Effect of ageing on the ability to adapt to a visual distortion during walking

Rients B. Huitema a,*, Wiebo H. Brouwer b, Theo Mulder c, Rienk Dekker a, At L. Hof c, Klaas Postema a

a Centre for Rehabilitation, University Hospital Groningen, P.O. Box 30.001, 9700 RB Groningen, The Netherlands
b Neuropsychology Unit, University Hospital Groningen, P.O. Box 30.001, 9700 RB Groningen, The Netherlands
c Institute of Human Movement Sciences, University of Groningen, P.O. Box 196, 9700 AD Groningen, The Netherlands

Received 25 November 2003; accepted 28 May 2004

Abstract

Degradation of major sensory systems such as proprioception, the vestibular system and vision may be a factor that contributes to the decline in walking stability in older people. In the present study this was examined by introducing a visual distortion by means of prism glasses shifting subject’s view 10 degrees to the right while subjects walked towards a target (exposure condition). Shifting the view while walking towards a target will cause subjects to alter their heading in such a way that their walking trajectory describes a curvilinear path. It was expected that older people, when compared to young people, would have greater difficulty adjusting their heading and would show a greater decrease in heading stability, quantified by means of the standard deviation of the lateral position (SDLP). This was indeed the case. When performance in a pre- and post-exposure condition, in which subjects walked without prism glasses, were compared to each other, older people (O group) showed a greater decrease in heading stability than young people (Y group) and middle aged people (M group). Furthermore, it appeared that during the exposure condition adaptation effects were present in the Y and M group, which were absent in the O group. It is discussed that this adaptation is a form of realignment of the proprioceptive and visual system. The absence of realignment in the O group is argued to be caused by degradation of the proprioceptive system, which results in a lowering of the proprioceptive bias of vision.

© 2004 Elsevier B.V. All rights reserved.

Keywords: Ageing; Prism paradigm; Realignment; Heading stability; Proprioception

1. Introduction

Falls in older people during walking often result in serious injuries. Reported numbers vary but approximately one third of community living people over 65 years of age report one or more falls each year [1–3]. Approximately 20% of these falls require medical attention and almost 10% result in a fracture [2,4]. Although much is still unknown about factors associated with falls and gait stability in older people, age related changes in sensory input may play an important role.

Three major sensory systems can be distinguished, which provide feedback about the position of our body relative to the environment: proprioception, the vestibular system and vision. It has been well documented that these systems degenerate with age. Older people show a decreased sensitivity of joint receptors in both ankle and knee [5] and the perception-threshold for vibratory stimuli increases with age [6]. Age-related changes have been reported also for the vestibular system and include a decline in primary vestibular neurons and up to 40% reduction of hair cells [7,8]. Regarding the visual system, reduction of the ability to deduce heading from optical flow, reduction in contrast sensitivity, decreased depth perception, restriction of the visual field and reduced acuity are specific age-related changes [9–12]. Although vision declines substantially with age, older people still rely heavily on the visual sense and some experiments report that older people are even more dependent on visual information for maintaining balance during gait than younger people [13,14].
To assess the effects of visual distortions on motor performance and the ability to adapt to these distortions, the prism adaptation paradigm is a frequently employed experimental procedure. Although experiments have been performed in which walking subjects wore prism glasses [15,16], no experiments have investigated the ability to adapt to these distortions during walking and, until now, the prism adaptation paradigm has not been applied to a gait related experiment. In a typical prism adaptation experiment subjects perform a motor task, usually throwing or pointing to a target, while wearing prism goggles [17,18]. During the task, named the exposure condition, motor performance and visual input have to be adapted and realigned. By adding a pre-exposure and post-exposure condition, in which the task is performed without prism goggles, the after-effect of the prism adaptation can be assessed. In these throwing or pointing experiments two specific adaptation mechanisms can be distinguished: strategic perceptual-motor control and adaptive spatial (re)alignment [19,20].

Strategic perceptual-motor control refers to a relatively fast working type of adaptation. It can be viewed as a feed forward system, based on knowledge of results, in which the difference between task-goal and perceived performance is used to adjust the (motor) output. For example, when a subject has just started the exposure condition in a target-pointing task with prism goggles shifting the visual field to the right and he intends to point at a target perceived straight ahead, he will point towards a position to the right of the target. During the pointing movement he might adjust his movement to the left, properly pointing at the target, but in subsequent trials he will already initiate a movement more to the left. This adjustment, probably initially based on a cognitive-verbal strategy ("I know I deviate to the right, therefore I point more to the left"), is referred to as strategic perceptual-motor control.

