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A.H. Wertheim

PILOT STUDIES ON OBJECT MOTION
PERCEPTION DURING LINEAR SELF-
MOTION AFTER LONG DURATION CEN-
TRIFUGATION OF HUMAN SUBJECTS

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TNO-report IZF 1993 B-3
A.H. Wertheim

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SUMMARY

Four experiments are reported. They were carried out with the purpose of investigating whether we could use and optimize a particular experimental paradigm to investigate the effects of long duration centrifugation of human subjects. The method involved the psychophysical measurement of visual thresholds for perceiving object motion during self-motion on a linear track sled (acquired by the TNO Institute for Perception from the European Space Agency). Since the experiments were of a preliminary nature—we cannot (yet) draw definite conclusions as to their theoretical interpretation. Nevertheless it can be concluded that we have indeed developed an optimal method. In addition, we have arrived at two hypotheses, which can be tested in further research. According to the first hypothesis, long duration centrifugation affects the way in which visual information interacts with otolith reactivity. According to the second hypothesis, subjects who rely largely on visual information for a correct percept of egomotion are more susceptible to centrifuge induced sickness than others.

Pilot-studie over de objectbewegingsperceptie gedurende lineaire eigenbeweging na 'angdurig verblijf van mensen in een centrifuge-gondel

A.H. Wertheim

SAMENVATTING

Vier experimenten worden gerapporteerd. Zij werden uitgevoerd met het doel na te gaan of een bepaalde experimentele methode geschikt is, en kan worden geoptimaliseerd, voor onderzoek naar effecten van een langdurig verblijf van mensen in de gondel van een centrifuge. De methode betreft de psychofysische bepaling van drempels voor het zien van beweging van een visuele stimulus, terwijl de waarnemer middels een lineaire sleebaan heen en weer wordt bewogen (het betreft hier de slee van de European Space Agency, die momenteel bij het Instituut voor Zintuigfysiologie TNO is gestationeerd). Omdat de experimenten in de eerste plaats een verkennend karakter hadden, kunnen (nog) geen definitieve conclusies getrokken worden met betrekking tot de theoretische betekenis van de vergaarde data. Wel kan worden geconcludeerd, dat de ontwikkelde methode optimaal is. Bovendien hebben de resultaten tot twee hypothesen aanleiding gegeven. Volgens de eerste hypothese beïnvloedt het centrifugeren de wijze waarop visuele informatie interacteert met informatie afkomstig uit de otolieten. Volgens de tweede hypothese zijn personen die sterk afhankelijk zijn van visuele informatie voor het onderhouden van hun perceptie van eigenbeweging, gevoeliger voor het ontstaan van door de centrifuge geïnduceerde bewegingsziekte, dan anderen.

1 INTRODUCTION

In an experiment performed several years ago, former astronaut Dr. W.J. Ockels was rotated in the gondola of a human centrifuge for a period of 1.5 hours, with a centrifugal force equal to 3G. Since he was lying on his back and since the gondola could swing out, the resultant of the centrifugal and gravitational forces acted on his body in the x-direction (which is the same direction as in which gravitation acts on our body when normally lying on our back). After centrifugation Ockels was motion sick for many hours and recognized that his symptoms corresponded largely to those which characterize space sickness. This discovery prompted a series of further experiments, carried out to confirm this finding, first with three astronauts, and later with students and Air Force pilots as subjects (see for some detailed reports Bles et al., 1989; Bles & De Graaf, 1993; Bles & Van Raay, 1988; Ockels et al., 1989, 1990). It was suspected that the symptoms of sickness were caused at least partly by some kind of adaptation or recalibration of the vestibular system. Since in such centrifuge experiments there appeared to be time available for some additional experimentation, they provided an opportunity for carrying out a number of pilot studies related to the issue of vestibular adaptation. Their particular purpose was to see if a method, which was being developed in another research project—to assess psychophysically the brain's assessment of ego-velocity during self-motion (see Wertheim & Bles, 1984; Wertheim & Mesland, 1993)—could be used here to obtain insight into these vestibular adaptation or recalibration processes.

It should be emphasized here that the results of the present experiments cannot not yet be regarded as definite. Dependent of the state of affairs with the other project mentioned above, the measurement procedures in the present experiments were not (yet) optimal in all cases. Nevertheless we chose to proceed with the centrifuge associated pilot studies, and not to wait until the other project was finished, simply because such centrifuge experiments are very expensive and do not happen very often. Thus we felt that we should not miss an opportunity to participate in them and at least carry out some preliminary studies, and in addition, we suspected (rightly so) that the studies to be reported here, would contribute to the other project as well. Hence, the present report should be seen as a progress report, as a summary of preliminary research, such as is customary before a definite investigation can be undertaken.

The work reported here was carried out under project B92-40, and has received additional funding from the European Space Agency (ESA) and from the Netherlands Organization for Scientific Research (NWO). Experiments I to III have been carried out in collaboration with Ir. R.J.A.W. Hosman from the Department of Aeronautics of Delft University of Technology, from which some of the equipment was borrowed, and whose graduate students, P. Zeppenfeld and M. Beuning, also participated. Experiments III and IV were carried out in collaboration with B.S. Mesland, a graduate student stationed at the TNO Institute for Perception, as part of her PhD requirements.

2 THEORETICAL BACKGROUND

Since the theoretical rationale underlying the experimental methodology of these experiments has extensively been described elsewhere (e.g. Wertheim, 1981, 1987, 1990, 1991; Wertheim & Bles, 1984; Wertheim & Van Gelder, 1990; Wertheim & Mesland, 1993), it will here be described in general terms only.

When we move around in space, the image of the visual environment sweeps across our retinae. But, normally, the perceptual system does not take this as evidence that the environment is moving: we keep seeing a stationary world. Apparently the visual system "knows" that the retinae themselves move in space—and how—and uses this information when interpreting retinal image motion. On the neurophysiological level, this "taking into account process" can be described formally as a comparison process between two signals. One signal, henceforth to be termed the "retinal signal" encodes retinal image velocity. The other signal, here to be called the "reference signal", encodes the velocity of the eyes in space. We may conceptualize these signals as vectors, and the visual system as carrying out a comparison between them. When the signals are equal, image motion on the retinae must have been caused entirely by movements of the eyes in space. The visual system then "concludes" that it's the eyes that move, and not the environment. Consequently, a percept of a stationary environment is generated. But when we look at a visual stimulus that moves in space (against a dark or unstructured background) while we ourselves—i.e., our eyes—also move in space, the situation is different. Now the two signals differ. The visual system then considers their (vectorial) difference as caused by real motion of the stimulus, and consequently generates a percept of a stimulus moving in space with a velocity proportional to this vectorial difference. Hence the percept of object motion or stationarity relative to external space depends on whether retinal and reference signals are equal or not. If for some reason the reference signal is incorrect, we make a perceptual error and misperceive the velocity, motion or stationarity of visual objects in space.

When we say that a reference signal is incorrect, it means that the visual system receives incorrect information about how the eyes move in space. To understand why such information might be incorrect, it should be understood where it stems from: it derives from two other neural signals, one encoding how the eyes move in the head and one encoding how the head moves in space. The signal which encodes how the eyes move in the head is usually called the "efference copy" (it is thought to be generated by the oculomotor units in the brain in parallel with commands to the oculomotor musculature). The other signal, the one which encodes how the head moves in space, originates from various sources, prominent amongst which are vestibular afferents (other sources are visual afferents which stem from optic flow from the retinae, afferents from the neck muscles, other kinaesthetic feedback, and possibly also particular cognitions as to how we think we are moving). The "efference copy" and the signal which encodes head movements in space—the "head in space signal"—should also be viewed as vectors:

they are added (vectorially) to yield a compound vector that encodes how the eyes move in space. It is this compound vector which is carried by what we have called the reference signal. Obviously, if vestibular reactivity is affected after a long stay in the centrifuge, the vestibular input to the ("head in space" component within the) reference signal will be affected. Consequently the reference signal will change and, as mentioned above, errors in the perception of object motion and stationarity (relative to external space) may occur during movements of the head in space.

