Effects of Acceleration-Induced Reductions in Retinal and Cerebral Oxygenation on Human Performance

Rodney J. Croft; Roger Kölegård; Arne Tribukait; Nigel A. S. Taylor; Ola Eiken

BACKGROUND: Ischemic hypoxia induced by suprathreshold G-force loading can adversely affect vision, cognition, and lead to loss of consciousness (LOC). The purpose of this study was to determine whether reductions in cerebral oxygenation, caused by subthreshold G-forces (up to +4 G_z and of limited durations that do not lead to LOC), would affect visual perception and working memory performance.

METHODS: Sixteen subjects performed visual perception and working memory tasks both before and during G_z exposures (+1, +2.2, +3, +4 with leg pressurization, +4 with leg and abdomen pressurization) within a human-use centrifuge.

RESULTS: As measured using near-infrared spectroscopy, blood oxygenation over medial prefrontal cortex was similar in the +1 and +2.2 G_z conditions, but was reduced to a similar extent in the +3 and +4 G_z conditions. In parallel, visual perception accuracy was reduced in the +3 and +4 G_z conditions, with no difference between the +3 and +4 G_z conditions. No change in reaction time was seen. Conversely, neither accuracy nor reaction time changes were observed for the visual working memory task.

DISCUSSION: These results indicate that although visual working memory is not affected, the ability to visually discriminate between stimuli is reduced at G-forces as low as +3 and +4 G_z. This may have important ramifications for pilots who are routinely subjected to such forces.

KEYWORDS: visual discrimination, memory, cerebral oxygenation, retinal oxygenation, human-use centrifuge.

Croft RJ, Kölegård R, Tribukait A, Taylor NAS, Eiken O. *Effects of acceleration-induced reductions in retinal and cerebral oxygenation on human performance.* Aerosp Med Hum Perform. 2021; 92(2):75–82.

Impaired oxygen delivery to the central nervous system (CNS) remains a cardinal aeromedical issue.[5] It can occur, not only during accidental exposure to low ambient pressure,[27] but in high-performance aircraft, due to reduced arterial pressure at head level.[15] Numerous perceptual, cognitive, emotional, and psychomotor symptoms have been documented during in-flight, hypobaric hypoxia.[25,32] Those effects of CNS hypoxia differ considerably among individuals, can be insidious, and are often not readily recognized by the affected individual.[25]

Flying an aircraft requires efficient visual perception, requiring both the functional integrity of the eye and central neural functions responsible for the detection and discrimination of stimuli. Visual perception and recognition are also closely intertwined with cognitive functions necessary for scanning and interpreting the cockpit instruments. Furthermore, the pilot's ability to adequately process and respond to visual information requires an effective working memory,[21,24] which is related to frontal-lobe activity,[33] and is typically associated with voluntarily, and actively, keeping in mind information necessary for solving present or imminent cognitive tasks.[22] The sense of vision is, however, quite sensitive to hypoxia,[23,28] with hypoxic impairment of visual sensitivity and acuity having been established at altitudes of 2000–4000 m (see Leber and colleagues[19]). Some CNS functions of significance for the pilot's ability to adequately respond to visual information, which include logical reasoning and running memory, begin to deteriorate at 3000–4000 m above sea level.[29]

During a sharp turn in a high-performance aircraft, the resultant gravitoinertial force vector, acting in the head-to-seat

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This manuscript was received for review in July 2020. It was accepted for publication in November 2020.

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DOI: https://doi.org/10.3357/AMHP.5731.2021

direction ($+G_z$; henceforth G denotes $+G_z$), may attain a value several-fold that of the Earth's gravitational force, resulting in a marked drop in head-level arterial pressure. The effects of the ischemic hypoxia induced by sustained (> 2 s) high G loading are typically more distinct and dramatic than those caused by hypobaric hypoxia. A gradual increase in G loading will, in due course, lead to a sequence of signs and symptoms, which include reduced peripheral vision, loss of central vision, and G-induced loss of consciousness (G-LOC).[38] That the visual symptoms attributable to retinal ischemia precede G-LOC, is routinely used by fighter pilots as an early warning signal to reduce the G load.[1,10]

However, whether functional impairments precede the subjectively discernible visual symptoms is also of crucial importance. Levin et al.[20] reported reduced performance on a visual working memory task that was independent from visual perception, during exposure to G loads that were unlikely to be subjectively distracting.

