

The influence of non-visual signals of walking on the perceived speed of optic flow

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Supervised by Dr A. Pelah

Declaration

The reported experiments were performed as my Part II Physiology project during Lent term 1998. All work except as noted below was performed entirely by me, including the writing of software programs used for the control and analysis of experiments. Collaboration was undertaken with Alastair Bell on the experiments comparing overground and treadmill walking.

I would like to acknowledge supervision by Dr Adar Pelah, and discussions on methodology with Hartwig Distler.

Adrian Thurrell

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The Influence of Non-visual Signals of Walking on the Perceived Speed of Optic Flow

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Introduction

How do we judge the speed of motion of objects we see around us? The eyes provide information concerning the position and velocity of an object relative to themselves, but the eyes may also be moving through space. Any estimation of the true velocity (absolute velocity) of an object from visual cues must be able to deal with the motion of the eyes, or perceived motion will always be relative to the observer and therefore considerably less useful or even dangerously misleading. Considerations of the mechanism of this process during eye movements and passive ego-motion have tended to fall into one of two main theoretical approaches.

The traditional view, the *inferential theory* (Helmholtz, 1964), states that the brain compares a neural signal encoding the velocity of the image of the object upon the retina with a neural signal encoding the velocity of the retina itself. The velocity of the retina here corresponds to the velocity of the centre of gaze (i.e. in world co-ordinates, ms^{-1}) rather than the rotation of the eye (in $^{\circ}\text{s}^{-1}$). If the absolute velocity of the retinas and the relative velocity of the object to the retinas are vectors, their sum will equal the absolute velocity of the object. With this mechanism some means must be used to obtain the retinal velocity, and a combination of head motion from the vestibular apparatus and eye rotation within the head from efference copy signals would seem ideal.

A major problem with this, however, is the poor response of the vestibular system at low frequency. The vestibular system, comprising the semi-circular canals and otolith organs, relies on the interplay between inertia, elasticity and viscosity to signal head movement. As a 2nd order system it has a finite bandwidth of motion detection such that during walking, though the movements over the course of a single stride may be detected, movements of a lower temporal frequency including overall body velocity can not. At low temporal frequency, vision can perform this role, but in its absence another system is required. Thus, when moving at a constant velocity, (e.g. on a moving train,) the absence of vestibular signals of acceleration means that no direct sensation of ego-motion is actually felt and it is the landscape outside that appears to be rushing past.

The alternative view, known as *direct perception* (Gibson, 1966; 1979) is that the motion of the object can be derived directly from certain invariant cues e.g. the rate at which areas of the background disappear and reappear on opposite sides of the object. This method never encodes motion relative to the movement of the eyes themselves and so their spatial co-ordinates need not be estimated. However, as motion is determined in relation to the background of the object of interest, this method relies on the assumption that the background is stationary. This assumption being violated causes the common illusion on trains of thinking one's own train is moving, when in actuality another train is moving on the adjacent platform. The movement results in a visually induced sensation of ego-motion orvection.

An attempt has been made to reconcile these two approaches (Wertheim, 1994) into a more general inferential theory of motion perception. However, this theory deals only with passive self-motion where vestibular and/or visual signals alone reveal head motion. Passive motion, even for humans who are often passively moved inside vehicles, may involve a learned system dependent on previous experience. A more natural method of movement is walking, where there are many more cues to ego-motion: efference copy as well as proprioception. Such cues would be compatible with a modified inferential theory as an alternative measure of head velocity in space. Proprioceptive signals from the legs, trunk and neck

together with efference copy of movement commands would encode the motion of the head with respect to the ground.

Deficiencies in the passive inferential model can be demonstrated when active motion, e.g. walking, results in no relevant vestibular information but does have an effect on visual object velocity perception. In an experimental paradigm involving treadmill walking, the active motion does not result in any gross displacement of the subject's head and as a result the vestibular stimulation caused would not be expected to signal the subject's walking velocity. Thus in this paradigm an effect on object motion from proprioceptive signals of walking velocity can be isolated.

Ivry and Diener, (1991) report that patients with cerebellar lesions are impaired in velocity perception tasks and in internal timing tasks (Ivry and Keele, 1989; Ivry, Keele, and Diener, 1988). If, as they suggest, the cerebellum were used in timing and velocity estimation in normal subjects, then altering the activity of the cerebellum in a systematic way, with an activity such as walking, would interfere with other activities requiring accurate timing or velocity information.

The present investigation considers whether walking velocity affects velocity perception in order to distinguish between the inferential and direct theories of motion perception. The task set was to adjust optic flow velocity displayed on a large screen to match a target optic flow velocity over a range of walking speeds. Any influence of walking velocity on matched optic flow velocity would suggest that proprioceptive signals due to walking were used in the processing of visual motion signals.

