey D. Monitoring of mental performance during spaceflight. Aviat Space Environ Med 2000;71(9 Suppl):A69-75.
- 60. Manzey D, Lorenz B. Mental performance during short-term and long-term spaceflight. Brain Res Brain Res Rev 1998;28(1-2):215-21.
- 61. Manzey D, Lorenz B, Poljakov V. Mental performance in extreme environments: results from a performance monitoring study during a 438-day spaceflight. Ergonomics 1998;41(4):537-59.
- Manzey D, Lorenz B, Schiewe A, Finell G, Thiele G. Dual-task performance in space: results from a single-case study during a short-term space mission. Hum Factors 1995;37(4):667-81.
- 63. Manzey D, Lorenz TB, Heuers H, Sangals J. Impairments of manual tracking performance during spaceflight: more converging evidence from a 20-day space mission. Ergonomics 2000;43(5):589-609.
- 64. Martens R, Landers DM. Motor performance under stress: a test of the inverted-U hypothesis. J Pers Soc Psychol 1970;16(1):29-37.
- 65. McGlynn GH, Laughlin NT, Bender VL. Effect of strenuous to exhaustive exercise on a discrimination task. Percept Mot Skills 1977;44:1139-47.
- 66. McMorris T, Graydon J. The effect of exercise on cognitive performance in soccer-specific tests. J Sports Sci 1997;15(5):459-68.
- 67. Mierau A, Girgenrath M, Bock O. Isometric force production during changed-Gz episodes of parabolic flight. Eur J Appl Physiol 2008;102(3):313-8.
- 68. Mills FJ. The endocrinology of stress. Aviat Space Environ Med 1985;56(7):642-50.
- Miyamoto Y, Shimazu H, Nakamura A. Plasma catecholamine and cortisol concentrations during acceleration stress. Eur J Appl Physiol Occup Physiol 1995;70(5):407-12.
- 70. Miyoshi T, Nozaki D, Sekiguchi H, Kimura T, Sato T, Komeda T, et al. Somatosensory graviception inhibits soleus H-reflex during erect posture in humans as revealed by parabolic flight experiment. Exp Brain Res 2003;150(1):109-13.

56

- 71. Mouelhi Guizani S, Bouzaouach I, Tenenbaum G, Ben Kheder A, Feki Y, Bouaziz M. Simple and choice reaction times under varying levels of physical load in high skilled fencers. J Sports Med Phys Fitness 2006;46(2):344-51.
- Navon D, Gopher D. On the economy of the Human-Processing System. Psychological Review 1979;86(3):214-255.
- Newman DG, Callister R. Analysis of the Gz environment during air combat maneuvering in the F/A-18 fighter aircraft. Aviat Space Environ Med 1999;70(4):310-5.
- Niven JI, Whiteside TC, Graybiel A. The Elevator Illusion: Apparent Motion of a Visual Target During Vertical Acceleration. Proj Mr005. 13-6001, Subtask 1, Rep 89. Res Rep U S Nav Sch Aviat Med 1963;36:1-15.
- 75. Nowak DA, Hermsdorfer J, Schneider E, Glasauer S. Moving objects in a rotating environment: rapid prediction of Coriolis and centrifugal force perturbations. Exp Brain Res 2004;157(2):241-54.
- 76. Obminski Z, Wojtkowiak M, Stupnicki R, Golec L, Hackney AC. Effect of acceleration stress on salivary cortisol and plasma cortisol and testosterone levels in cadet pilots. J Physiol Pharmacol 1997;48(2):193-200.
- 77. Reid GB, Eggemeier FT, Shingledecker CA. Subjective workload assessment technique. Air Force Flight Test Center Edwards AFB CA 1982;Technical report ADP001142.
- Ross HE, Reschke MF. Mass estimation and discrimination during brief periods of zero gravity. Percept Psychophys 1982;31(5):429-36.
- Sadoff M. Effects of high sustained acceleration on pilots' performance and dynamic response. Washington, D.C.: Sci./Techn. Info. Div., NASA; 1964. Report No.: NASA TN D-2067.
- Sand DP, Girgenrath M, Bock O, Pongratz H. Production of isometric forces during sustained acceleration. Aviat Space Environ Med 2003;74(6 Pt 1):633-7.
- 81. Schmidt RA. A schema theory of discrete motor skill learning. Psychol Rev 1975;82:225-60.
- Schoene H. On the Role of Gravity in Human Spatial Orientation. Aerosp Med 1964;35:764-72.