To prevent G-LOC, the pilot is equipped with an anti-G suit (AGS), which, in combination with muscle-straining maneuvers, can generate the necessary arterial pressure to sustain retinal and cerebral perfusion.[37] The AGS comprises an inflatable bladder covering the legs and lower abdomen. The pressure in the bladder is automatically regulated as a function of the G level. The leg portions of the bladder improve venous return and increase peripheral blood-flow resistance, and thereby arterial pressure, whereas the abdominal portion counteracts G-induced downward displacement of the heart, and hence reduces the drop in head-level arterial pressure.[9] A peculiarity with the action of the abdominal bladder of the AGS is that the increased intra-abdominal pressure, and the resulting elevation of the diaphragm, if combined with increased G load, results in compression of the dependent parts of the lungs, resulting in shunting of deoxygenated venous blood into the systemic circulation.[2,13] Thus, during prolonged G exposure, the desirable effect of the abdominal bladder on local arterial pressure may be counteracted by concomitant hypoxemia. During 4-min exposures to moderate G loads (4-5 G), the accompanying hypoxemia is more pronounced if the entire AGS is inflated than if the abdominal portion of the bladder remains unpressurized.[10]

A measure of the combined effect of hypoxemia and reduced arterial pressure at head level is the deoxygenation of the cerebral frontal lobes, which can be recorded by means of near-infrared spectroscopy (NIRS[31]). Reduced oxygenation in the frontal cortex has been regarded a predictor of G-LOC.[18,30,35] Nevertheless, if more subtle impairments of cerebral function could be detected, and related to reductions in cortical oxygenation, then this would be of considerable value to efforts aimed at supporting the operational integrity of pilots of high-performance aircraft.

The aim of the present study was to establish whether reductions in head-level arterial pressure and arterial oxygenation, as created within a human-use centrifuge and by an AGS, might influence two visual functions. One of those functions is comparatively more sensitive to retinal deoxygenation (visual discrimination).[8] The other is regarded to be highly dependent on the integrity of the CNS (visual working memory).[7]

METHODS

Subjects

There were 16 healthy individuals, 13 men and 3 women (mean age 28.2 y, SD 10.8), who participated as test subjects. Each subject provided written, informed consent before participating, and was free to withdraw from the study at any time. The protocol and experimental procedures were approved by the Regional Human Ethics Committee in Stockholm, Sweden.

Equipment

The experiments were performed in a 7.25-m radius human-use centrifuge (ASEA, Västerås, Sweden) at the Royal Institute of Technology (Stockholm, Sweden). Subjects were seated in a mock seat of the Gripen 39 fighter aircraft. The centrifuge gondola is tangentially pivoted so that the resultant of the gravitational and inertial force vectors is always directed head-to-seat. The centrifuge was controlled by an open-loop system, employing preset G-time profiles. G force was measured using an analog accelerometer mounted approximately at the level of each subject's heart. Throughout each experiment, the subject was monitored via closed-circuit video, and could communicate with the experimenters by means of a two-way intercom system.

Subjects were dressed in overalls and an extended-coverage pneumatic AGS, as used within the Gripen 39 aircraft (for details, see Eiken et al.[9]). For these experiments, suits were modified so that independent pressurizing of the abdomen and legs could be achieved.[9] As in the aircraft, pressurization commenced at 2 G, with pressure increasing linearly with increments in G force to a maximum of 2.9 kPa at 4.0 G. For G-forces ≤ 2 G, the suit was pressurized to 1.3 kPa to facilitate its rapid inflation and application of a counter pressure. Suit pressure was automatically controlled through a regulator or G valve (Eros, F-5341, Eros, Plaisir Cedex, France).

Heart rates were derived from electrocardiographic recordings using a cardiometer (Datex-Engström, Instrumentation Corp, Helsinki, Finland), with the electrodes positioned in a precordial 5-lead arrangement. Systolic, diastolic and mean arterial pressures were measured continuously using a volume-clamp technique (Portapres, TNO, Amsterdam, The Netherlands), with the pressure cuff placed around the middle-phalanx of the third finger of the left hand, and with the reference pressure transducer taped to the skin of the forehead, at the level of the cerebral frontal cortex.

Capillary oxyhemoglobin saturation (S_pO_2) was measured continuously using a pulse oximeter (Nellcor Puritan Bennett Inc., Pleasanton CA, USA), with the transducer placed on the second finger of the left hand. The oximeter has an accuracy of $\pm$ 2% across the range 70–100%, and has an acceptable resilience to motion artifacts, making it suitable for use in this experiment.

The oxygenation of the frontal cerebral cortex was measured using continuous-wave, near-infrared spectroscopy (NIRO-200NX, Hamamatsu, Japan). The transducer unit was positioned over the left prefrontal cortex between the first frontal-polar and third frontal locations (FP1, F3), as determined by the modified international 10-20 system for electroencephalography. To minimize the confounding influence of skin blood flow, the unit, comprising an emitter and a detector, was taped to the skin at a fixed interoptode distance of 4.0 cm.[16] To reduce intrusion of external light and loss of transmitted near-infrared light from the measuring area, the transducer unit was covered with an opaque bandage.

The near-infrared light is used to quantify tissue oxygenation from changes in oxygenated hemoglobin ($\Delta[O_2Hb]$).[36] The NIRS signal was recorded at 5 Hz, expressed relative to the 4-min baseline period preceding each trial, and averaged over 25-s periods. The theory, limitations, and reliability of cerebral oxygenation obtained from NIRS have been reviewed elsewhere.[4,11]

During each experimental trial, a visual perceptual task was administered, with stimuli presented separately in the fovea and periphery as a function of difficulty (i.e., an easy and more difficult version were administered), as well as a working memory task (on a computer monitor with the screen positioned 0.43 m from the bridge of the nose of the subjects). The order of those tasks was counterbalanced and randomly assigned across subjects, but due to data loss, complete counterbalancing was not achieved in the final data set described below. Data were presented using PsychoPy v1.83.01.