Methods

General Set-up

All experiments were performed using a free-running WOODWAY Exo43 treadmill powered not by

the electric motor but by the subject driving (i.e. walking on) the belt, unless otherwise stated. Optical flow stimuli were rear-projected onto a large (3x2 m) screen positioned 0.9 m in front of the subjects' head (see Fig. 1). The subjects wore welder's goggles to restrict peripheral vision to within the screen and also to reduce its luminosity by a factor of approximately 100. The stimuli was a regenerating tunnel of computed internal dimensions (width =2.24 m height =1.68 m length =9 m) consisting of 12 equally spaced large bright rectangles of line width =4 cm on a dark background, luminosity =0.004 cdm^{-2} . The tunnel was horizontally but not vertically symmetrical as the far point was raised to the subject's eye-level when walking on the treadmill, this point being approximately 75% of the height of the tunnel. A small (0.14° diameter) fixation point, luminosity =1.09 cdm^{-2} was presented at the far point and the subject instructed to fixate it during all trials. Individual rectangles increased in size, using rules of perspective and varied in brightness as a trapezoid function of distance: maximum luminosity of 1.09 cdm^{-2} between 1.35 and 2 m distance from the observer. The screen resolution was 1024x768 pixels and the image refresh rate was 70 Hz. An LCD projector (SANYO) was controlled in real time from an INTEL Pentium MMX 200MHz computer programmed in Borland Turbo Pascal via a CAMBRIDGE RESEARCH SYSTEMS Visual Stimulus Generator (VSG) card.

Recording Methods

The treadmill speed was measured using a DC motor acting as a sensor attached to the treadmill rear spindle. The analogue output from the motor was electronically filtered and digitally recorded using the analogue to digital converter on the VSG card: input range -5.12 to +5.12 V giving a speed range of -12 to +12 kmh^{-1} . Finally the digital signal was passed through a binomial filter of bandwidth 8.7 Hz. Walking steps were also recorded using a piezo-electric sensor attached to the underneath of each subject's left shoe, producing a pulse when the subject placed their foot on the treadmill. From this the

gait parameters of stride frequency and length were obtained. All parameters were sampled and recorded once per frame (70Hz) and cumulative distance was also calculated as the integral of speed. Stored results were analysed subsequent to experimental trials using software written for this purpose and the Microsoft Excel 97 spreadsheet program.

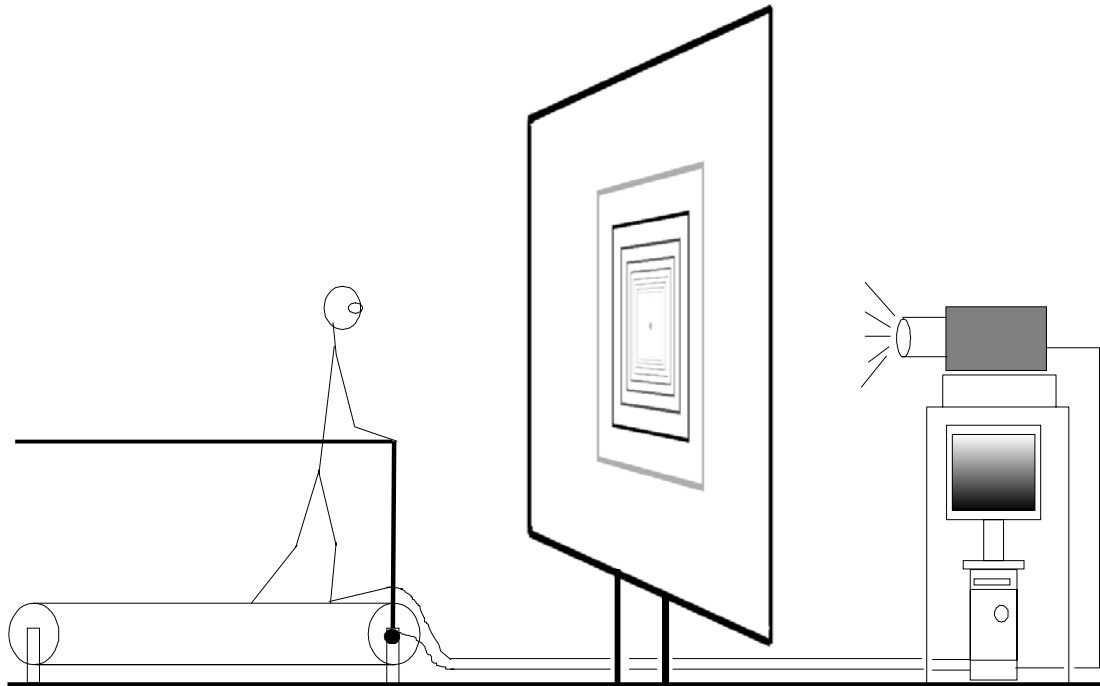


Figure 1. The experimental set-up. The screen subtended a visual angle of $59^\circ \times 48^\circ$ at the nodal point of the eye.

Results

Experiments were performed both to investigate walking on the treadmill and to investigate influences between walking velocity and optic flow speed.

I. *Effect of treadmill tilt upon subject effort*

A comparison of the effort of walking overground and self-driven treadmill walking was conducted as self-driven treadmill walking was thought to require significantly more effort. A possible way to reduce this effort was to tilt the treadmill.

The resting heart rates for two subjects were measured using a POLAR Accurex NV heart rate monitor whilst they stood still on the treadmill. They were then required to walk at a “very slow” speed for 3 min; heart rate was monitored throughout and averaged over the last 2 min. The subjects stopped (stood) between trials until their heart rate had returned to its resting level and then the procedure repeated at instructed walking speeds: “slow,” “normal,” “fast,” and “very fast,” for each trial. This process was repeated for overground walking, treadmill walking at 0° inclination, and treadmill walking at 2.3° (4%) inclination. The difference between the average resting values before all trials and the average value for a given speed and tilt was calculated.