This yields the experimental method to assess the effects of long duration centrifugation on vestibular functioning: we should simply measure whether after centrifugation errors occur in the perception of object motion and stationarity during vestibular stimulation (e.g., during egomotion). From these errors we can learn what happened to the reference signal, i.e. what happened to the vestibular afferents from which it is constructed.

3 EXPERIMENTAL PARADIGM

Several years ago the TNO Institute for Perception acquired a linear track sled from ESA, originally used for vestibular research on board the 1985 D1-Spacelab mission. This apparatus allows us to move subjects in a controlled fashion along a linear track (max ampl 6 m) at a given velocity, which enables us to perform the kind of experiments required for our purpose.

The basic idea is to move a subject on the sled (in forward or backward direction) in between two screens parallel to the sled's track. On the screens we present a stimulus pattern that can be moved independently parallel to the sled's track, also in either forward or backward direction. We then adjust the velocity of the stimulus pattern until the subject, who is moving between the monitors, reports that it is seen as stationary (relative to external space, i.e. relative to the screen, not relative to herself). Since at this point—the Point of Subjectively Perceived Stationarity (PSS)—the pattern is seen as stationary in space, the retinal signal must be equal to the reference signal. In other words, retinal image velocity at the PSS is a quantitative measure for the reference signal: all we need to do is to calculate retinal image velocity at the PSS. If we measure the reference signal in this way, there are three possible outcomes.

- 1 No perceptual errors occur: at the PSS the stimulus pattern is indeed physically stationary in space. In this case retinal image velocity at the PSS—the reference signal—is exactly equal to the velocity of the eyes in space, which means that the reference signal is correct, i.e. we may assume that it receives correct vestibular input.

- 2 Perception is in error: at the PSS the stimulus moves actually slightly in the same direction as egomotion. In this case retinal image velocity at the PSS—the reference signal—is slightly less than ego velocity. Hence the reference signal is too small (it has a gain less than 1), which implies that its vestibular input is insufficient: it provides an underestimation of head velocity in space to the visual system.
- 3 The opposite perceptual error occurs: at the PSS the stimulus moves actually slightly in the direction opposite to egomotion. In this case retinal image velocity at the PSS—the reference signal—is slightly larger than ego velocity. The reference signal, being too large (with a gain larger than 1), then provides an overestimation of head velocity in space to the visual system. This would suggest that its vestibular input is too strong.

Basically this is the experimental paradigm which allows us to measure the effects of centrifugation on vestibular functioning: we just measure if after centrifugation the gain of reference signals during egomotion has changed.

However, the situation is actually somewhat more complex. The point is that the above theoretical reasoning only holds if the reference signals of our subjects consist only of vestibular afferents. But, as mentioned above, they usually include an efference copy component (when eye movements are made), and a "head in space component" which only partly stems from vestibular afferents, and which is affected by information from other sources as well (e.g., from optic flow across the retinae). How then can we be sure that it is really the vestibular input to the reference signal which is affected by centrifugation. To reach such a conclusion we must set up the experiment in such a manner that we can be reasonably sure reference signals receive only vestibular and no other inputs.

This implies additional experimental requirements. First, we should provide the subject with a straight forward head stationary fixation point to prevent the occurrence of eye movements in the head. That should keep the efference copy component in the reference signal at zero level. But it makes the task for the subject somewhat more complex, because it requires the subject to keep the eyes focussed on the forward fixation point, while directing attention to the peripherally visible stimulus on the screens alongside the sled's track. Second, we should reduce the optic flow contribution to the ("head in space" component in the) reference signal to negligible levels. This can be done by carrying out the experiment in total darkness and by showing the visual stimulus on the screen only very briefly (see e.g. Wertheim, 1987, 1990). However, other inputs to the ("head in space" component in the) reference signal, such as somatosensory or cognitive influences, are less easily controlled. In the present studies we have assumed that they are not affected by centrifugation, but this assumption can be questioned (see Wertheim & Mesland, 1993).

In the experiments to be reported here, vestibular stimulation consisted of linear acceleration of the subjects on the sled. Therefore, within the vestibular apparatus only the otolith subsystem is stimulated. The otoliths function as linear accelerometers and generate vestibular afferents that encode linear ego (i.e., head) velocity in space. We thus assume that measuring reference signals during egomotion on the sled after centrifugation implies (in darkness and with only briefly visible stimulus patterns—see above) measuring whether, and how, centrifugation affects the otolith response.

4 EXPERIMENT I: ASTRONAUT SUBJECTS

4.1 Introduction

Soon after the initial discovery of "Sickness Induced by long duration Centrifugation" (SIC) by Ockels—at the Netherlands Laboratory of Air and Space Medicine (NLRGC) in Soesterberg, next to the TNO Institute for Perception—a first attempt was made to investigate this phenomenon systematically with three former astronauts as subjects. The purpose of this centrifuge experiment was to compare the sensation of SIC to space sickness (see Bles et al., 1989; Ockels et al., 1989, 1990). This occasion provided the first opportunity for a sled experiment. Its purpose was to see whether we could obtain indications of an effect of centrifugation on otolith afferent reactivity.

4.2 Method

Subjects were seated on the ESA-sled and could be moved sinusoidally forward and backward at a frequency of 0.15 Hz, and a maximum speed of linear egomotion of 109.5 m/s in forward and backward direction. The subjects were seated with the head fixed to the chair on the sled. They were instructed to keep their eyes focussed on a small fixation light that was positioned straight in front of the eyes, at 2 m in front of the end point of the sled's forward motion on the track. Thus, when moving on the sled, no eye movements relative to the head were made (apart from very small vergence eye movements). EOG was measured continuously to verify if indeed no eye movements were made (which was the case), and the EOG trace was recorded on line on computer disc. Next to the sled's tracks, opposite to each other, and at eye level, two large video monitors (40 x 40 cm) were placed, parallel to the tracks. The monitors and their electronic support system were borrowed from the department of aeronautics of Delft University of Technology. When the sled reached its maximum velocity, just before the subjects head moved between the monitors, a black and white checkerboard pattern was briefly made visible on the screens (400 ms). Hence the pattern was always seen peripherally, as the subject kept looking straight ahead (see Fig. 1).



Fig. 1 Experimental set up (the eye fixation point is positioned at the place where the photograph was taken).

During its brief presentation, the pattern either remained stationary on the screens or moved forward or backward at a given velocity, i.e. with or against the direction of the sled. The velocity of the pattern was controlled by the experi-

menter, who could adjust it by hand with a potentiometer while reading its setting from a digital volt meter. The experiment was carried out with the main lights in the experimental room extinguished, but not in total darkness. The room remained visibly quite well due the fact that we simply could not monitor the experimental apparatus in total darkness. The subjects were asked to report verbally, by means of an intercom system, whether they saw (peripherally) motion of the checkerboard pattern on the screen and if so, in which direction. Care was taken to remind the subjects that we wanted to know if they saw the patterns move on the screens, i.e. in *space*, and not relative to themselves.