The visual perception task consisted of a series of pairs of linear, sinusoidal black/white gratings in the shape of a circle (2.4° visual arc), presented concurrently to both the left and right of a central fixation cross, which was at eye level (**Fig. 1**). Individual gratings were presented concurrently with a solid white border around their perimeter. The objective of the task was to press a response button whenever a grating-pair was detected, and to withhold a response when a nontarget was presented (the white perimeters without enclosed gratings; see Fig. 1). The equally probable stimuli were presented either centrally or peripherally (centered 2.4° and 14.6° of visual arc, respectively, to the left and right of the fixation stimulus), and were either nontargets, easy targets, or difficult targets (equiprobable). In addition, continuous visual noise was added for the duration of the task to increase overall difficulty (random white kinetic dots on a gray background). The difficulty level was adjusted using a calibration procedure such that it was equivalent for each subject, and for each of the foveal and peripheral presentations (see below). As shown in Fig. 1, each trial began with the presentation of a white fixation cross (200 ms) which was replaced by a blank (black) screen (200 ms), and then by a target or nontarget stimulus-set (250 ms). A response was permitted from the interval beginning 100 ms after the stimulus onset, for a period of 1100 ms. A total of 48 stimuli were presented (8 instances of each of the 6 possibilities), lasting 77 s.

As shown in **Fig. 2**, the working memory task consisted of the sequential visual presentation of a fixation mark (250 ms), a blank screen (250 ms), a set of white letters (the memory set) from the Latin alphabet presented simultaneously for 2 s, and a blank screen for 3 s (during which subjects needed to commit those letters to memory). They were then presented with an experimental (probe) stimulus for 1 s. That stimulus was a single letter that may, or may not (equiprobable), have been within the memory set. Subjects were asked to respond with a button press if that letter was from the memory set. A response was permitted from the interval beginning 200 ms after the onset of the probe screen, for a period of 2.3 s. A total of 16 probe stimuli were presented (half targets), lasting a total of 130 s. Letters were white Arial font, with a width approximately 2.4° visual arc, presented at eye level and center-justified relative to the midpoint of the horizontal field of view. Difficulty (number of letters in the memory set, with a maximum of two on one line) was matched across subjects using a calibration task.

Calibration trials were administered for both cognitive tasks prior to commencing the experimental sessions. These were used for three reasons: 1) to determine the stimulus characteristics for each individual, so that these tasks would be 'difficult but achievable', and thereby avoid ceiling and floor effects; 2) to ensure the stimulus difficulties were equivalent across individuals; and 3) to provide two discrete difficulty levels within the visual perception task. Within that task, those outcomes were achieved by varying the opacity of the gratings, and, within the working memory task, they were produced by varying the number of letters in the memory set (4–10). A stair-casing technique was used for the visual perception task, whereby the minimum opacity value that resulted in a sequence of three correct responses for a given location/difficulty combination was used for the subsequent experimental trials for that location/difficulty combination. Working memory calibration involved two presentations of each memory set length (sequentially from the smallest to largest number of letters), with the largest memory set that resulted in correct responses for both trials being used for the subsequent experimental trials.

Procedure

Each subject was instrumented, equipped with an AGS, and familiarized with both cognitive tasks at 1 G with the centrifuge gondola parked, and then with the centrifugation procedures, using a pre-experimental exposure to 2.2 G. Thereafter, each subject was tested under five conditions:

1. 1 G;
2. 2.2 G with pressurization (≈0.4 kPa) of the full AGS;
3. 3 G without pressurization of the AGS;
4. 4 G with pressurization to 2.93 kPa of the full AGS [4 G(f)]; and
5. 4 G with the legs, but not the abdominal bladder of the AGS pressurized [2.93 kPa; 4 G(l)].

Each centrifuge run started with a G-force increase to idle speed (1.4 G), and thereafter by 0.2–0.3 $G \cdot s^{-1}$ to the target G-plateau. After 30 s at each plateau, the subject commenced the cognitive tasks, which were completed about 3.5 min later. On completion, the load was decreased (0.5 $G \cdot s^{-1}$) to 1.4 G,