- Sergio LE, Kalaska JF. Changes in the temporal pattern of primary motor cortex activity in a directional isometric force versus limb movement task. J Neurophysiol 1998;80(3):1577-83.
- 84. Shadmehr R, Mussa-Ivaldi FA. Adaptive representation of dynamics during learning of a motor task. J Neurosci 1994;14(5 Pt 2):3208-24.
- 85. Tenenbaum G, Yuval R, Elbaz G, Bar-Eli M, Weinberg R. The relationship between cognitive characteristics and decision making. Can J Appl Physiol 1993;18(1):48-62.
- 86. Weinberg RS, Ragan J. Motor performance under three levels of trait anxiety and stress. J Mot Behav 1978;10(3):169-76.
- Welch RB, Cohen MM, DeRoshia CW. Reduction of the elevator illusion from continued hypergravity exposure and visual error-corrective feedback. Percept Psychophys 1996;58(1):22-30.
- Whiteside T. Hand-eye coordination in weightlessness. Aerosp. Med. 1961;32:318-22.
- Wicke RW, Oman CM. Visual and graviceptive influences on lower leg EMG activity in humans during brief falls. Exp Brain Res 1982;46(3):324-30.
- Wiegmann D, Shappell S, Fraser J. HFACS analysis of aviation accidents: A north american comparison. Aviat Space Environ Med 2002;73(3):257.
- 91. Wright WG, DiZio P, Lackner JR. Perceived self-motion in two visual contexts: dissociable mechanisms underlie perception. J Vestib Res 2006;16(1-2):23-8.
- 92. Wright WG, DiZio P, Lackner JR. Vertical linear self-motion perception during visual and inertial motion: more than weighted summation of sensory inputs. J Vestib Res 2005;15(4):185-95.
- 93. Yerkes R, Dodson J. The relation of strength of stimulus to rapidity of habit-formation. Journal of Comparative Neurology and Psychology 1908;18:459-82.

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13. CURRICULUM VITAE

Personal Details

Name	Simon Guardiera
Birth name	Göbel
Date of birth	January 23 rd 1978
Place of birth	Troisdorf-Sieglar, Germany
Family status	married to Dr. Petra Guardiera
Nationality	German

Education

2004 - 2008	Ph.D. Student at the Institute of Physiology and Anatomy,	
	German Sport University Cologne, Germany	
2001-2004	Undergraduate Student at the German Sport University	
	Cologne and the University of Cologne, Germany	
	Degree: Bachelor's degree for teaching O level and A level	
	GCEs (Ordinary and Advanced Level General Certificates of	
	\underline{E} ducation) at grammar schools in the subjects mathematics	
	and sport ("Erstes Staatsexamen für die Lehrämter für die	
	Sekundarstufen I und II in den Fächern Mathematik und	
	Sport")	
1997-1998	Civilian Service at the Johanniter Child Hospital, St. Augustin,	
	Germany	
1988-1997	Grammar school student at the Stadtgymnasium Köln-Porz,	
	Cologne, Germany	
	Degree: General qualification for university entrance	

14. SUMMARY

Several scientific studies have examined human motor performance during phases of increased terrestrial gravitational acceleration (+Gz), and found deficits e.g. in tracking, pointing and force production tasks. In the latter case, +Gz provoked highly exaggerated arm forces when subjects used an isometric joystick. Since several high-performance aircraft are controlled by such sticks this force exaggeration might impair flight stability and could therefore compromise pilots' safety during +Gz flight maneuvers as loops and turns. However, several questions in this context remain unclear: Is the observed force exaggeration in +Gz reduced by training? Do +Gz-experienced fighter pilots show the same force exaggeration like +Gz-inexperienced subjects? Are manual displacements with a regular joystick used in different aircraft affected by +Gz as well? Does +Gz have an impact on motor learning processes? Such questions all relate to the operational background of pilots flying high-performance aircraft and answers might help to improve pilots' flight trainings and their working lives.