The PSS, the point of subjectively perceived stationarity was defined as the midpoint between two opposite thresholds, the "with-threshold" and the "against-threshold". The with-threshold is the threshold for perceiving motion on the screens in the same direction as the sled. The against-threshold is the threshold for perceiving motion on the screens in the direction opposite to the direction in which the sled moved.

The thresholds were obtained with the so called staircase method. Thus the with-threshold was obtained as follows: the first time the pattern was made visible it moved at its maximum (70 cm/s) velocity across the screen in the same direction as the sled. This was always clearly above threshold. When the subject reported that motion was perceived in the with-direction, the experimenter adjusted the potentiometer to reduce the velocity of the pattern at the next presentation. When the subject mentioned for the first time that the pattern appeared to be stationary or to move in the other direction (opposite to the direction of the sled), pattern velocity was increased on the next trials, until it was again seen as moving with the sled. After this, pattern velocity was reduced again and so on. After four such turning points the measurement was ended and the mean of the velocities of the pattern at these three turning points was calculated. For the sake of reliability, the measurement was then repeated once again, and the mean of the two calculated means then served as the threshold score. The against threshold was measured similarly, starting with a trial in which the pattern moved at 70 cm/s in the direction opposite to that of the sled. From these threshold velocities retinal image velocity at each of the two thresholds was calculated as the difference between the velocity of the sled (109.5 cm/s) and the threshold velocity of the patterns. The mean of these two threshold retinal image velocities then served as the retinal image velocity at the PSS, i.e. this value reflected reference signal magnitude.

This whole experiment was carried out three times, once before the subjects entered the centrifuge, once about 20 minutes after they had left the centrifuge, and once another 2 hours later.

4.3 Results

The results are summarized in Fig. 2.

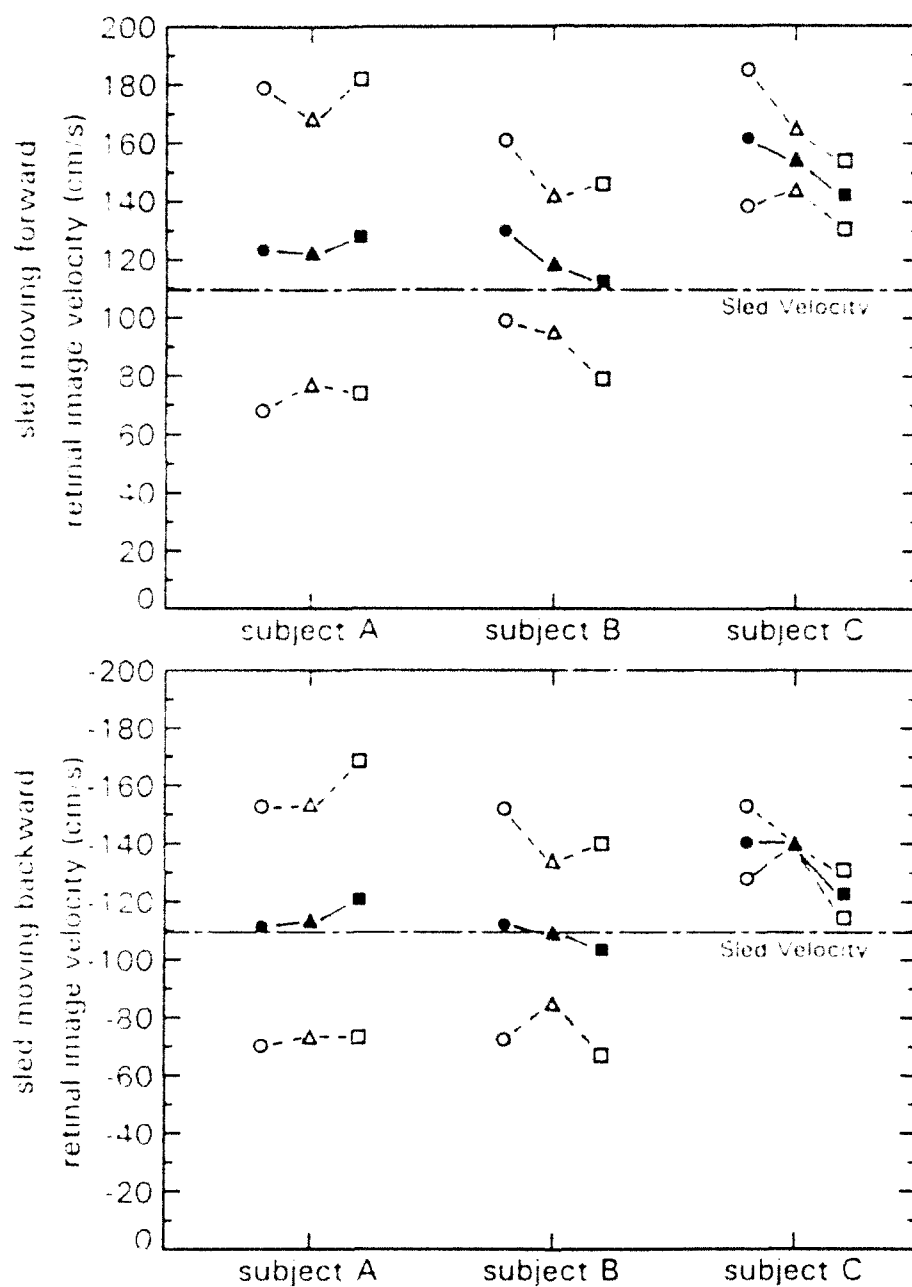


Fig. 2 With thresholds (lower dotted lines), against thresholds (upper broken lines) and PSS (drawn lines) expressed in terms of retinal image velocity before centrifugation (circles), 20 min after centrifugation (triangles) and 2 hours after centrifugation (squares). Ego velocity in space (sled velocity) was 109.5 cm/s. Note that the closed symbols describe the magnitude of the reference signal. Each data point mean of two replications. Upper panel: sled moving forwards. Lower panel: sled moving backwards.

As can be seen, the reference signal appeared to be slightly oversized in conditions where the sled moved in forward direction, and appeared to be slightly smaller (more or less correct with subjects A and B) when the sled moved in backward direction. There was no systematic effect (across subjects) of centrifugation on the magnitude of the reference signal. The size of the no motion range, i.e. the distance between the two opposite thresholds, varied largely between subjects. All subjects showed a small reduction of this no motion range at the first measurement taken after the centrifuge run.

In this experiment (as in all centrifugation experiments) the severity of motion sickness after centrifugation was measured. It appeared that the subject who suffered most (subject C) was also the one whose reference signal gain deviated most from 1 on all trials (see Fig. 2).

4.4 Discussion

No clear effect of centrifugation on the reference signal was found, apart from the suggestion that the no motion range was slightly decreased after centrifugation. However, this result should be considered with great caution.

First, it should be noted that during forward sled motion reference signal magnitude was larger than it should be, i.e. larger than sled velocity. This is in contradiction to an experiment, performed much later in the context of the other project mentioned above. In that study, which was carried out in absolute darkness, we measured the temporal modulation of the reference signal during the same sinusoidal sled motion as in the present study. It was then found that the modulation reflected the velocity profile of the sled motion in that it was also sinusoidal, but with a gain of approximately 0.8, i.e. reference signal magnitude was smaller than sled velocity (see Wertheim & Mesland, 1993, experiment IV). That result was explained theoretically as follows: reference signals which are composed only of an otolith component are likely to be slightly undersized, because in normal daylight situations they should be properly sized. The point is that in day light circumstances there is optic flow of the environment during ego-motion. As mentioned earlier, this creates an additional component in the reference signal. (It should be noted that no strict additive model is implied here. The precise characteristics of the modification of reference signals by optic flow from the retinae are as yet unknown. Thus when speaking of the "addition of a visual component" we only mean to say that optic flow has the effect of somehow increasing reference signal magnitude.) If a reference signal would already be properly sized without such a visual component, it would become too large in normal day light circumstances, and that would cause illusory motion of the environment. Since usually no such illusions happen in normal day light circumstances, reference signals composed of both a visual and an otolith component are correctly sized. Therefore, without this visual component, i.e. in total darkness, reference signals are undersized.