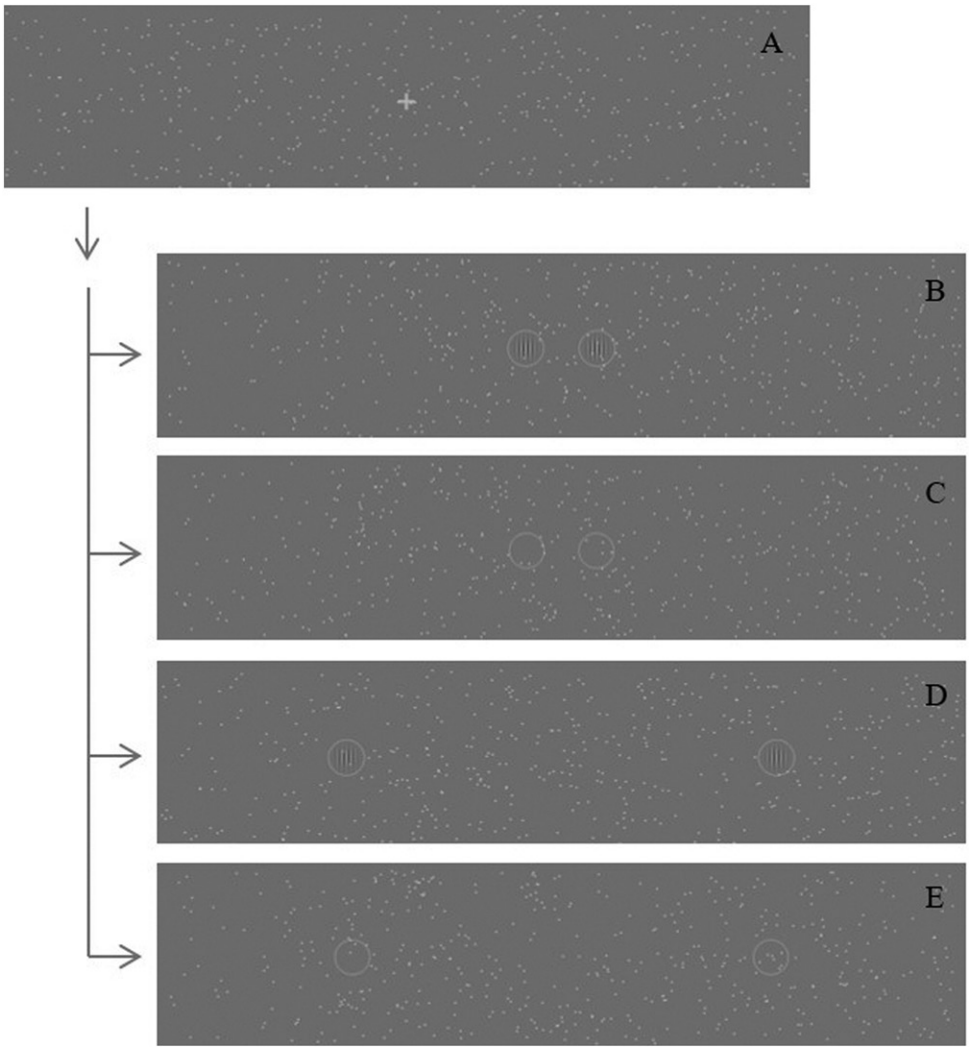

Fig.1. Visual perception task: Subjects first viewed the top screen (A) containing a centrally located cross. This was then replaced by one of the randomly assigned screens (B-E), each of which contained two circles positioned equidistant from the center, but within either the narrow (foveal) or peripheral fields of view. Subjects pressed a button if the screen contained a pair of circles with parallel lines (grating) within the perimeter (i.e., B and D). These were targets, while the nontarget stimuli (C and E) lacked this grating. Note that consistent with the difficulty of the task, the target and nontarget stimuli are deliberately very difficult to discern.

and thereafter to 1 G. Between each of the runs, there was a recovery period of at least 5 min (1 G), and the order of the treatments was alternated and balanced among subjects in a Latin-square manner.

Statistical Analyses

For each of the visual perception and memory tasks, d-Prime (a measure of discriminability based on signal detection theory)[14] was used to verify that subjects could perform the task adequately. Where a subject's d-Prime score in the 2.2 G condition was less than 0.5, in either the working memory task overall or the easy foveal condition of the visual perceptual task, data from that task for that subject were excluded from further analysis. This is because such data demonstrated a poor ability of the subject to detect the difference between the targets and nontargets, and, given that all subjects could discriminate during the practice tasks, that implies inadequate engagement in the task during the control condition. Thus, potential changes within the G-force manipulation conditions became potentially meaningless. Furthermore, interpolation for missing data cells was used where missing data was minimal (no more than 10% of cell means missing for a subject). This resulted in $<$ 1% interpolation in each of the two tasks.

For the visual perception task, button presses to targets (or null responses for nontargets) within 100–1100 ms of stimulus presentation were classified as correct responses. Accuracy was calculated as the percentage of trials with correct responses, and reaction time as the latency for correct target responses (relative to target onset). These were determined separately for easy foveal, difficult foveal, easy peripheral, and difficult peripheral stimuli.

For the working memory task, button presses to targets (or null responses for nontargets) within 200–2300 ms of probe presentation were classified as correct responses. Accuracy was calculated as the percentage of trials with correct responses, and reaction time as the latency for correct responses (relative to probe onset).

Data are reported as means with standard errors of the means ($\pm$ SE), unless stated otherwise (SD). Note that, due to some missing data, the sample size varied from 13 to 15 across the analyses. However, as the subjects corresponding to the particular missing cells varied across the analyses, all 16 subjects contributed to at least some of the analyses. Where applicable, the relative deviations from the original sample size can be seen in the degrees of freedom values.