Adaptive spatial alignment is a much slower process and refers to the changes taking place within a sensory system to make its represented space realign with the represented space of another sensory system. In the previously mentioned example proprioceptive limb space does, at first, not align with visual limb space. During the pointing task, if performed under the proper circumstances, the proprioceptive representation of space will gradually align towards the visual representation of space. However, when a subject is able to fully optimise task performance using constant visual feedback, realignment will hardly take place [19]. In the previous example this would be the case when the complete pointing trajectory is visible to the subject. Concealing a part of the pointing trajectory would prevent constant visual feedback, facilitating realignment. Realignment will cause an after-effect typical for a prism adaptation task: in the mentioned pointing experiment, using prism goggles shifting the visual field to the right, subjects will point left of the target after removal of the goggles.

In the current experiment the prism adaptation paradigm is used for distorting the visual input while subjects walk. Although the paradigm does not directly apply to walking, it is possible that similar effects occur in a walking experiment. When walking towards a target while prism goggles shift the view to the right, subjects will reach the target but their walking trajectory will show a curve right of the midline [15,16]. If realignment were to take place during the exposure condition, in time the curve would decrease and subjects would start walking straighter. In the post-exposure condition an after-effect would then be present resulting in a walking curve left of the midline. However, since there is a constant visual feedback during this exposure condition, it is expected that realignment will hardly take place. Hence, a typical prism adaptation after-effect will most likely be absent.

Instantly after the prism goggles are removed, subjects will have to readjust their heading. Since this readjustment is driven by visual, proprioceptive and vestibular input, a decrease in the latter two may have a negative effect on it. Welford describes in a model, derived from the signal detection theory, that signals from sensory organs and signals within the central nervous system have to be distinguished against a background of random activity. A decrease in signal amplitude leads to a decrease in signal-to-noise ratio, which causes a slowing of performance in older people [21,22]. Based on this theory, it is expected that the decrease in proprioceptive and vestibular output will cause the heading readjustment to take longer in older people, which may have a negative effect on the heading stability. This expectation is verified by recording subject’s walking trajectories before, during and directly after wearing prism goggles. Heading stability will be defined in terms of subject’s deviation from the optimum walking trajectory. It is expected that older people will show a larger decrease in heading stability than younger people when they have to adjust to large changes in visual input.

2. Methods and materials

2.1. Subjects

Thirty-six healthy subjects, divided into three age-groups, participated in the study: 12 young people (Y group), 12 middle aged people (M group) and 12 older people (O group). The age and sex distributions of these groups are presented in Table 1. During intake an anamnesis was taken by means of a standard questionnaire concerning medical history and current use of medication. Furthermore, a short physical examination was performed in which motor ability and possible vestibular disorders were assessed. No subject had a history of motor, vestibular or neurological disorders and all subjects had normal or corrected to normal vision. Subjects in the Y group were recruited from hospital staff and students. Subjects in both the M and O group were recruited through local newspaper advertisements. They all were physically active and lived independently. The study was approved by the hospital’s ethics committee and an informed consent was obtained from each subject.
2.2. Materials

During the experiment subjects wore prism glasses inducing a 10° shift of the visual field to the right. The glasses were covered on the sides preventing subjects from not looking through the glasses. The prism glasses could be worn in combination with glasses already worn by subjects. As a safety precaution subjects wore a girdle that was loosely held by the experimenter not limiting the subjects in their movements. The experiment was carried out in a section of 7.8 by 4.0 metres of a larger gait lab, separated by means of curtains. The section was low on visual stimuli: apart from the targets the section was completely empty, no clearly visible details were present on the white walls or white curtains and the floor had a plain grey colour. The area was illuminated by 12 fluorescent tubes, each 36 W, fitted in a 3.0 m high plain ceiling. A two-dimensional ultrasonic positioning system (adapted version of a motion analysis system, [23]) assessed the position of subjects while walking. The positioning system was attached to a belt around the waist, close to the centre of mass of the subjects. Data from this device were recorded using a 200 Hz sampling frequency and further processed on a personal computer using Matlab 5.3. Time related samples were converted to position related X,Y-coordinates (see Fig. 1) with a resolution of 5.0 mm in the X-direction and 4.0 mm in the Y-direction.