Walking surface	Fitted polynomial
Treadmill 0°	$HR=0.50xWV^2+6.66xWV$
Treadmill 4°	$HR=0.73xWV^2+4.16xWV$
Overground	$HR=0.66xWV^2+1.93xWV$

Table 1. Power output of subject AT measured using changes in heart rate, with best fit curves predicting heart rate from walking velocity. Comparison of the linear terms of the fitted polynomials suggests that a treadmill tilt of ~7° would result in subject effort similar to overground walking. 3° was used to prevent subjects from noticing the incline and changing their walking style as a result. HR = heart rate, WV = walking velocity.

Heart rate was assumed to be linearly related to power output and hence subject effort within the test

range. Polynomial functions (Table 1) were fitted to the data (Fig. 2). The linear components were assumed to be due to the treadmill resistance (as it is a rolling resistance) and the squared terms assumed to be due to the subjects' internal resistance (as this is due to acceleration of the legs). Increasing tilt reduced the size of the linear term towards that of the overground walking value with little effect on the squared term. Extrapolation suggested that a tilt of $\sim 4^\circ$ (7%) would be necessary to remove the effect of the treadmill resistance. However, a value of 1.65° (3%) was used on subsequent experiments to prevent the subjects from noticing the tilt and altering their walking style as a result.

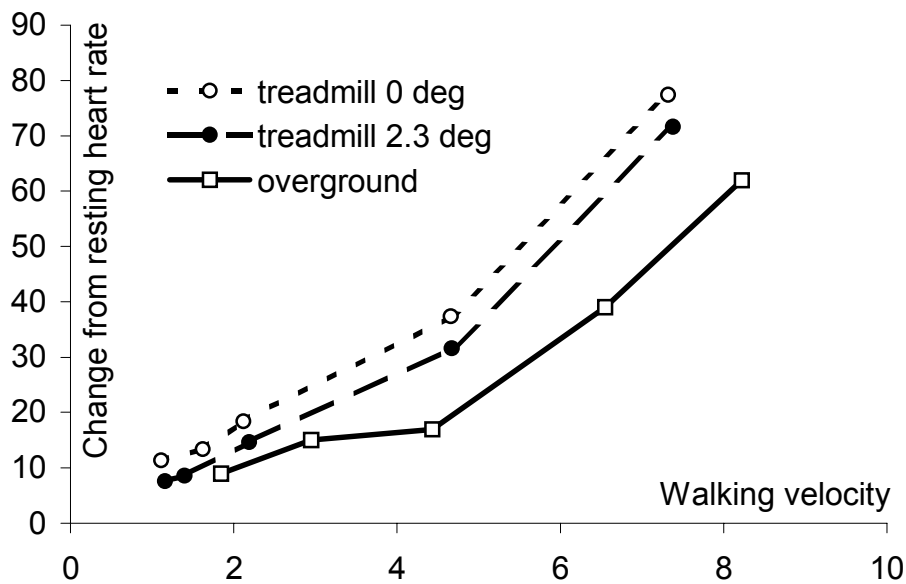


Figure 2. Comparison of treadmill walking at two tilt levels plotted against overground walking, as measured by subjects' power output. Changes in subject (AT) heart rate from rest (standing) plotted against walking speed on three surfaces: overground; treadmill at 0° and treadmill at 2.3° . Five subjective speeds were used for each surface.

II. Comparison of self-driven treadmill and overground walking

Self-driven treadmill walking is a new technique, so some comparison to overground walking is

necessary. Seventeen subjects were instructed to walk at one of five subjective speeds: “very slow,” “slow,” “normal,” “fast” or “very fast” under three different conditions: overground walking on a solid floor; and treadmill walking with and without an optic flow stimulus. Each condition had 26 trials, one fake and five at each speed presented in a controlled order to minimise order effects. For treadmill trials with an optic flow stimulus, optic flow speed was identical to measured treadmill speed i.e. gain=1 consistent with the computed internal dimensions of the tunnel. Each trial consisted of a 20 m course, computed on the treadmill but marked-out in overground trials, while average speed and gait parameters were measured over the central 10 m in the overground trials and the last 10 m in treadmill trials. Gait parameters were calculated manually by counting steps during overground walking and from periodic variations in recorded walking velocity during treadmill walking.

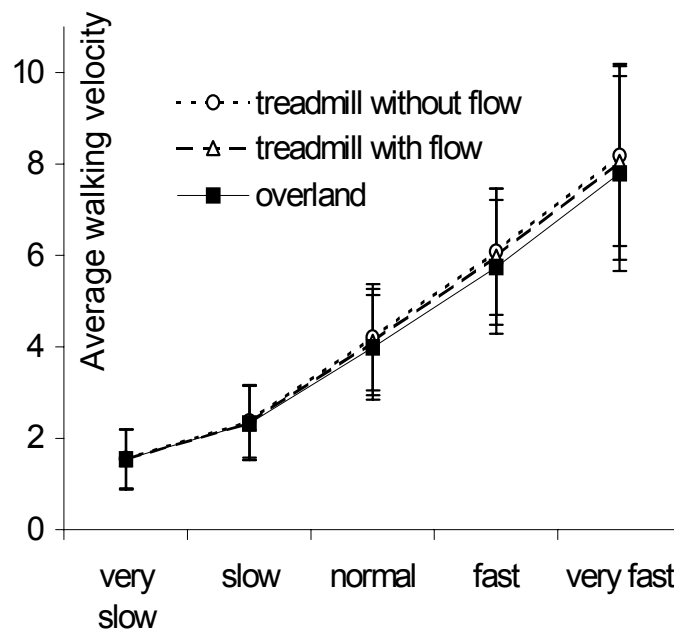


Figure 3. Comparison of overground and self-driven treadmill walking. Walking velocities averaged over the 10 subjects who completed all 3 conditions plotted against subjective walking speeds. The three conditions show no difference. Error bars denote S.D. (For all subject results see Appendix 1).