To determine the effect of the G-force manipulation on the physiological data, repeated measures ANOVA was performed for each of cerebral oxygenation, mean arterial pressure, heart rate and oxyhemoglobin saturation (S_pO_2), where G-force was the independent variable (1, 2.2, 3, 4 [leg pressurization only; 4 G(l)] and 4 G [full pressurization; 4 G(f)]); Huynh-Feldt adjusted values are reported where appropriate. As these comparisons are descriptive rather than inferential, Tukey's

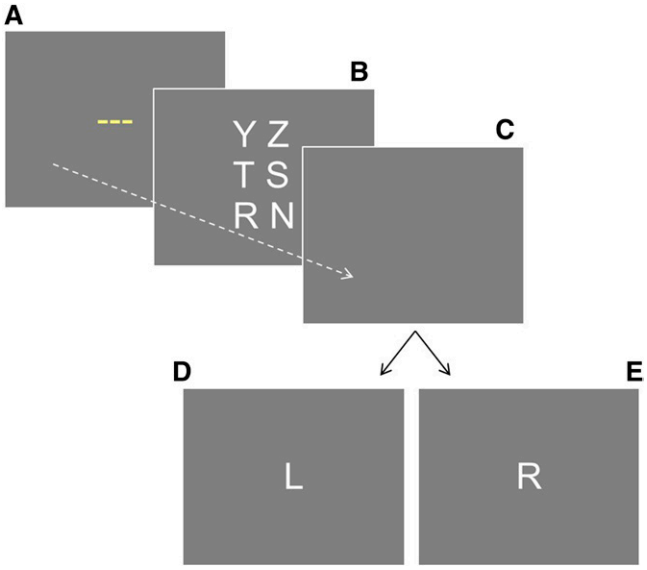

Fig. 2. Working memory task: Subjects viewed a fixation mark (A), followed by a set of letters that needed to be remembered (memory set; B), a blank screen (C) and then a stimulus (probe) screen containing just one letter (screen D or E). Subjects responded (button press) if the letter displayed (on screen D or E) was included within the memory set. Such letters were targets (e.g., 'R'), while other letters were distractors (nontargets; e.g., 'L').

LSD was used to determine the nature of those significant relationships (i.e., no adjustment for multiple comparisons was made).

To determine whether the subjects were able to perform the visual perception task adequately during the 1 and 2.2 G control conditions, and whether the difficulty manipulation was successful, a repeated measures ANOVA was performed using d-Prime as the dependent, and control level (1, 2.2 G), difficulty (easy, difficult) and visual field (fovea, periphery) as the independent variables. A similar ANOVA was performed for the memory task (but without visual field or difficulty). To determine the effect of the G-force manipulation on cognition, repeated measures ANOVA was performed for each of accuracy and reaction time, for each of the visual perception and memory tasks, using contrasts that were set up to match effects of G-force on cerebral oxygenation (i.e., the target most relevant to perceptual and cognitive function). Specifically, matching cerebral oxygenation findings (see Results), the average of 3 G, 4 G(l) and 4 G(f) was compared to the average of 1 and 2.2 G. For visual perception, the interactions of this linear change with visual field and difficulty were also assessed. As these comparisons were hypothesis-driven with fewer than the G-force degrees of freedom, an adjustment for multiple comparisons was not used.

RESULTS

Mean arterial pressure differed as a function of G-force, (F[4,48] = 64.72; $P < 0.001$; partial eta-squared = 0.84; **Table I**, **Fig. 3**); 1 G was higher than 2.2 G ($P < 0.001$); 2.2 G was higher than 4 G(f), 4 G(l) and 3 G (all $P < 0.001$); 3 G was lower than 4 G(f) ($P = 0.032$) but not 4 G(l) ($P = 0.536$); 4 G(l) and 4 G(f) did not differ from each other ($P = 0.090$). As a consequence, perfusion of some tissues above heart level may have been less than ideal. Heart rate similarly differed with G-force exposure (F[4,52] = 88.54; $P < 0.001$; partial eta-squared = 0.87; Table I); 1 G was lower than 2.2 G ($P < 0.001$); 2.2 G was lower than each of 4 G(f), 4 G(l), and 3 G (all $P < 0.001$); 4 G(f), 4 G(l), and 3 G did not differ from each other ($P > 0.521$).

Oxyhemoglobin saturation (S_pO_2) varied with G-force, but also with changes in counter pressure (F[4,52] = 13.09; $P < 0.001$; partial eta-squared = 0.50; Table I, Fig. 3). As a consequence, S_pO_2 was higher for 1 G than 2.2 G ($P = 0.028$); 2.2 G was similar to 3 G ($P = 0.613$) but higher than 4 G(l) and 4 G(f) ($P < 0.002$); 3 G was higher than 4 G(f) ($P = 0.001$) and 4 G(l) ($P = 0.050$), but 4 G(l) and 4 G(f) did not differ ($P = 0.107$). Finally, cerebral oxyhemoglobin ($\Delta[O_2$ Hb]) differed as a function of G-force (F[4,52] = 9.26; $P = 0.002$; partial eta-squared = 0.42; Table I, Fig. 3); 1 G did not differ significantly from 2.2 G ($P = 0.170$), whereas 4 G(f) ($P = 0.008$), 4 G(l) ($P = 0.023$) and 3 G ($P = 0.004$) were each lower than 2.2 G; 4 G(l), 4 G(f), and 3 G did not differ from each other ($P > 0.208$).