Along the lines of this reasoning, one explanation for the present finding that reference signals were so large, could be that the room was not really darkened, which may have created an additional visual component in the reference signal.

The creation of an optic flow component in the present experiment could also explain why no effect of centrifugation was observed on the magnitude of the reference signal: centrifugation may have opposite effects on the otolith and the visual components of the reference signal, effects which cancel each other. For example, the centrifuge may have had the effect of reducing the otolith response due to adaptation, while at the same time the visual component is increased. In fact there are indeed indications that when otolith feedback becomes unreliable (i.e., during space flights), the importance of optic flow within the system responsible for human spatial orientation is greatly increased (Bles & Van Raay, 1988; Young & Shelhamer, 1990).

But there is also a second reason why the absence of complete darkness may have affected the results: relative motion between the patterns and the contours of the monitors themselves may have been noticeable, and subjects may have tried to cancel that relative motion. This can be done by comparing the retinal image velocity of the contours of the monitors or the experimental room with the retinal image velocity of the pattern. If so, the subjects compared two retinal signals instead of a retinal with a reference signal, i.e. no inferences can then be made about reference signals.

Another argument why we should be hesitant about the results of this first pilot study—and probably a more important one than the theoretical arguments about a visual component as mentioned above—is that, although the threshold measurement procedure appeared to be satisfactory with respect to the ease with which the subjects could report what they perceived (no ambiguities), its experimental design was actually rather sloppy.

We should doubt the methodological rigidity of this method, because the thresholds were obtained by adjusting the potentiometer by hand. The step size in velocity (the velocity change) between two consecutive trials was neither constant, nor very precise. It varied considerably, dependent on whether the experimenter thought he was close to the threshold or not. If we would have used longer measurement sequences (i.e., taking many small steps) we would have been more precise. However, this was prevented by time pressures.

Another reason for not taking the present results too seriously is of course that a sample of three former astronauts as representative for a normal subject population. Not only is the sample quite small, but these astronauts were also highly trained physically and well acquainted with situations of abnormal egomotions.

The only significant finding across all subjects was that the reference signal was slightly larger during forward egomotion than during backward egomotion. In the later experiment, mentioned above (Wertheim & Mesland, 1993, experiment IV), where the temporal modulation of the reference signal was measured during the same sinusoidal sled motion, it was found that the response sinus (the modulated reference signal) had a small offset relative to the stimulus sinus (i.e., the sinusoidal sled motion), which caused the reference signal to be smaller during backward than during forward egomotion. Since this also explains the presently observed forward-backward difference in reference signal magnitude, we may conclude that at least in this respect we need not doubt the results of the present study.

5 EXPERIMENT II: STUDENT SUBJECTS

5.1 Introduction

This experiment was carried out at the occasion of the second investigation of centrifuge induced motion sickness (see Bles & De Graaf, 1993). It was again performed in collaboration with Hosman from Delft University of Technology, and with the help of the same apparatus from its Aeronautics Department. In this experiment we used a sample of subjects which may be assumed to be more representative of a normal subject population, and we used a somewhat more precise threshold measurement procedure. The purpose of the study was twofold. First we wanted to see if the results would now be different from those obtained with the three astronauts. Second, in this experiment all subjects were centrifugated three times, their head being positioned at different angles inside the gondola. We wanted to see if any effect of centrifugation in the sled experiment was dependent on this factor.

5.2 Method

The experiment was identical to experiment II, apart from the following aspects: six female students from Utrecht University, between 20 and 25 years of age, participated as paid volunteer subjects. In this experiment each subject participated in three centrifuge runs (each one lasting for 1.5 hrs) on consecutive days. During one centrifuge run they were positioned in supine position in the centrifuge, the resultant force of 3G (resultant of the gravitational and centrifugal force) acting in the x-direction (frontal-dorsal). In a second run they were positioned with the head turned over sideward, the resultant force thus acting in the y-direction of the head (perpendicular to the temple), and in a third run their head was positioned such that the resultant force acted largely on the head in the z-direction (from above). After each centrifugation the subjects were seated on the sled as described in experiment I. Since the sled moved only in

forward-backward direction—which means that sled acceleration is always in the x-direction—it was expected that if centrifugation has any effect on the reference signal, it should be most prominent after centrifugation in that same x-direction.

Since there was only half an hour available for measurements on the sled, the threshold measurement method could not be changed to last longer. Thus it was decided to improve the method by trying to measure the with and against thresholds in one measurement sequence, which could then last longer. Thus the measurement sequence began with a clearly above threshold velocity of the checkerboard pattern on the monitors, e.g. the with direction. After the subjects report that motion in that direction was perceived indeed, the pattern was, at the next trial, moved at the same high velocity, but now in the against direction. After a correct response, the next trial consisted again of the pattern moving in the with direction, but now with a lower velocity. When the subject saw pattern motion correctly, it was, at the following trial, presented again with a similarly reduced against motion, and so on until motion in (either one direction) was not any more perceived. We then increased pattern velocity on the next trial of that direction and so on. The measurement was stopped after 10 trials in each direction.

Measurements were taken in two blocks, one with the sled moving in forward direction and one while it moved backward. The whole experiment was carried out once before and once after each centrifuge run.

5.3 Results

These subjects were considerably less motion sick after the centrifuge runs than the three astronauts from the earlier study, and several of them even showed no signs of motion sickness at all. Nevertheless all subjects participated in the sled experiments. However, because of unforeseen technical difficulties, pre-centrifuge baseline measurements before the z-centrifugation runs could not be carried out properly with all but one of the subjects. We also lost data with two subjects in the pre-centrifuge baseline conditions before the y-direction centrifugation runs. Therefore, rather than comparing each post-centrifuge measurement with its own pre-centrifuge baseline, we averaged all successful pre-centrifuge baseline measurements and used this mean score as the baseline against which the post-centrifuge scores were to be compared.