No order effects were found between trials. The relation between the walking velocities of individual subjects in the overground and the treadmill trials showed no consistent effect of walking surface across subjects (see Appendix 1). When averaged across subjects there were no differences between the conditions (Fig. 3). Gait parameter analysis of subjects was too noisy to reveal any change in stride length or frequency between conditions (see Appendix 2). When asked about any perception of treadmill tilt no subjects reported such awareness.

III. Comparison of Self-driven and Motor-driven Treadmill Walking Gait Parameters

A comparison of gait parameters between self-driven and motor-driven treadmill walking, combined with a previous study comparing motor-driven and overground gait parameters, would allow a second comparison of overground and self-driven treadmill walking.

One subject was instructed to walk on the treadmill, which for this experiment alone was motor-driven, while the set speed of the treadmill was varied between 1.5 kmh^{-1} and 9 kmh^{-1} in 0.5 kmh^{-1} steps. The subject was then instructed to walk on the treadmill self-driven, starting as slow as possible and gradually increasing speed to 9 kmh^{-1} over 10 min. The stride length, stride frequency and average speed over the stride were recorded for each step in both conditions.

Comparison of the best fit functions of gait parameters between motor-driven treadmill walking and self-driven walking revealed an approximate 7% increase of stride length at the expense of stride frequency for a given speed (Table 2, Fig. 4). A study (Stolze et al, 1997) comparing overground walking and motor-driven treadmill walking revealed an approximate 7% decrease of stride length at the expense of stride frequency for a given speed. Thus it would seem that self-driven treadmill gait parameters are more comparable to overground gait parameters than those for motor-driven treadmills.

Power source	Function for stride frequency	Function for stride length
Self	$SF=0.60 \times WV^{0.63}$	$SL=0.93 \times WV^{0.37}$
Motor	$SF=0.64 \times WV^{0.61}$	$SL=0.86 \times WV^{0.39}$

Table 2. Fitted power functions for gait parameters of subject AGB showing the 7% decrease in stride frequency and 7% increase in stride length during self-driven rather than electrically powered walking as determined by the coefficient. The 3% change in the exponent shows a small change in the ratio of the gait parameters between surfaces at different speeds. The changes in gait parameters between overground and motor-driven treadmill walking from another study (Stolze et al, 1997) suggest that self-driven treadmill walking is more similar to overground walking than motor-driven treadmill walking. SF = stride frequency, SL = stride length, WV = walking velocity.

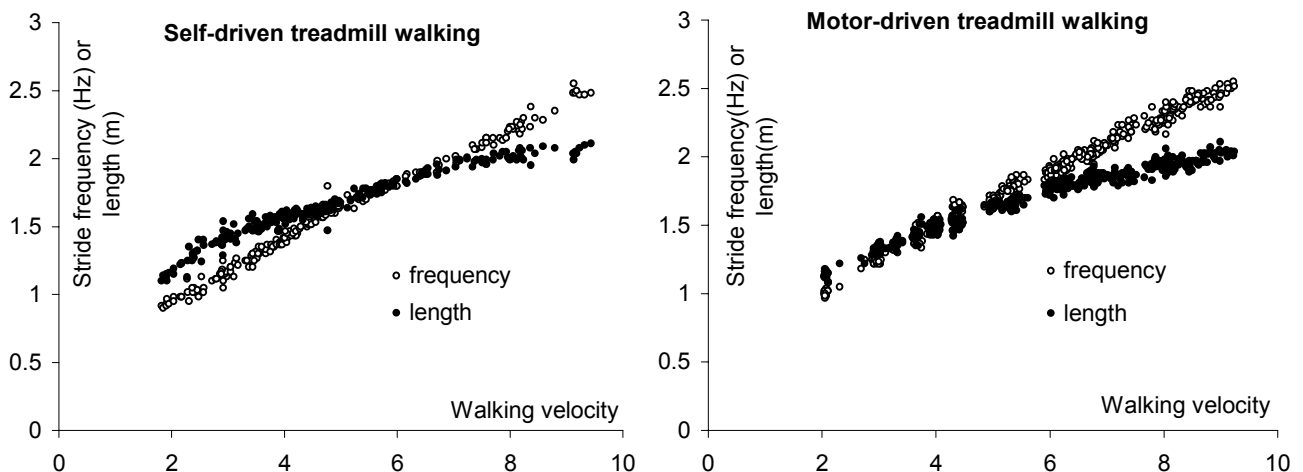


Figure 4. Gait parameters during electrically powered and self-driven treadmill walking showing the similarity in behaviour between surfaces for subject AGB.

IV. Effect of gain upon walking velocity

A report (Prokop et al. 1997) showed that subjects walking on a treadmill would respond to changes in

the closed-loop gain between walking velocity and optic flow speed. In that report, the control of optic flow was closed-loop as walking velocity on the treadmill determined optic flow speed, which in turn the subject used to determine their walking velocity. The gain refers to the relative speed of the optic flow compared with the walking velocity. The direction of the effect shown suggested that optic flow speed is used by subjects as a measure of self-motion in the control of walking velocity, the size of the effect should therefore reveal the strength of this control.