Demonstrating that subjects could perform the visual perception task adequately during the control conditions (1 G and 2.2 G), d-Prime was high (> 2.1 in all conditions), and was reduced in the difficult relative to the easy condition (F[1,12] = 10.48; $P = 0.007$; partial eta-squared = 0.47; **Fig. 4**). Although not statistically significant, the mean d-Prime score was lower in the peripheral relative to the foveal fields of view (F[1,12] = 3.5; $P = 0.080$; partial eta-squared = 0.233; Fig. 4), which raises the possibility that the difficulty manipulation was less robust in the peripheral field. The mean accuracy of the combined 3 G, 4 G(l) and 4 G(f) average was lower than that of the combined 1 G and 2.2 G average (F[1,14] = 6.06; $P = 0.027$; partial eta-squared = 0.30; Fig. 4). This contrast did not interact with difficulty, visual field or the interaction of difficulty and visual field ($P > 0.149$). Reaction time was not affected by G-force, the interaction of G-force with visual field or the interaction of difficulty and visual field (Fig. 4).

Demonstrating that the sample could perform the working memory task adequately during the control conditions (1 G and 2.2 G), d-Prime was high in both conditions (> 1.8). However, neither working memory accuracy nor reaction time was affected by G-force (F[1,14] < 1.63; $P > 0.222$; partial eta-squared < 0.10; Fig. 4).

DISCUSSION

The present study was designed to determine whether graded reductions of cerebral and retinal oxygenation, manipulated by applying different levels of G-force using a human-use centrifuge, would affect either visual discrimination or working memory. Visual discrimination accuracy was reduced at 3 and 4 G, but unaffected at 2.2 G, whereas the visual working memory task was unaffected by all G elevations.

Table I. Means (and Standard Errors) Are Shown for the Physiological Variables as a Function of G-Force Condition.

	1 G	2.2 G	3 G	4 G(f)	4 G(l)
Cerebral Oxygenation Index ($\Delta[O_2$ Hb])	75.0 (1.6)	74.1 (1.8)	71.2 (1.6)	71.4 (1.5)	71.1 (1.4)
Mean Arterial Pressure (mmHg)	55.0 (2.4)	36.0 (3.2)	19.1 (2.6)	23.6 (2.5)	20.7 (2.7)
Heart Rate (bpm)	68.8 (2.4)	78.8 (3.1)	100.9 (4.0)	100.6 (3.8)	99.5 (3.2)
Oxyhemoglobin Saturation (%)	96.1 (0.3)	94.8 (0.6)	94.3 (0.8)	90.7 (1.0)	92.5 (0.9)

That G-force reduced accuracy, but did not affect reaction time, suggests there was no speed-accuracy trade-off, and thus this result can be interpreted as an impairment in visual perception. Notably, the visual perception decrement was not influenced by either the difficulty or the location of those stimuli (foveal vs. peripheral). At a neurocognitive level, visual discrimination requires a range of neural processes that are also required for visual working memory, and so it might be expected that an impairment in visual discrimination would also result in an impairment of working memory. However, in the present study, the visual stimuli used for the working memory task were exceedingly easy to discriminate, providing a high degree of dissociation (independence) between the visual perceptual and mnemonic processes (functions). As a consequence, the results suggest that, as well as G load not noticeably affecting visual working memory, the visual processing impairment seen in the visual discrimination task was not sufficient to interfere with the relatively trivial visual processing demands associated with the visual working memory task.

Assuming that the visual impairments described above were caused by local tissue hypoxia, then it seems that the impairments were likely attributable to retinal, rather than cerebral ischemia. During exposure to a gradually increasing G load, there is typically a sequence of symptoms that starts with loss of peripheral vision, followed by loss of central vision and eventually by loss of consciousness.[15] Those symptoms are attributable to local ischemia due to the G-dependent multiplication of the hydrostatic pressure drop in the arteries between the heart and the head.[15] That less G elevation is required to induce critical ischemia in the retina than in the cerebral cortex, despite lower arterial pressure at the level of the cortex, can be explained by two mechanisms. Specifically, at increased G loads, the "siphon effect" within intracranial blood vessels may act to preserve flow, and hence oxygenation of the cerebral cortex, even when local arterial pressure drops to zero.[17] Secondly, to perfuse the retina, arterial pressure at eye level needs to be high enough to overcome the intraocular pressure.[26] It can be estimated that eye-level mean arterial pressure in the present 3-G exposure was about 22–26 mmHg (i.e., mean arterial pressure at the level of the prefrontal cortex was 18–20 mmHg). Since the intraocular pressure at 3 G is about 14 mmHg,[9] the effective perfusion pressure in the retinal vessels is likely to have been only 8–12 mmHg. Although nominally somewhat higher than in the 3-G exposure, eye-level mean arterial pressure was also low in the 4-G exposures (Fig. 3), suggesting markedly reduced retinal perfusion in these conditions.