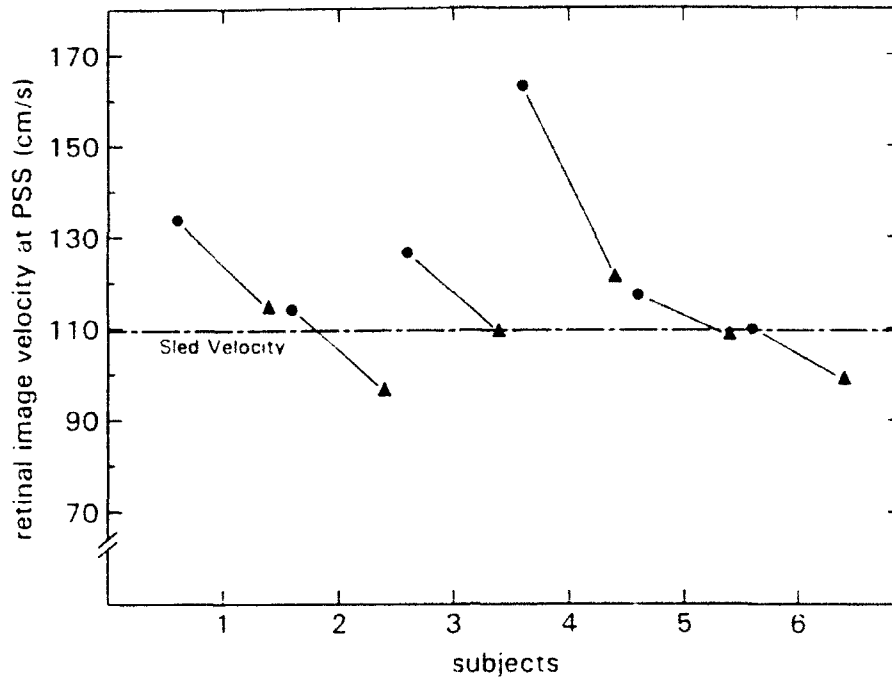


Fig. 3 Retinal image velocity at the PSS, i.e. reference signal size, at forward (circles) and backward (triangles) sled motion. Individual data, averaged across all conditions.

As can be seen in Fig. 3, we again observed that the reference signal was larger (statistically significant) when the sled moved forward than when it moved backward. On average, however, the baseline value of reference signal magnitude in the pre-centrifugation (sled forward) conditions, was not statistically different from those observed with the astronauts in experiment I.

However, this time we observed that after the x-direction centrifuge run, the reference signal had on average (just significantly: $p < 0.05$) increased. After the y- and z- centrifuge runs this was not the case (see Figs 4 and 5).

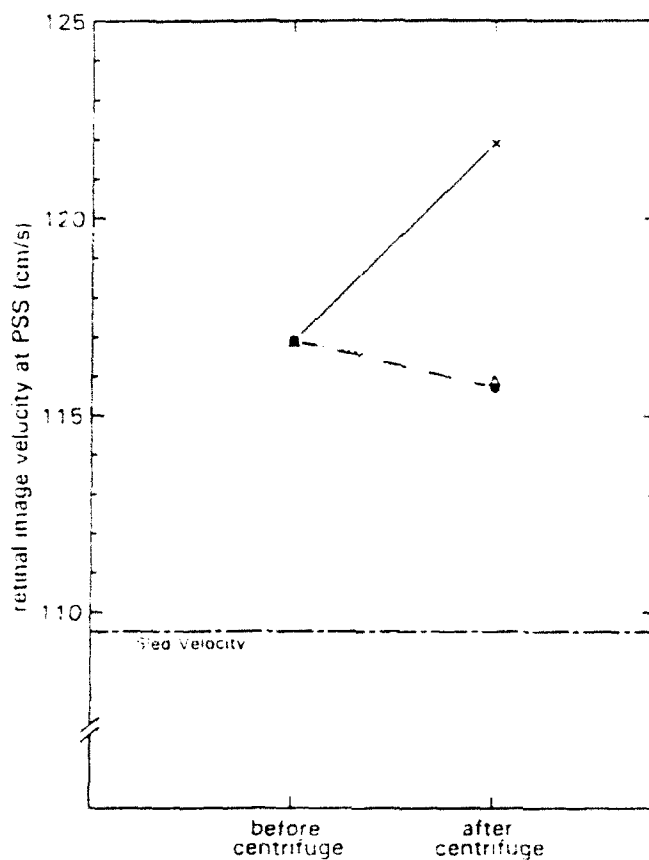


Fig. 4 Retinal image velocity at PSS, i.e. reference signal magnitude, before and after centrifugation. Data averaged across subjects and forward and backward sled motion. Centrifugation in the x-direction (drawn line), in the y-direction (dotted line) and in the z-direction (broken line). Note that only centrifugation in the x-direction had a (statistically significant) effect on the reference signal.

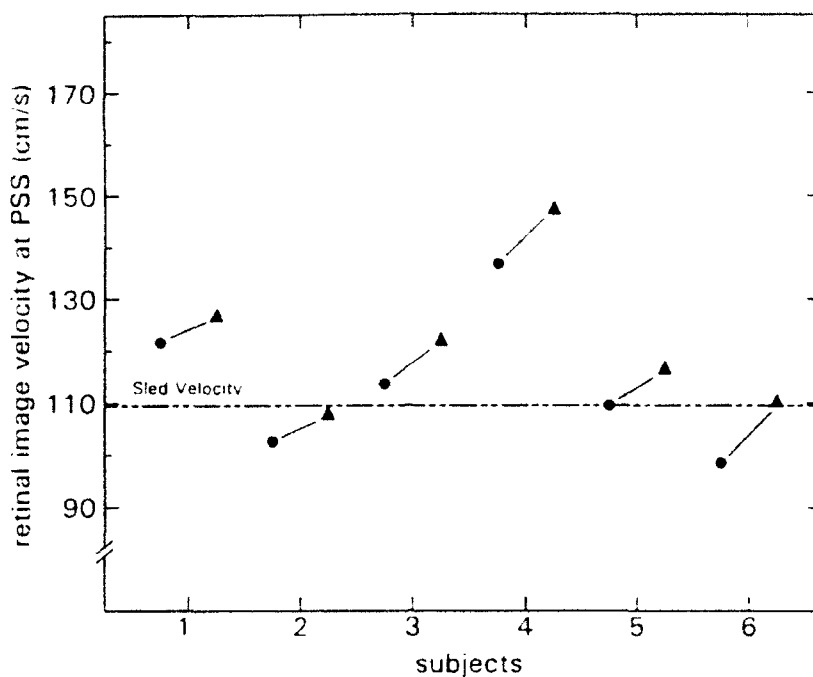


Fig. 5 Retinal image velocity at the PSS, i.e. reference signal magnitude, for all subjects before and after centrifugation in the x-direction. Data averaged across forward and backward sled motion. Circles: before centrifugation; triangles: after centrifugation.

There was no indication that the no motion range was in any systematic way affected by centrifugation, because the method used did not allow for the precise determination of the with- and against-thresholds.

5.4 Discussion

The results of this experiment were encouraging, but not yet satisfactory. This time a small systematic change (increase) was observed in the magnitude of the reference signal after centrifugation in the x-direction. In addition, the effect of sled direction (forward vs backward) was replicated.

But we should not jump to conclusions. One reason is that reference signal magnitude in the baseline conditions was, on average, still approximately equal to that of the astronauts in experiment II: group mean reference signal magnitude was 113.6 cm/s. Hence the reference signal was still larger than expected if it would have consisted of only an otolith component. Since the light level in the experimental room was the same as in the prior study, this should not be surprising. It supports the hypothesis that a visual component was present in the reference signals. As suggested in the discussion of experiment I, it is conceivable that the increase in reference signal gain after centrifugation does not reflect

an effect on the otolith response, but on this visual component, or on the manner in which visual and otolith information interact on the level of the reference signal (as mentioned earlier, we do not know whether they add linearly; the interaction may be quite complex).

Another reason to be hesitant about trusting the data is that, although the subject population may have been more representative, the method may still have biased the results, as it still included a manual procedure in which the step changes in pattern velocity between trials were not standardized. Moreover, each measurement sequence was stopped after a fixed number of trials, independent of the performance of the subjects. Already early in the experiment it became clear that some subjects take longer than others to reach a reliable indication that the threshold is reached. The unreliability of this hand operated threshold measurement procedure may also have been the underlying cause for the large individual differences in baseline magnitude of the reference signal: some of them did indeed have slightly undersized reference signals (see Fig. 5). Therefore it was decided to design a standard, computer controlled, threshold measurement procedure.