2.3. Procedure and design

The experiment consisted of three conditions: a pre-exposure, an exposure and a post-exposure condition. In all three conditions subjects had to walk towards a target: a 10 cm diameter ball. For each subject the target heights were adjusted to just above the subject’s head. Both targets were hung at 65 cm from the far opposing walls, resulting in a distance between the targets of 6.8 m. Before measurements commenced, the ultrasonic positioning system was calibrated by determining the X,Y-coordinates while subjects were positioned exactly underneath the balls. The coordinates of these two positions were used in the analysis to determine the midline, which connected the two balls.

Subjects were instructed to constantly focus on the ball and to walk towards the ball where they actually saw it, stand still underneath it, turn around, focus on the ball on the opposite side and again walk towards where they saw it. During the pre-exposure condition subjects wore no prism glasses and were instructed to walk one cycle to the first ball and back to the second ball. In the subsequent exposure condition subjects had to walk eight cycles to the first ball and back to the second ball while wearing prism glasses. After completing the exposure condition, subjects were instructed to keep focussing on the ball while the experimenter removed the prism glasses. Immediately after the glasses were removed subjects had to start walking towards the ball, stand still underneath it, turn around and walk towards the ball on the opposite side. This cycle was the post-exposure condition.

During the complete experiment subjects had to await instructions from the experimenter (“walk towards the ball”, “turn left”, “walk towards the ball”, “turn right”) before taking actions. All cycles and conditions were performed without pauses in between. Depending on the walking speed of the subject a complete cycle (two walks and two turns) took 15–20 s. Proper application of the prism glasses between the pre-exposure and exposure condition took about 20 s. Removal of the prism glasses between the exposure and post-exposure condition was instantly and subjects were instructed to start walking towards the ball the moment the glasses were removed.

2.4. Dependent variables

When subjects walk from point A to B the optimum walking trajectory would be a straight line. A way to determine the amount subjects deviate from this trajectory is by calculating the standard deviation of the lateral

![Fig. 1. Walking trajectory and heading-error. When subjects walk from A to B wearing prism glasses they will show a curved walking trajectory. The heading-error is defined as the angle between the subject’s heading and the correct heading. In theory this heading-error should equal the prismatic shift.](image-url)
position (SDLP):

\[
SDLP = \sqrt{\frac{1}{n} \sum_{i=1}^{n} (y_i - \bar{y})^2}
\]  

(1)

in which \( n \) is the number of sampling intervals in the trial, \( y_i \) is the lateral deviation at each sample interval and \( \bar{y} \) the mean lateral deviation of the trial. For each walking trial during the pre- and post-exposure condition this is equivalent to the distance subjects deviated from the virtual midline connecting the two balls: the more a subject deviated from the midline the higher the SDLP.

To determine whether there were differences between age-groups during the exposure condition, the mean heading-error (MHE) was determined. The heading-error is defined as the angle between the subject’s heading and the virtual line connecting the subject’s position and the target (the correct heading, Fig. 1). In theory this heading-error should equal the prismatic shift [16]. Some studies, however, show that parameters like walking speed or perceived target height may influence the heading-error [15,24]. As it is shown in Fig. 1, calculating the heading-error requires differentiating the walking trajectory to obtain subject’s heading. This procedure introduces a high degree of noise. Furthermore, the heading-error is very sensitive to walking induced body sway, especially when the subject is close to the target. Therefore, the heading-error needs to be averaged over all the sampling intervals of all trials, resulting in one MHE for the complete exposure condition:

\[
MHE = \frac{1}{Nn} \sum_{j=1}^{N} \sum_{i=1}^{n} (\text{subject heading} - \text{correct heading})
\]

\[
= \frac{1}{Nn} \sum_{j=1}^{N} \sum_{i=1}^{n} \left( - \frac{dy_j}{dx_j} - \tan \left( \frac{y_j}{x_j} \right) \right)
\]  

(2)

in which \( N \) is the number of trials (16 in exposure condition) and \( n \) is the number of sampling intervals per trial.