Considering such low retinal perfusion pressures, as estimated on the basis of present measurements of mean arterial pressure and on previous data,[11] the relatively modest reduction in visual discrimination accuracy seems somewhat surprising. Presumably, without AGS the subjects would, on average, have lost peripheral vision at about 3.5 G. Indeed, although the effect size (30%) of the reduction in visual discrimination accuracy attributable to the G-force manipulations (Fig. 4) would normally be described as moderately large,[6] when considered relative to the mean performance level of the 1-G control condition, the magnitude of the impairment was only approximately 2%. So, the impact of G exposure on the subjects would appear small, and whether this level of impairment is operationally relevant remains an important empirical question.

Given that such a small change in visual discrimination performance was identified, it is noteworthy that the present experimental paradigm was able to differentiate between visual discrimination and working memory function – particularly given the inherent difficulties of obtaining measures of cognition that are not overly confounded by the psychological and physiological effects of centrifugal acceleration. Accordingly, the present paradigm may represent a useful means with which to extend our understanding of the differential effects of low-G exposure on cognition.

Even though the present 3- and 4-G exposures induced substantial reductions in cerebral oxygenation, no effect of deoxygenation was found for working memory performance, a cognitive function that relies heavily on attention and short-term memory capability, but very little on visual processing (particularly in the present study, where large, easily discriminable stimuli were used). Research in monkeys (invasive) and humans (fMRI) has shown that the neural structures most strongly underpinning working memory (and in particular the retention of task-relevant stimuli) are the bilateral prefrontal cortices (Danskin et al.[7]). As the NIRS probe of the present study assessed oxygenation over the left frontal cortex, this would provide an approximate measure of oxygenation in lateral prefrontal cortices. Therefore, the null result from the present working memory task is in line with the fact that cerebral functions are more resilient than retinal functions to headward acceleration, not only because of the aforementioned intraocular pressure and "siphon" effects on local perfusion, but presumably also because CNS functions appear less sensitive to hypoxia than do retinal functions (Leber et al.[19] and Peacock et al.[29]). Somewhat at variance with the present results, Levin and coworkers[20] found that memory encoding (lateral prefrontal cortex[7]) was reduced by 10%, whereas memory retrieval was intact during exposure to G loads corresponding to 70% of the relaxed G tolerance. Although the observations by Levin et al.[20] are yet to be replicated, Biernacki and colleagues[3] reported