If the relatively large size of the reference signals (as observed with some of the subjects in the pre-centrifuge conditions prior to centrifugation) was indeed due to a visual component in the reference signal, we should expect reference signal magnitude in baseline conditions to be reduced if we perform the experiment in absolute darkness. If we then observe no increase in reference signal after centrifugation, that would suggest that centrifugation has a specific (enlarging) effect, not on the otolith response, but on the manner in which visual information modulates the reference signal.

6 EXPERIMENT III: STANDARD PROCEDURE

6.1 Introduction

This experiment was again similar to experiments I and II. It was carried out in conjunction with another centrifuge experiment in which subjects were again rotated at $3G_x$ for a 1.5 hrs period (see Bles & De Graaf, 1993). There were three differences with the earlier experiments.

First, now a computer driven threshold measurement procedure was used.

Second, we tried to prevent subjects from perceiving any contour of the environment, with the help of large black curtains, which were placed around the tracks of the sled. The fixation light was also dimmed considerably. In addition we tried to prevent dark adaptation of the eyes by switching the lights on for a few

minutes before and after each threshold measurement. This procedure really created absolute darkness around the subjects.

Third, an additional sequence of control measurements was taken. This was considered necessary, because the centrifuge induced increase of reference signal magnitude, observed in experiment II, was so small. From an experiment performed in the context of the other research project mentioned earlier, it appeared that the effect of centrifugation observed in experiment II may have been a chance finding: it seemed to be of a magnitude comparable to the natural variation of measurements which occurs when a threshold is measured twice (see Wertheim & Mesland, 1993, experiment I). Hence, in this experiment two subject groups participated: an experimental group, of which measurements were taken before and after the centrifuge run, and a control group, which did not participate in the centrifuge experiment, but whose thresholds were measured before and after a similar 2 hrs waiting interval.

6.2 Method

The experiment (Wertheim, 1992) was again performed in collaboration with R.J.A.W. Hosman from the Department of Aeronautics of Delft University of Technology. The measurements were carried out together with M. Beuning, who also optimized the computer program (which had been written earlier by P. Zeppenfeld of Delft University of Technology; see Zeppenfeld, 1991). The control group was investigated with the help of B.S. Mesland as part of her PhD research program.

The computer program for determining the thresholds consisted of an adapted version of what is known as the PEST-procedure. The PSS was defined as in experiment I, i.e. as the midpoint between the (separately measured) with- and against- threshold. The procedure was as follows: when the *with threshold* was measured, pattern velocity at the first trial was 70 cm/s in the direction *opposite* to the sled. At the next trials, as long as the subject still correctly reported having seen motion in that direction (opposite to the sled), pattern velocity was reduced with a step of 16 cm/s. At a certain point pattern motion is not any more perceivable. The subject then reports that the pattern appears to be stationary on the screens, but the computer continues to reduce the velocity of the patterns at the following trials, and when it passes the zero velocity point it begins to increase the velocity of the pattern in the *with* direction (with the same large step size). This continues until the first trial on which the pattern is finally seen as moving in the direction *with* the sled. At that point the subject is familiarized with all possible percepts. At the next trial the computer reduces the with-velocity of the pattern, but now the step size of the velocity change is halved (8 cm/s). If the subject still perceives with-motion of the pattern the computer continues to reduce the with-velocity of the pattern for a maximum of 3 trials. If it takes more trials before the subject reports stationarity of the

pattern, the computer doubles the step size of the velocity change for the next trial and so on. As soon as the pattern is seen as stationary again, the with-velocity of the pattern is increased again, but the computer then again halves the step size of the velocity change. This procedure has the effect of allowing the subject to gradually approach a step size velocity change of 1 cm/s. At this point the procedure is ended and the last pattern velocity is taken as the with-threshold pattern velocity. Similarly, the against-threshold is measured, which begins with a pattern velocity of 70 cm/s in the same direction as the sled. (Further details about this procedure and its validity vis a vis other staircase methods can be found in Taylor & Creelman, 1967.) Measurements were taken with the sled moving either in forward or backward direction, each threshold being measured once before and once after the centrifuge run (or waiting interval).

The experimental group consisted of 7 male helicopter pilots from the Royal Netherlands Air Force, between 23 and 36 years of age. The control group consisted of 1 female helicopter pilot (aged 26), and 6 female and 4 male paid volunteer students from Utrecht University (aged between 18 and 24 years).

6.3 Results

In the experimental group we lost one subject because his against thresholds were so high, we could not measure them. This appears to be a problem inherent to the method, and there is little that can be done about it (see also Wertheim & Mesland, 1993). We also lost one other subject with whom we were not able to obtain baseline measurements before centrifugation, because of a technical failure. Hence data are reported here for only 5 subjects from the experimental group. In the control group 3 subjects were lost because of very high against-thresholds. Hence we report here the data of only 8 control subjects. In this experiment, as in experiment II, none of the subjects showed severe symptoms of centrifuge induced sickness.

In contradistinction to the prior experiments, this time the magnitude of the reference signal was indeed slightly undersized in the baseline measurements of 4 out of the 5 subjects of the experimental group, and also in all measurements of the control group. On average, reference signal gain in all conditions (apart from the experimental conditions after centrifugation) was 0.92.

Fig. 6 shows that after the centrifuge run there appeared to be a small increase in the magnitude of the reference signal for all subjects in the experimental group. With 4 of the 5 subjects in this group the effect was, however, extremely small (much smaller than in the prior experiment), and well within the range of measurement noise. On the other hand, in the control group half the subjects showed a similar increase in reference signal magnitude, the other half showing a decrease of approximately the same magnitude.

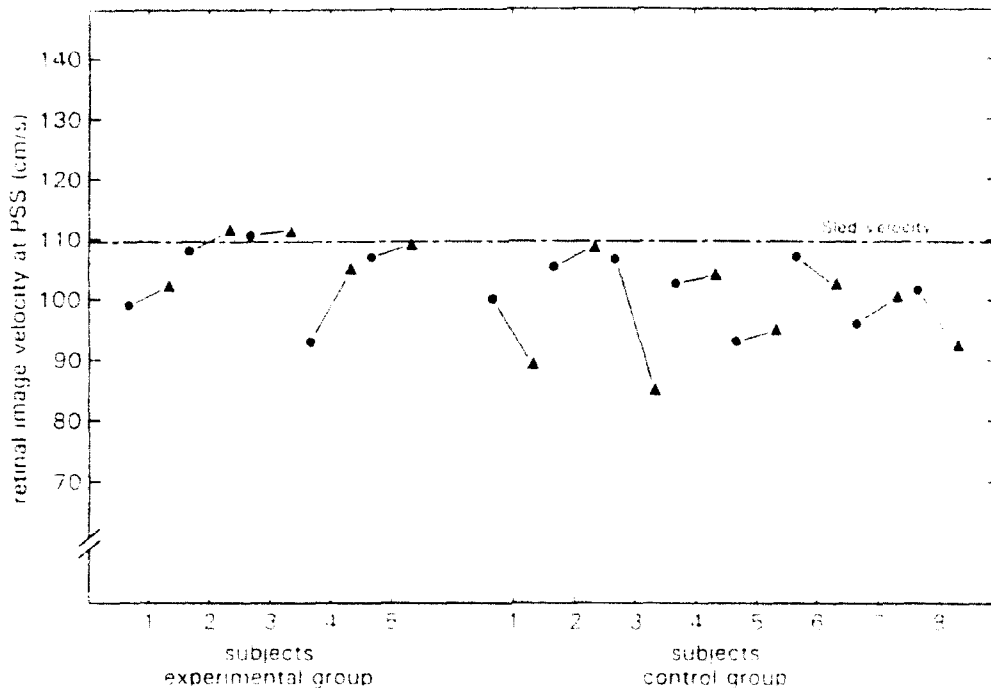


Fig. 6 Retinal image velocity at PSS, i.e. reference signal magnitude, averaged across forward and backward sled motion conditions. Individual data from experimental group and control group. Circles: baseline measurements; triangles: measurements after centrifugation (experimental group) or after a 2 hours waiting interval (control group).