Protocol A

Three subjects were instructed to walk at a constant “slow” velocity on the treadmill with a moving optic flow stimulus for 5 min. The speed of the optic flow was determined by the measured speed of the treadmill multiplied by a gain factor. The gain was equal to one for the first 85 s of the trial; then its value was altered in a half-cosinusoid fashion to a test value over 30 s; this was maintained for 70 s until the gain was reduced over 30 s back to a value of one. This process was repeated six times with intervening rest pauses with different test gain values presented in a random order. Test gains varied from 0.5 to 1.5.

Protocol B

Four subjects were instructed to walk at a constant “normal” velocity when the optic flow stimulus was presented and to stand still when blank. Optic flow was presented for 25 s per trial with a 5 s blank pause in between trials. Gain was altered between trials, alternating between test values and one, starting with one.

Protocol C

One subject was instructed to walk at a constant “normal” velocity for 9 min. The gain factor was constant at a value of one for 1 min and then varied sinusoidally with a cycle period of 2 min, an

amplitude of 2 and a mean of one.

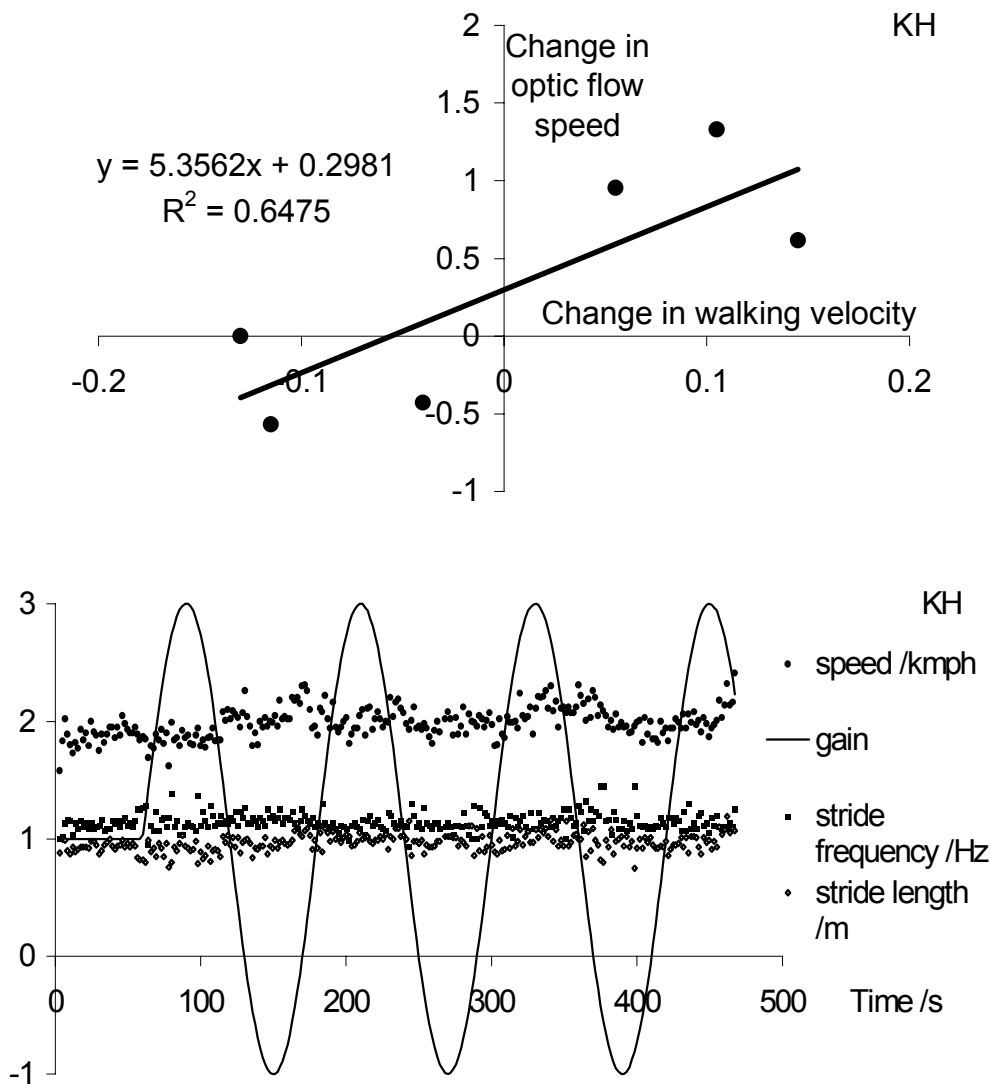


Figure 5. Subjects were instructed to walk at a constant velocity during changes in gain in order to test for an influence of changes in optic flow on the control of speed of walking. **Top.** One subject showed an effect of gain changes on walking velocity with protocol A, but not in the direction expected from the results of Prokop et al. (1997). **Bottom.** The same subject run using protocol C; a repeat of the previous study (Prokop et al. 1997), showed no effect of gain changes on walking velocity.

Due to the variability of subjects' normal walking velocities, all analysis was based on the changes between the test phase and the average of the two straddling control phases. Using protocol A, of three

naive subjects tested, two showed no significant effect of changes in gain on walking velocity, while the remaining subject showed an increase in walking velocity when the test gain was increased. The subject may have been sub-consciously trying to match the optic flow speed with their walking velocity (Fig 5a). With protocol B, one experienced and three naive subjects were used, none of whom showed any effect of gain on walking velocity. The one naive subject run on protocol C showed no effect of the gain changes on walking velocity (Fig 5b).