Besides these applied questions, another fundamental question is striking: Why do subjects produce exaggerated isometric forces in +Gz? According to literature some possible reasons like mechanical aspects, disturbed vision or proprioceptive deficits cannot explain this effect, while other aspects, like computational stress, physical activation, vestibulo-spinal activity or psycho-physiological stress might indeed explain the observed force exaggeration in +Gz. However, valuable scientific data supporting these latter theories are missing.

Therefore, in order to enhance the current knowledge of applied as well as basic research topics on motor performance in +Gz, this thesis contains the investigation of both questions on motor performance related to flight operations as well as possible causes of the +Gz-induced force exaggeration.

Pertaining to the research questions on motor performance related to flight operations we could show that the observed isometric force exaggeration in +Gz can be partly compensated by a prolonged task practice in +Gz, while an equivalent practice

conducted in normal gravitational acceleration adequate to simulation training on the ground was ineffective. Furthermore, long term adaptation to the +Gz environment could not be observed, since professional jet pilots frequently exposed to +Gz during practice flights only showed a slightly smaller deficit in isometric force production than +Gz-inexperienced subjects. We could further demonstrate, that neither manual displacements with a regular joystick nor subjects' ability to adapt their motor performance to unknown situations are affected negatively by +Gz.

The investigation of possible causes of the observed force exaggeration in +Gzshowed that also computational stress seems unlikely as an underlying reason for the force increase in +Gz, since the cognitive demand investigated by the dual task approach did not vary with the +Gz-level. We could further show that physical exercise impairs isometric force production, but since this effect differed qualitatively to the observed force exaggeration in +Gz, physical activation does probably not explain this force exaggeration in +Gz, either. In contrast, the present thesis describes experiments on force production during phases of linear vection supporting the assumption that increased vestibulo-spinal activity might be a cause of the observed force exaggeration in +Gz. Additionally, +Gz-related psychophysiological changes might also be a relevant factor, as we could demonstrate that +Gz induces a comprehensive increase in various stress hormone concentrations going along with a decrease in perceived physical and mental state. Since manual displacements were neither affected by +Gz, vestibular stimulation nor physical activity, these underlying mechanisms seem to affect only forces, but do not apply for displacements.

15. ZUSAMMENFASSUNG

Zahlreiche Studien haben die menschliche Motorik in Phasen erhöhter Erdbeschleunigung (+Gz) untersucht und Defizite z.B. bei Folge-, Zeige- und Kraftproduktionsaufgaben gefunden. Im letzteren Fall führte +Gz zu stark überhöhten Armkräften, wenn die Probanden einen isometrischen Joystick verwendeten. Da viele Hochleistungsflugzeuge durch solche Joysticks kontrolliert werden, könnten diese überhöhten Kräfte die Flugstabilität beeinträchtigen und daher die Sicherheit der Piloten während +Gz Flugmanövern wie Loopings und Kurven gefährden. Jedoch bleiben zahlreiche Fragen in diesem Kontext unklar: Reduziert sich die Krafterhöhung in +Gz durch ein Training? Zeigt sich bei +Gz-erfahrenen Piloten die gleiche Krafterhöhung wie bei +Gz-unerfahrenen Probanden? Sind manuelle Auslenkungen mit einem regulären Joystick wie er in anderen Flugzeugmodellen genutzt wird ebenfalls durch +Gz beeinträchtigt? Hat +Gz auch einen Einfluss auf Prozesse des motorischen Lernens? Solche Fragen beziehen sich alle auf den operativen Hintergrund von Piloten, die Hochleistungsjets fliegen, und entsprechende Antworten könnten helfen, die Flugausbildung und den Arbeitsalltag solcher Piloten zu verbessern.