To establish if adaptation effects occurred during the exposure condition, the gradient of the line fitting the SDLps of the consecutive exposure trials was calculated (GRADS). During the exposure condition the SDLP is not a suitable measure for heading stability, since the optimum walking trajectory is not a straight line. However, the SDLP does quantify the amount subjects deviate from a straight line, i.e. the lower the SDLP the straighter the walking trajectory. Since the start and end points of the curved walking trajectory equal the positions of the balls, a straighter walking trajectory implies that the deviation from the midline declines. Therefore, a negative GRADS indicates that the subject’s walking trajectory became straighter and that the deviation from the midline declined during the exposure condition. The average SDLP over all exposure trials (SDLPexp) was calculated to quantify the mean amount a subject deviated during the exposure condition.

Walking speed for each trial was calculated as the mean walking speed over the middle four metres of the walked trajectory. This way acceleration effects at the start and deceleration effects at the end of the trial did not influence the calculated walking speed. Averaging walking speed over trials resulted in a mean walking speed for each condition (\( V_{\text{pre}} \), \( V_{\text{exp}} \), \( V_{\text{post}} \)).

2.5. Statistical analysis

To test whether age-groups differed in pre-post differences on SDLP, a repeated measures analysis of variance (ANOVA) was performed on SDLP with one within-subjects factor CONDITION with two levels, pre-exposure and post-exposure [pre, post] and one between-subjects factor AGE-GROUP with three levels, young, middle aged and old [Y, M, O]. To determine whether age-groups were comparable in heading stability during the pre-exposure condition, a comparison of age-group [Y, M, O] means was made by one-way ANOVA for SDLPpre. Furthermore, comparisons of age-group [Y, M, O] means were made by one-way ANOVA for SDLPexp and MHE to determine whether the age-groups showed equal main exposure effects during the exposure condition. To verify whether possible between-age-groups differences in SDLPexp and MHE could be explained by differences in speed, a comparison of age-group [Y, M, O] means was made by one-way ANOVA for \( V_{\text{exp}} \). To test for differences between male and female subjects, comparisons of gender-group [male, female] means were performed by one-way ANOVA for SDLPpre, SDLPexp, SDLPpost, \( V_{\text{pre}} \), \( V_{\text{exp}} \), \( V_{\text{post}} \) and MHE. If a significant effect was found in an ANOVA, a Bonferroni corrected post hoc analysis was performed.

Age-group [Y, M, O] means on GRADS were compared by means of one-way ANOVA. GRADS represents the gradient of the best linear fit through all SDLps of the consecutive exposure trials. Therefore, a between-groups comparison of GRADS is equivalent to the linear TRIAL × AGE-GROUP effect of a repeated measure ANOVA with one within-subjects factor TRIAL with 16 levels [trial 1, trial 16] and one between-subjects factor AGE-GROUP [Y, M, O]. However, by performing an ANOVA on GRADS, post-hoc analysis on the linear TRIAL × AGE-GROUP effect become available. The between-groups comparison of GRADS assumes a linear relationship between SDLP and TRIAL. This linear relationship was used faute de mieux.

All variables were checked for outliers by means of box plots and for normal distribution by means of P–P plots.

3. Results

Fig. 2 shows the mean walking trajectories of the three age-groups. All three conditions, pre-exposure, exposure and post-exposure, are presented in the figure. The upper curves of the exposure condition represent the trajectories...
from A to B and the lower graphs of the exposure condition represent the trajectories from B to A. In the first post-exposure condition subjects walked from A to B and in the second they walked from B to A.

A repeated measure ANOVA for SDLP during pre-exposure and post-exposure-1 condition showed a significant main effect for AGE-GROUP \[ F(2, 33) = 4.29, \ P = 0.022 \] and a significant main effect for CONDITION \[ F(1, 33) = 37.8, \ P < 0.001 \]. More importantly, a significant AGE-GROUP \times\ CONDITION interaction was found \[ F(2, 33) = 4.06, \ P = 0.027 \]. Bonferroni corrected post hoc analysis showed a significantly larger post-pre effect (SDLP\text{post} - SDLP\text{pre}) for the O group compared to the Y group (\(P = 0.024\)).