The investigations into the effects of optic flow speed upon walking velocity all revealed the absence of the effect reported by Prokop et al. (1997). All but one subject showed no effect of a change in optic flow gain on walking velocity and the remaining subject showed an effect opposite to that reported by Prokop et al. (1997) though in agreement with a previous finding (Konczak, 1994). No subject during any trial showed an effect similar to that reported by Prokop et al. (1997) even when their protocol was followed as closely as possible.

A number of remaining differences between the experimental set-ups may have been the cause of the variation. Prokop (1997) used a set-up in which the movement of the subject on the treadmill belt (sensed at waist level) was used to update the speed of the moving belt, imperfections in this arrangement may have contributed to instability in the subjects' gait. The change from electrically powered to self-driven treadmill walking removes the possibility of effects produced due to such instability in the Prokop set-up. Conversely, the extra cues to stationarity in the self-driven set-up, i.e. holding onto the treadmill rails, may be reducing the size of innate mechanisms of ego-motion control. The present study used goggles simply to restrict peripheral vision and darken the display, whereas the previous investigation used goggles that also contained prismatic lenses to simulate binocular convergence and accommodation in the subject, such that the display appeared at near infinity. These effects combined with the visible graininess of the image in this experiment may have contributed to the lack of immersion that subjects reported. Subjects may have ignored changes in the stimulus speed due to settling into a rhythm, as their

instructions were to walk at a constant velocity. The time subjects had to settle into this rhythm was reduced in B but again no effect was found. During protocol C the visual stimulus was constantly altered so subjects were given little opportunity to settle into a rhythm, but an effect was not produced suggesting that settling into a rhythm was not the reason the Prokop et al. (1997) effect was not replicated.

V. *Effect of gain altered walking velocity upon perceived optic flow speed*

An investigation of the effect of walking on motion perception may reveal shortfalls of the direct perception theory and also of the inferential theory as described by Wertheim (1994). If an effect is found, the inferential theory as described by Wertheim (1994) can provide no explanation, but an addition to the model combined with phenomenal regression (see discussion) can.

Four Subjects were instructed to stand, whenever the fixation point was made large (1.11° diameter) and to view the optic flow stimulus presented at constant speed (3 kmh^{-1}). During subsequent trials, when the fixation point was small (0.14° diameter), subjects were informed that optic flow speed was dependent upon walking velocity and instructed to walk at such a speed as to result in a tunnel speed equal to that of the previously viewed target. Subjects were instructed to stand still when no tunnel was displayed between trials. The closed-loop gain factor between walking velocity and optic flow speed was altered randomly from 0.6 to 1.4 in steps of size 0.2 between trials. Thus to maintain target speed subjects must walk at between 1.875 kmh^{-1} and 5 kmh^{-1} , well within the comfortable range for all subjects. There were a total of 80 trials of 15 s each, of which five were displaying the target stimulus, these occurred on the first trial and every 16th trial thereafter. The walking velocity during the last 10 s of each trial was averaged and a blank pause of 5 s occurred between trials.

The control of optic flow speed was such that high gains required low walking velocities to match optic flow speed. All subjects showed an effect of increased gain (low walking velocities) increasing

matched optic flow speed, over the range of gain and walking velocity values investigated. The spread of values of walking velocities for each gain value was greater than expected, such that some were probably not in the subjects' comfortable range of walking velocities. This may have biased the results to higher values at low walking velocities (high gains) and lower values at high walking velocities (low gains) (Fig 6).

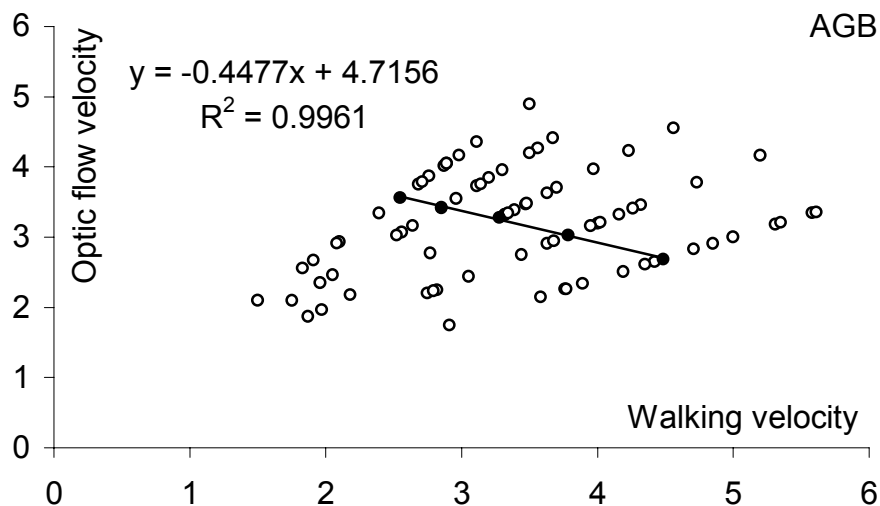


Figure 6. Subjects were required to walk at such a speed that optic flow velocity remained as close as possible to a previously presented target velocity during changes in walking velocity to optic flow velocity gain. The groups of values are each at a single gain value so have the same optic flow velocity/ walking velocity ratio. The effect may, however, be due to points on the left being shifted right and therefore upwards due to subjects being below their comfortable range of walking velocities, and shifted left and down on the right due to subjects being above their comfortable ranges. White: individual trials, black: averages at a particular gain. (For individual subject results see Appendix 3.)