Again a significant ($p < 0.03$) effect was observed of the direction of sled motion: when the sled moved in forward direction, the reference signal was larger than when it moved backward, just as observed in the prior experiments.

6.4 Discussion

In this experiment we seemed to replicate the finding from experiment II (see Fig. 5), that reference signals increase slightly after centrifugation. However, it could still be argued that the effect is again a chance finding. The increase in reference signal after centrifugation was very small and, as can be seen in Fig. 6, on average the effect was of a magnitude well within the range of the repeated measurement variability observed in the control group. It is very difficult to establish whether such an effect is of statistical significance, especially with an experimental group of such small size.

What can be said about the magnitude of reference signals in the present experiment. The presence of a completely darkened environment did indeed reduce reference signal gain to less than 1, as expected. Nevertheless, in the present

study, reference signal gain was still considerably higher than the approximate value of 0.8 as consistently observed in later studies (Wertheim & Mesland, 1993). Was there still a small residual visual influence on the reference signal? When asked after the experiment, most subjects indeed confirmed that the environment was absolutely dark. However, there appeared to be one remaining source of visual information. In cases where the threshold measurement sequence took longer than two or three minutes (which often happened), the after glow of the phosphor on the screens became visible. The optic flow, which was thus generated across the eyes during movements of the subjects on the sled, may still have caused the generation of a small visual component in the reference signal. This explanation was tested later, as we shall see, in experiment IV, and also in the experiments from the other research project mentioned earlier (Wertheim & Mesland, 1993) where we observed the lower 0.8 reference signal gain. In those studies we used exactly the same conditions of darkness, but with the additional requirement for subjects to wear dark sun glasses, which prevented them from seeing the after glow. This is one example of how the current pilot studies yielded information that could be used in the other project (another example is that in the cause of the present pilot studies the computer driven threshold measurement procedure was developed).

As mentioned above, the finding that the experimental group again showed a small but consistent increase in reference signal magnitude, may or may not be significant. However, even if we take the effect at face value, the possibility that a small visual component was still present in the reference signal, implies that we still do not know whether this would be an effect on the otoliths or on this visual component. Actually, the latter seems the more likely, because when the reference signal would have consisted of only an otolith component, a decrease of reference signal size after centrifugation might have made more sense: adaptation of the otoliths is more likely to reduce their response than to enhance it.

As stated earlier, it is theoretically possible that the centrifuge has opposite effects on the otoliths (decreasing their response) and on this small visual component (increasing its magnitude). If so, we may end up with no effect at all or with a slight increase in reference signal magnitude. This issue can only be decided upon if we replicate the centrifuge experiment once more, but with the absolute and complete elimination of any visible background information, i.e. with conditions in which monitor glow cannot be seen because subject wear dark sun glasses.

It should be noted here, that if, in such a replication, we would indeed observe reference signals with a gain of approximately 0.8 (as observed in the later Wertheim & Mesland studies quoted above), and if we would in addition observe either no effect of centrifugation on, or a slight reduction of the reference signal, then we would be more justified to hypothesize that centrifugation acts somehow on the manner in which reference signals are modified visually.

If so, that may have some explanatory power for a phenomenon which is reported by almost all subjects who have spent a considerable time in the centrifuge. The phenomenon is hard to describe by naive subjects and seems to consist of a sensation that the visual world loses its stability during ego-motion, or during movements of the head, if these are made in any plane not perpendicular to the earth's gravitational field. Some subjects have referred to this sensation (which is often nausea provoking) as some kind of perceptual lagging of the visual world: at the beginning of the head movement the visual world seems initially to "stay behind" and then to "catch up" after the head movement is finished. This seems to suggest that the reference signal is initially too small and that its visual compensation (it becoming larger through the addition of a visual component from optic flow)—especially the time course of development of this compensation—is affected. In other words, the compensation of too small reference signals by visual information may have become too slow.

This implies an interesting hypothesis: subjects who rely heavily on visual information for generating reference signals—i.e., subject who have a relatively large visual component because they have only a relatively small otolith component in their reference signal, may suffer more from symptoms of centrifuge induced sickness (and probably also from space sickness) than others. This hypothesis is in accord with the fact that in experiment I, subject C was most sick. His reference signal was very large, so that we may assume that his visual component was very large too. On the other hand, in experiments II and III none of the subjects suffered much from symptoms of sickness (although some degree of perceptual lagging of the visual world was always reported). This includes subject 4 of experiment II (see Fig. 5), who had a very large reference signal, which was comparable to that of subject C in experiment I. That seems at odds with the hypothesis. However, in those first two experiments the procedure for measuring the PSS was questionable, so we should not take the data from these two subjects as either supportive or contradictory to the hypothesis.

In stead, to see if some support for this hypothesis can be found, we need to compare subjects who suffer severely from sickness after centrifugation with subjects who don't. This was the purpose of the last of the pilot experiments reported here.

7 EXPERIMENT IV: COMPARISON WITH SIC

7.1 Introduction

This experiment was performed with new equipment, acquired by the TNO Institute for Perception after the stimulus display monitors and their hardware support system had to be returned to Delft University of Technology. The study was carried out in close collaboration with both B.S. Mesland and M. Beuning.

7.2 Method

The new displays were much smaller (20×22 cm) than the original ones, and the stimulus patterns did not consist of checkerboards, but of a vertical sinusoidal grating (spatial frequency 0.15 cycles/deg). Pilot measurements, taken with these monitors indicated that, because the new monitors were so small, it was hard to perceive the stimulus peripherally. Therefore the monitors had to be placed at a certain angle with the sled track (22 deg), so that they were turned a little toward the eyes. This enlarges the area on the peripheral retina in which the stimulus image projects, and thus makes it better visible. However, it also reduces slightly the retinal image velocity of stripes that are stationary on the screens while subjects move on the sled. The retinal image velocity of such a stationary stimulus then becomes 8% (one minus the cosine of 22 deg) slower than in the prior experiments. Hence in this experiment, retinal image velocity had to be calculated as 92% of the difference between sled and pattern velocities.

With gray filters placed in front of the screens in combination with dark sun glasses, we were able to darken the visual environment completely. No afterglow of the monitors was perceivable, also not after a long period of adaptation to darkness.

Reference signal magnitude was measured in a control condition before and in an experimental condition approximately 30 min after 1.5 hrs of $3G_x$ centrifugation. All thresholds were measured three times within each condition and the PSS was calculated as their mean. Measurements were only taken during sled motion in forward direction.

In this study 15 paid volunteer subjects (14 male and 1 female) participated. They were students from Utrecht University and some junior staff of the TNO Institute For Perception. In all other aspects the present study was identical to the experiment performed with the experimental group in experiment III.

7.3 Results

We lost one subject because of malfunctioning of the apparatus, two subjects who could not, or refused to, keep their eyes focussed on the fixation mark (which prevented a proper determination of retinal image velocity), two subjects because of extremely high against thresholds, and one because of extremely high with-thresholds. Hence only data from 9 subjects are reported.