A significant between-group (age) effects was found for \(V_{\text{exp}}\). Bonferroni corrected post hoc analysis showed no significant effects. No significant age-group effects were found for SDLP\text{pre}, SDLP\text{exp} and MHE (Table 2). A significant difference between male and female subjects was found on \(V_{\text{pre}}\) and \(V_{\text{exp}}\) (\(V_{\text{pre-male}} = 1.25 \text{ m/s}, \ V_{\text{pre-female}} = 1.12 \text{ m/s}; \ P = 0.012\); \(V_{\text{exp-male}} = 1.27 \text{ m/s}, \ V_{\text{exp-female}} = 1.14 \text{ m/s}; \ P = 0.034\)). All other variables (SDLP\text{pre}, SDLP\text{exp}, SDLP\text{post}, \(V_{\text{post}}\) and MHE) did not show significant sex differences.

Fig. 3 shows the average SDLP for each age-group during the exposure condition. In the figure it appears that the SDLP

![Fig. 2. Mean age-group walking trajectories. Upper curves of the exposure condition represent trajectories from A to B and lower curves of the exposure condition represent trajectories from B to A. In post-exposure condition 1 subjects walked from A to B, in post-exposure condition 2 subjects walked from B to A.](image)

![Fig. 3. Average SDLP for each age-group during exposure condition.](image)

<table>
<thead>
<tr>
<th>Variable</th>
<th>Young</th>
<th>Middle aged</th>
<th>Older</th>
<th>(P) value*</th>
</tr>
</thead>
<tbody>
<tr>
<td>SDLP\text{pre} (m)</td>
<td>0.03 (0.01)</td>
<td>0.03 (0.02)</td>
<td>0.03 (0.01)</td>
<td>NS</td>
</tr>
<tr>
<td>SDLP\text{exp} (m)</td>
<td>0.12 (0.01)</td>
<td>0.13 (0.02)</td>
<td>0.13 (0.02)</td>
<td>NS</td>
</tr>
<tr>
<td>(V_{\text{exp}}) (m/s)</td>
<td>1.25 (0.17)</td>
<td>1.26 (0.13)</td>
<td>1.10 (0.21)</td>
<td>0.040</td>
</tr>
<tr>
<td>MHE ((8^\circ))</td>
<td>9.3 (2.5)</td>
<td>9.8 (2.0)</td>
<td>10.2 (1.5)</td>
<td>NS</td>
</tr>
</tbody>
</table>

Values are mean (\(\pm\)S.D.); NS: not significant.
* One-way ANOVA.

![Table 2: Age-group mean values](image)
declines only for the Y and M group. The gradient of the best linear fit indeed showed a significant between-groups effect \( F(2, 33) = 4.87, P = 0.014 \). Bonferroni corrected post hoc analysis showed a significant effect between the Y and O group only \( (P = 0.012) \). Post hoc \( T \)-tests revealed that only the Y and M group had significantly lower than zero gradients \( (P = 0.002 \) and \( 0.001) \). The O group did not show a significantly lower than zero gradient \( (P = 0.475) \).

The sawtooth pattern of the curves for the Y and M group in Fig. 3 suggests that the walking direction might influence the SDLP during the exposure condition, since all the odd numbered trials represent walks in one direction and even numbered trials walks in the opposite direction. However, the figure also shows that this effect is opposite for the Y and M group, that is, even numbered trials for the Y group appear to have a lower SDLP whereas for the M group they appear to be higher. So, not surprisingly, a post hoc comparison of SDLP means between odd and even numbered trials was not significant. Within the age-groups the effect appeared to exist as well, but again, the effect was not the same for every subject within a group. We are not sure yet what may have caused this effect, but we suspect a different offset of the positioning system per subject. A way to deal with the effect causing the saw tooth would be to average the SDLP over every two trials. However, for the analysis of the SDLP gradient this would have had no effect whatsoever: the linear slope of the remaining eight mean trials would be exactly the same as the one of the original 16 trials.

4. Discussion

In the current experiment older people showed a significantly larger effect on the SDLP pre-post difference than the middle aged or young people. It is important to notice that this effect is not the typical prism adaptation after-effect. The non-linear walking trajectory in the post-exposure condition was to the right of the midline, which is the same side as the curved walking trajectory during the exposure condition. If a typical prism adaptation after-effect had been present, the walking curve would have been to the left of the midline in the post-exposure condition.