The effect of gain on matched optic flow was the reverse of that expected. A major criticism of this experiment was that the effect may not have been due to walking velocity but to the limiting effects of the changes in gain themselves. Due to the variability in the subjects' matched walking velocities, subjects were walking at velocities over the majority of their ranges suggesting that subjects would have walked

faster or slower to match optic flow velocity but were unable to do so, thus skewing the results. A closed-loop protocol was used, as optic flow is closed-loop during natural walking. However, linking the optic flow to the walking velocity in this manner may have caused more problems than it solved especially in the interpretation of results.

VI. *Effect of walking velocity upon perceived optic flow speed*

The results of the previous experiment may have been due to the limiting factor of subjects' walking velocities. The experiment was altered to overcome this by introducing an open-loop paradigm i.e. optic flow not dependant on walking velocity.

Again a target optic flow speed (3 kmh^{-1}) was presented and on subsequent trials subjects were instructed to match the target speed. However, control of optic flow speed was now by a potentiometer (range of adjustment 0 to 6 kmh^{-1}) mounted on the treadmill controlled by the subjects' right hand (all subjects were right-handed). The potentiometer had a random offset for each trial to prevent subjects learning its correct position. During each trial subjects were also required to walk at one of five subjective walking velocities determined by instructions displayed on the screen between trials. Trials were split into blocks of five such that each block contained one trial at each speed and the target speed was displayed after every three blocks. Trials were 15 s each with 5 s gaps between trials during which walking instructions but no optic flow was shown. Instructions e.g. "fast," "target," were displayed with a letter height of 2.23° . For subjects AP (rerun) and GJ a modified protocol was used: to reduce the use of memory in recalling the target velocity for comparison during later trials, target presentations were increased to one after every block of five test trials. A total of five subjects were used.

All subjects were accurate at matching optic flow speed in the standing condition, and all subjects showed an effect of increased walking velocity resulting in increased matched optic flow. An increase of

matched optic flow speed would imply a decrease in perceived optic flow speed compared to veridicality. Three subjects showed this effect to be closely centred around the “normal” walking velocity, such that the best match (i.e. veridical) was obtained at the subjects’ “normal” walking velocity. One subject showed this effect to be centred around zero walking velocity. The remaining subject was tested twice and showed both types of behaviour: centred around zero then around “normal” walking velocity (Fig 7).

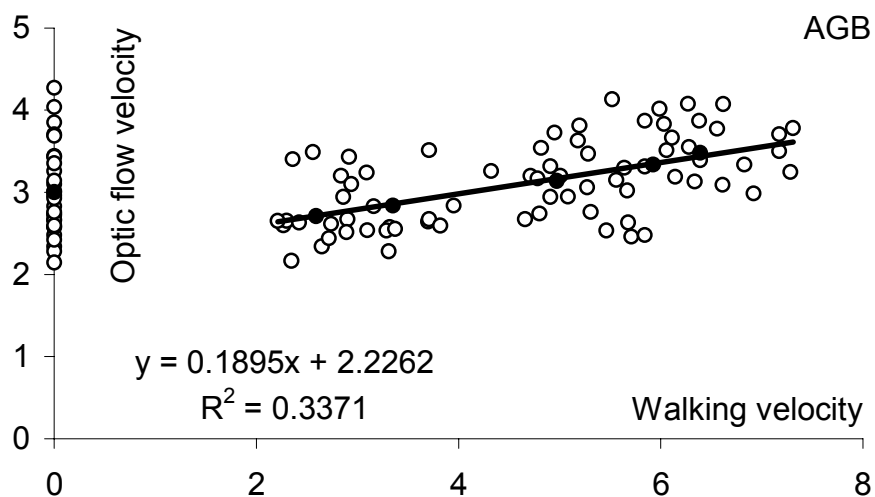


Figure 7. Subjects were required to either walk at 5 constant subjective velocities or to stand still (when the target was presented) during each trial; they were also required to match optic flow velocity to a previously presented target velocity using a hand-held potentiometer. A large effect of walking velocity upon matched optic flow velocity was found for all subjects. White: individual trials, black: averages for each subjective walking velocity. (For individual subject results see Appendix 4.)

Discussion

As the use of self-driven as opposed to motor-driven treadmills is a new technique (this is the first such investigation), there were concerns about how this method would affect the results obtained. It was felt

that using self-driven treadmills would over-come a number of limitations of computer-controlled motor-driven treadmills, namely, that the closed-loop algorithms used to control the treadmill speed and the latency of their feedback cause much instability in subjects' walking patterns. The experiments run to determine the applicability of self-driven treadmill walking to overground walking suggest that self-driven treadmill walking is in the respects considered more similar to overground walking than motor-driven treadmill walking.

Tilting the treadmill to 1.65° offsets some of the increase in effort of treadmill walking compared to overground walking. The results of the ten subjects who walked on the treadmill with and without optic flow and overground suggest that, in terms of speed, self-driven treadmill walking is similar to natural walking. In addition the analysis of gait parameters, in combination with the results of Stolze et al. (1997), suggests also that gait parameters during self-driven treadmill walking are very similar to those during overground walking.

Absence of an effect of gain change on walking velocity was robust across a number of subjects and minor changes in protocol. People are often passively moved such that optic flow need not always be linked to walking, but we rarely experience novel combinations of optic flow while actually walking (except perhaps on airport travelators). As a result we are practised at disregarding optic flow in the control of speed of self-motion, but we should find it hard to ignore the fact that we are walking in perceiving the speed of visual object motion. This observation may help to account for the present findings.