Neben diesen anwendungsorientierten Fragen ist eine andere, grundlegende Frage auffallend: Warum produzieren Probanden erhöhte isometrische Kräfte in +Gz? Entsprechend der Literatur sind einige potentielle Gründe wie mechanische Aspekte, gestörtes Sehvermögen oder propriozeptive Defizite nicht in der Lage diesen Effekt zu erklären, wohingegen andere Aspekte, wie kognitive Belastung, körperliche Aktivität, vestibulo-spinale Aktivität oder psycho-physiologischer Stress tatsächlich die beobachtete Krafterhöhung in +Gz erklären könnten. Allerdings fehlen nützliche wissenschaftliche Daten, die diese letzten Theorien unterstützen würden.

Daher beinhaltet diese Promotion die Untersuchung sowohl von Fragen zur Motorik in Bezug auf fliegerische Tätigkeiten, als auch von möglichen Gründen für die +Gzbedingte Krafterhöhung, um so das aktuelle Wissen in anwendungs- und grundlagenorientierten wissenschaftlichen Themen zur Motorik in +Gz zu erweitern. Hinsichtlich der wissenschaftlichen Fragestellungen bezogen auf fliegerische Tätigkeiten konnten wir zeigen, dass die beobachtete Erhöhung isometrischer Kräfte in +Gz partiell durch ein anhaltendes Training in +Gz ausgeglichen werden konnte, wohingegen ein gleichwertiges Training bei normaler Erdbeschleunigung entsprechend eines Simulatortrainings auf der Erde unwirksam war. Darüber hinaus konnte eine längerfristige Gewöhnung an die +Gz Umgebung nicht beobachtet werden, da professionelle Jetpiloten, die in Trainingsflügen regelmäßig +Gz ausgesetzt sind, nur eine geringfügig kleinere Verschlechterung bei der isometrischen Kraftproduktion zeigen als +Gz-unerfahrene Probanden. Ferner konnten wir zeigen, dass weder manuelle Auslenkungen eines regulären Joysticks, noch die Fähigkeit der Probanden, ihre Motorik an unbekannte Situationen anzupassen, negativ durch +Gz beeinträchtigt sind.

Die Untersuchung möglicher Gründe für die beobachtete Krafterhöhung in +Gz zeigte, dass auch eine kognitive Belastung als zugrundeliegender Mechanismus für den Kraftanstieg in +Gz unwahrscheinlich ist, da der kognitive Aufwand bei der Untersuchung mittels der Doppeltätigkeitsmethode nicht mit dem +Gz-Level variierte. Darüber hinaus konnten wir zeigen, dass körperliche Aktivität die isometrische Kraftproduktion beeinträchtigt, sich dieser Effekt aber qualitativ von der beobachteten Krafterhöhung in +Gz unterscheidet, so dass körperliche Aktivität wahrscheinlich ebenfalls nicht der Grund für die erhöhte Kraftproduktion in +Gz ist. Im Gegensatz dazu beschreibt die vorliegende Promotion Experimente zur Kraftproduktion während Phasen von linearer Vektion, welche die Vermutung unterstützen, dass eine gesteigerte vestibulo-spinale Aktivität ein Grund für die erhöhte Kraftproduktion in +Gz ist. Zusätzlich könnten auch +Gz bedingte psychophysiologische Veränderungen ein relevanter Faktor sein, da wir zeigen konnten, dass +Gz umfassenden Anstieg in zu einem unterschiedlichen Stresshormonkonzentrationen führt, welche einhergeht mit einer Reduktion der wahrgenommenen körperlichen und mentalen Verfassung. Da manuelle Auslenkungen weder in +Gz, bei vestibulärer Stimulation noch bei körperlicher Aktivität beeinträchtigt waren, scheinen die zugrundeliegenden Mechanismen nur Kräfte, jedoch keine Bewegungen zu beeinflussen.