We argue that the deviating walking trajectory in the post-exposure condition is caused by problems older subject have to adapt to changes in visual stimuli. The removal of the prism glasses may, for a short period, have disoriented the subjects’ body representation leading to a decrease in heading stability, that is, a deviation from the optimum walking trajectory. Degradation of major sensory systems like the proprioceptive and vestibular system could be a plausible explanation for this result. With these systems fully intact, as they are in healthy young people, they form, together with vision, a highly redundant source of information about the position of our body relative to the environment. A young subject has several sources of information to overcome distortions in the information of one or more sensory modalities. With age this redundancy diminishes. All sensory information is required to maintain a correct representation of body position and distortion of any part of this information results in a distortion of this representation. A secondary cause of this effect may be a decrease in speed of information processing. It is well known that ageing causes such a decrease and this might contribute to the increase in time older people need to adapt to changes in visual stimuli.

Another clear difference between the age-groups was found during the exposure condition. Subjects in both the Y and the M group showed a significant decrease in SDLP while the SDLP of the O group appeared to remain level. This indicates that the Y and the M group somehow adapted to the prism distortion while the O group did not. To understand why this difference occurred it first needs to be established what kind of adaptation took place. For this matter it is illustrating to report that all subjects were asked afterward if they had realised that they had walked in a curve during the exposure condition. None of the older people had consciously experienced that they had walked in a curve. They all were convinced that they had walked in a straight line from ball to ball. Most of the subjects in the other age-groups were quite aware that they had walked in a curve however. If the decline in SDLP was caused by some form of strategic control, the lack in the O group to consciously detect that they walked in a curve could account for the absence of adaptation in this group. After the first few exposure trials subjects in both the Y and the M group knew they had to walk in a curve to reach the target and anticipated to this knowledge in consecutive trials. However, subjects were given the explicit instruction to walk towards where they saw the ball and not where they expected it to be. Initiating a curve to anticipate to previous results would mean that they did not fully follow this instruction. Furthermore, Fig. 3 shows that the adaptation in the Y and the M group is a rather slow process. This would suggest that the mechanism underlying the adaptation in these two groups might better be understood in terms of realignment.

To explain why no realignment occurred in the O group a better understanding of this type of adaptation is required. When two sensory modalities conflict with one another, each will influence the other to a greater or lesser extent in an attempt to resolve the intersensory discrepancy. The extent in which they influence each other is referred to as intersensory bias (for a review, see [25]) and depending on both cognitive and non-cognitive parameters the intersensory bias for each modality may be altered. In several experiments it has been established that in a typical prism adaptation experiment the visual bias of proprioception is about 80% and proprioceptive bias of vision is about 20% [25]. This means that after prism
adaptation the felt position of a target has shifted 80% towards the initially, at the start of the exposure condition, seen target position while the seen position of the target has shifted 20% towards the initially felt target position. The visual supremacy over proprioception in this experiment is referred to as visual capture.

The adaptation during the exposure condition observed in the Y and M group might very well be a reflection of the proprioceptive bias of vision. The proprioceptive modality influenced the visual modality in such a way that the walking trajectory became straighter. The proprioceptive and visual systems were realigning. The fact that most subjects in these groups reported that they were aware that they walked in a curve implies that realignment was not complete and that an intersensory discrepancy still existed. For the older people it is likely that degradation of the proprioceptive bias of vision and make the visual system even more dominant, that is, the proprioceptive modality will hardly influence the visual modality and no realignment will occur.

In the current experiment it is difficult to discriminate between the exact contributions of proprioception and the vestibular system to the representation of body position relative to the environment. Therefore, the lowering of the proprioceptive bias of vision with age might reflect degradation of the vestibular system as well. One might even consider the existence of an additional vestibular bias of vision and a lowering of that bias with age. However, to our knowledge such a bias has not yet been described in literature.

The apparent absence of realignment in the O group and the presence of realignment in the Y and M group do appear to contradict the interaction effect found between age-group and measurement on the SDLP in the pre-and post-exposure condition. Realignment should have caused an after-effect that would have made the subjects in the Y and M group deviate to the left in the post-exposure condition and so increasing their SDLP for this condition. However, as it was mentioned in the introduction, the presence of constant visual feedback will strongly suppress realignment and in this experimental design realignment is far from full. Furthermore, the design of the post-exposure condition is not suitable to expose typical after-effects. For this only the target should be visible to a subject and no visual feedback about the walked trajectory should be available. A possible experimental design to correctly reveal after-effects might be to strongly reduce subjects view angle during the post-exposure condition.

Acknowledgements

We greatfully thank Roy Stewart for his statistical expertise. This research was supported by ZonMw, project: 1435.0004(96-06-005).

References