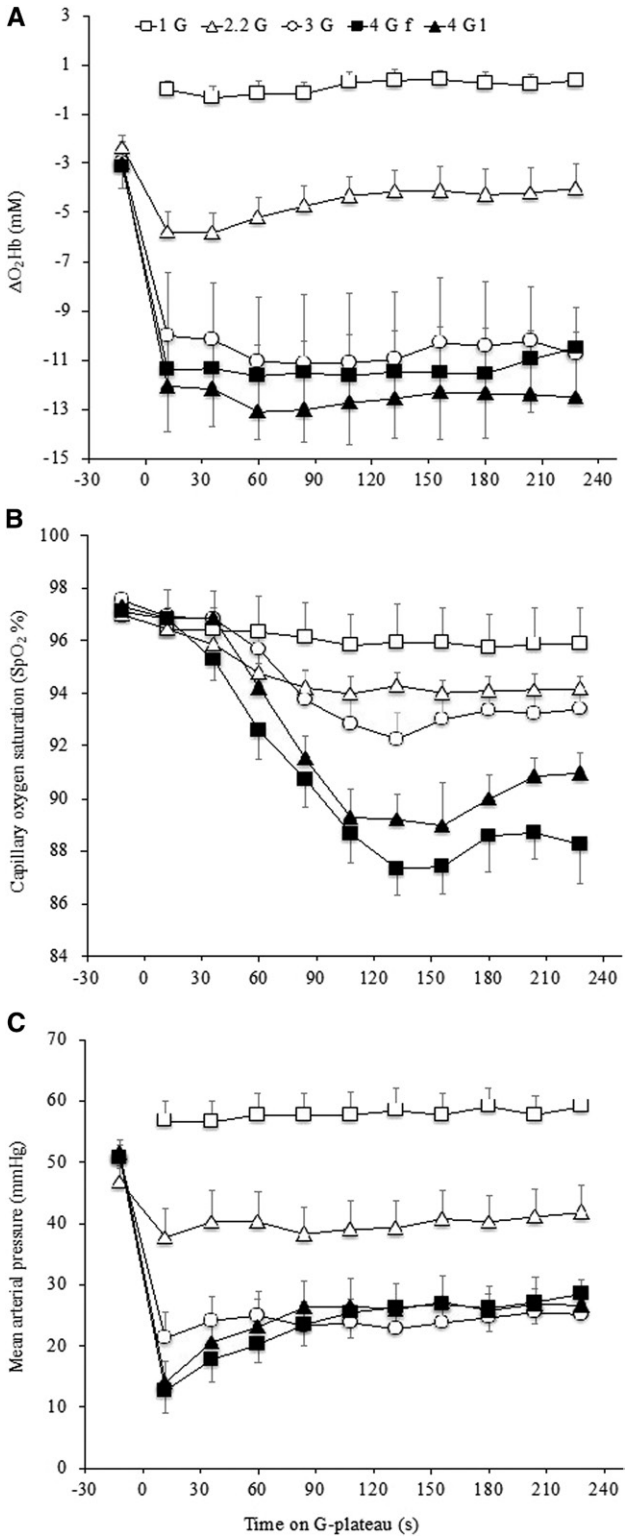

Fig. 3. Physiological variables are shown as functions of both the experimental condition and time spent at each G plateau, where time 0 denotes baseline values at 1 G before centrifugation. Data are means with standard errors of the means (N = 14) for changes in cerebral oxyhemoglobin (3A), as well as absolute values for capillary oxygen saturation (3B) and mean arterial pressure (3C).

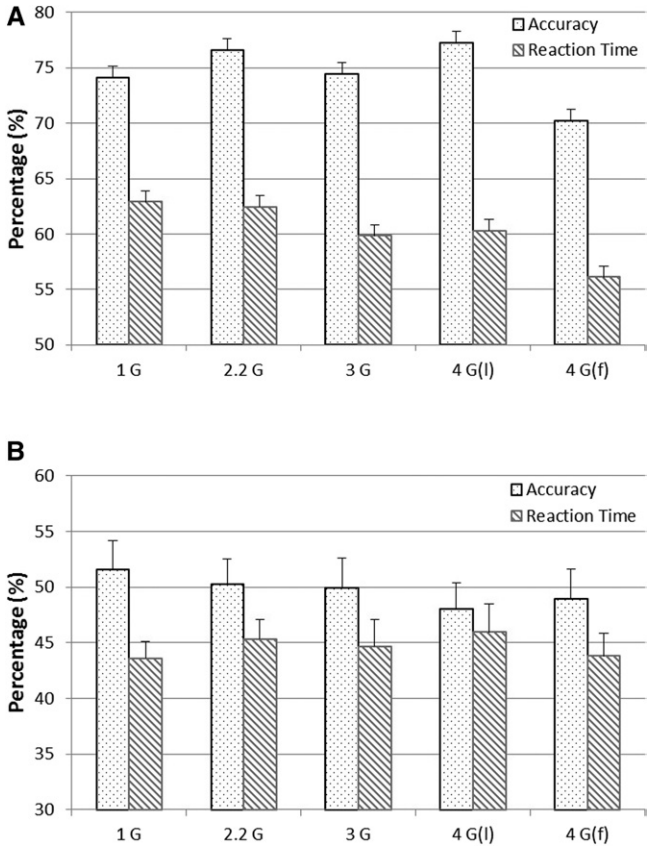

Fig. 4. Accuracy (%) and reaction times (% of 1 s) for the working memory task are shown (N = 15; 4A), as well as the accuracy (N = 14) and reaction times (N = 15) for the visual discrimination tasks (4B; collapsed across easy and difficult, foveal and peripheral conditions). Data are means with standard errors of the means, shown as a function of G-force conditions (defined on the abscissae).

impaired visuospatial memory performance at significantly higher G_z (+6.9), which may indicate that there is an effect on working memory at subthreshold G_z, but that the effect size (given the present sample size) was not large enough to be detected.

The present study included four experimental conditions: 2.2 and 3 G without AGS and 4 G with AGS, with and without pressurization of the AGS abdominal bladder. Of these, the 3 G and the 4 G with the full AGS pressurized might be considered operationally relevant. That exposure to 2.2 G did not affect visual perception suggests that our results were not confounded by vestibulo-ocular reflexes,[12] G-excess illusions[34] or other distracting influences associated with the rotation. Thus, the tangential acceleration of the centrifuge was similar in the 2.2 and 3.0 G exposures, and the difference in gondola roll displacement between the G loads was small (63° vs. 70°), suggesting similar stimulation of the semicircular canals in both of those G exposures. The rationale behind adding a 4-G condition without pressurizing the AGS abdominal portion was to exaggerate the hydrostatic pressure difference in arterial pressure between the level of the eyes and that of the cerebral cortex, thereby provoking hypoxia in the cerebral cortex more than the retina. The results, however, showed no significant differences between the 3-G and any of the 4-G conditions, neither in frontal cortex oxygenation nor in the visual discrimination and memory functions.

It is concluded that visual discrimination accuracy, but not visual working memory, was reduced by exposures to 3–4 G in

the head-to-foot direction. That discrimination impairment is attributed to G-induced retinal ischemia.

ACKNOWLEDGMENTS

This study was supported by the Swedish Armed Forces (Grant No: 922: 0905).

Financial Disclosure Statement: The authors have no conflicts of interest to report.

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