As shown in Fig. 7, reference signals in the pre-centrifuge conditions were now really less than one, mean reference signal gain being 0.76, which corresponds to the value of approximately 0.8 found in the Wertheim and Mesland (1993) experiments. There remained no evidence of a centrifugation effect.

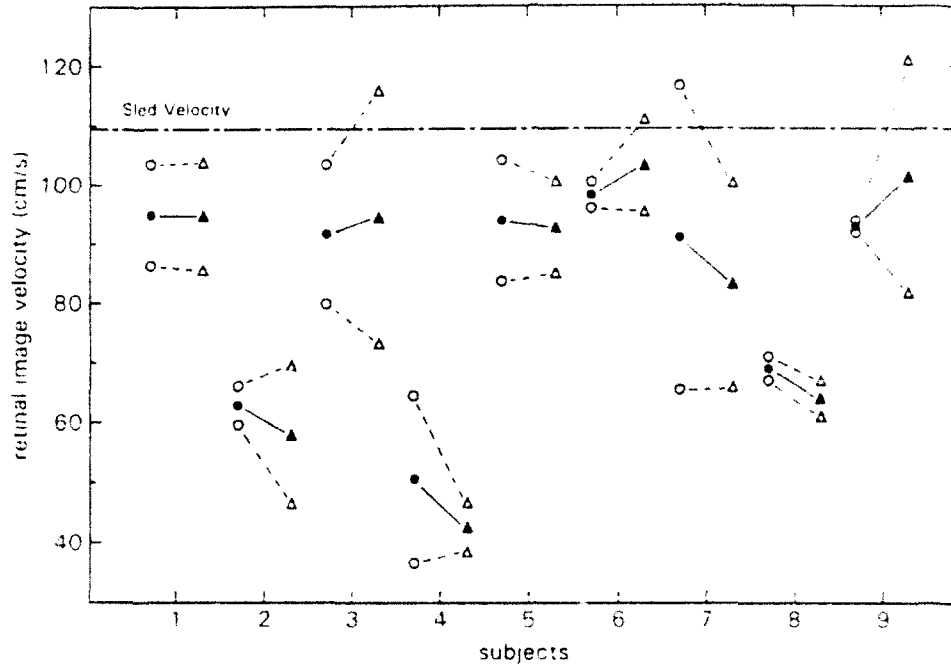


Fig. 7 Retinal image velocity at PSS at the with thresholds (lower dotted lines), the against thresholds (upper dotted lines) and at the PSS, where it reflects reference signal magnitude (drawn lines) for each subject. Each data point represents the mean of three replicated measurements.

Six subjects appeared to be severely motion sick after centrifugation, amongst which were two from which we were able to collect data. They happened to be the two subjects in our data set with the smallest reference signal: subjects 2 and 4 in Fig. 7. Their average reference signal gain was very low: 0.52 (the average gain of the remaining 7 subjects was 0.83). A third sick subject was the one with the very high with-thresholds, (from whose remaining data no PSS could be calculated). If the apparatus would have been able to record that high with-threshold, retinal image velocity at the PSS, i.e. the reference signal, would have been even less than that of the other two sick subjects.

7.4 Discussion

The results from this experiment suggest that when reference signals do indeed lack a visual component, they are not affected by centrifugation. Thus it seems that centrifugation does not affect reference signals which consist of only an otolith component. But that does not mean centrifugation has no effect at all. If we take the effects of centrifugation observed in experiment II (and maybe also in experiment III) at face value, and assume that in those experiments a (small) visual component was also present in the reference signal, another picture is

drawn. It consists of the hypothesis—mentioned in the discussion of experiment III—that centrifugation has an effect on the way visual information influences reference signals that include an otolith component, i.e. on how optic flow patterns across the retinae affect the brain's estimate of egomotion during linear ego motion. It seems that such compound reference signals become more sensitive to visual flow information, or, stated differently, after centrifugation, visual components in reference signals that include an otolith component become somewhat oversized. The finding, that those three subjects who really suffered from centrifuge induced sickness are those whose reference signal consisted of only a relatively small otolith component could be in line with such a hypothesis, because these subjects already rely heavily on visual information anyway, i.e. the visual component in their reference signals is already rather large to begin with.

8 SUMMARY AND GENERAL DISCUSSION

The experiments reported were intended to see if we could use a particular methodology to understand and measure the effects of long duration centrifugation on the vestibular functioning of human subjects. Some of the experiments showed no effects but others did. But in most of them there were still some flaws in the measurement procedure. However, even if we take their results at face value, it should be realized that it may have been difficult to obtain clear cut effects for yet quite another reason: we measured reference signals with subjects who moved (on the sled) perpendicular to the direction of the earth gravitational field. As mentioned earlier, the most salient perceptual effect of centrifugation (the visual "lagging" phenomenon) does not happen during head movements perpendicular to the gravitational direction. Therefore, the results might have been different if we would have been able to measure reference signal magnitude with subjects moving in another direction (e.g., vertically).

However, whatever the doubts we may have about the interpretation of the results of the present experiments, we are still able to draw some more definite conclusions:

- 1 Even in those experiments which were performed with less than optimal methods, we replicated the (later) finding from the Wertheim and Mesland (1993) studies, that reference signals during sled motion in forward direction are slightly larger than reference signals measured during backward sled motion. There remains a problem with subjects who have extremely high thresholds, but otherwise the method has now been optimized sufficiently—especially when viewed in concurrence with the methodological validation and reliability studies of Wertheim and Mesland (1993)—for use in more definite experiments.

- 2 The data have yielded a hypothesis as to a possible effect of centrifugation. According to this hypothesis, long duration centrifugation results in a change in the mechanism responsible for proper visual-vestibular interactions, rather than only in otolith responsiveness. The hypothesis can be tested by performing experiments similar to experiment IV, but with and without the presence of visual background information. The prediction would then be that only in conditions where visual information is present, an increase would happen in reference signal magnitude after centrifugation. The properties of this increase can be measured by varying such parameters as the luminance of the background information and the duration of the stimulus presentations on the screen (see also Wertheim, 1987).
- 3 Another, related, hypothesis is that subjects whose reference signal in normal day light circumstances includes a large visual component (and in total darkness only a small otolith component)—i.e., subjects who rely heavily on visual information for a correct perception of self-motion—are more prone to develop symptoms of centrifuge induced sickness, and probably also space sickness, than others.

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Soesterberg, February 1, 1993

A handwritten signature in black ink, appearing to be 'A.H. Wertheim', with a long horizontal flourish extending to the right.

Dr. A.H. Wertheim

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15. ABSTRACT (MAXIMUM 200 WORDS, 1044 BYTE) Four experiments are reported. They were carried out with the purpose of investigating whether we could use and optimize a particular experimental paradigm to investigate the effects of long duration centrifugation of human subjects. The method involved the psychophysical measurement of visual thresholds for perceiving object motion during self-motion on a linear track sled (acquired by the TNO Institute for Perception from the European Space Agency). Since the experiments were of a preliminary nature—we cannot (yet) draw definite conclusions as to their theoretical interpretation. Nevertheless it can be concluded that we have indeed developed an optimal method. In addition, we have arrived at two hypotheses, which can be tested in further research. According to the first hypothesis, long duration centrifugation affects the way in which visual information interacts with otolith reactivity. According to the second hypothesis, subjects who rely largely on visual information for a correct percept of egomotion are more susceptible to centrifuge induced sickness than others.		
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