The closed-loop experiment on the influence of gain-altered walking velocity on perceived optic flow speed (Experiment V.) revealed a possible limiting effect of subjects' finite ranges of walking velocities. When the loop was opened and optic flow velocity controlled manually, an effect of increased walking velocity reducing the perceived optic flow speed was apparent (i.e. a gradient change). In addition it was found that subjects may offset their perception of optic flow speed during walking by an amount that

results in veridicality at their “normal” walking velocity (i.e. variability of offset).

The proposed explanation for increased walking velocity decreasing perceived optic flow speed is that a form of *phenomenal regression* takes place. Phenomenal regression is the term used for interference between the perceived properties of an object and those that are directly sensed. An example occurs when a subject is shown a restricted (i.e. a single viewing angle) view of a tilted square piece of card. The subject is then asked to match the retinal image of the card to one of a selection of diamond shaped drawings of different relative dimensions. The matched shape is always closer to a square than the retinal image dimensions, as there is interference from the object’s perceived shape onto the perceived image properties below the level of awareness.

Optic flow speed is ambiguous on its own, as it may be due to self-motion and/or object motion. But when optic flow is compared with the velocity of the retina itself, it should reveal the absolute velocity of the observed object (the normal situation). If subjects were perfectly matching absolute object velocity (relative to the floor, i.e. the treadmill belt) a gradient of unity would be predicted through the matched optic flow speeds (see Fig. 8). On the other hand, if subjects were perfectly matching retinal image velocity (the task set), no influence of walking velocity would occur and the gradient would be zero. The gradients measured of between 0.16 and 0.34 suggest that there is some interference between the signals for absolute object velocity and retinal image velocity, the gradient should quantitatively reflect the amount of interference occurring. The variability of offset of the effect shown by subjects could be explained as perceived optic flow is interfered with, not only by absolute motion of the object, but also by the subjects’ walking velocity. During overground walking optic flow speed has a zero intercept and slope of one with walking velocity. If subjects were trying to match this situation, an interference with walking velocity would be manifest, similar to interference with absolute object velocity but offset to lower values of matched optic flow velocity, that could result in veridicality at the subjects’ “normal” walking velocities. Subjects may alter the amount of interference and hence the size of the offset to allow

perceptual veridicality at their “normal” walking velocity.

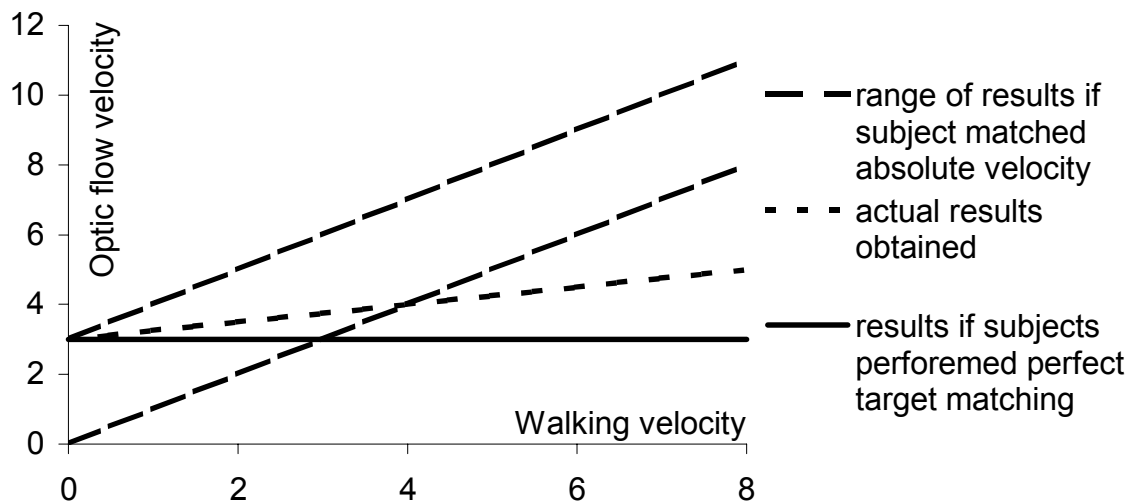


Figure 8. Theoretical and actual values of optic flow velocity for different subject behaviours. Slope of the actual results is proposed to be due to interference by perceptual absolute velocity and/or walking velocity. Subjects are aiming for a perfect match, but are unable to do so, presumably due to interference from their own walking speed.

The present findings are clearly contrary to the direct perception theory since this theory would predict no difference between perceived velocity with or without the proprioceptive signals from walking. However, a proposed addition to the inferential theory would account for the present findings by extending the passive self-motion inferential theory as described by Wertheim (1994) to encompass active self-motion during walking (Fig. 9, additions in bold type). With the modification, the perceptual processing on the retinal image indicated by the model would be the source of the phenomenal regression observed. Proprioceptive signals from walking are not required to match the target optic flow velocity veridically, the observation that they are used suggests that the sensory processing that occurs in normal walking cannot be ignored by the system.

Alternatively, the observed results may be due the activity of walking altering certain timing functions performed by the cerebellum (Ivry & Keele, 1989). These alterations may lead to perceptual errors in

speed matching, since these also require timing estimations to be made. However, this would provide no explanation for the variability of the offsets in the observed matched optic flow velocity curves. To differentiate between these possibilities requires investigation using visual stimuli of a nature unrelated to walking (i.e. not optic flow), such as horizontally moving gratings, where the inferential theory would predict there to be no effect of walking velocity, whereas the timing interference hypothesis would.

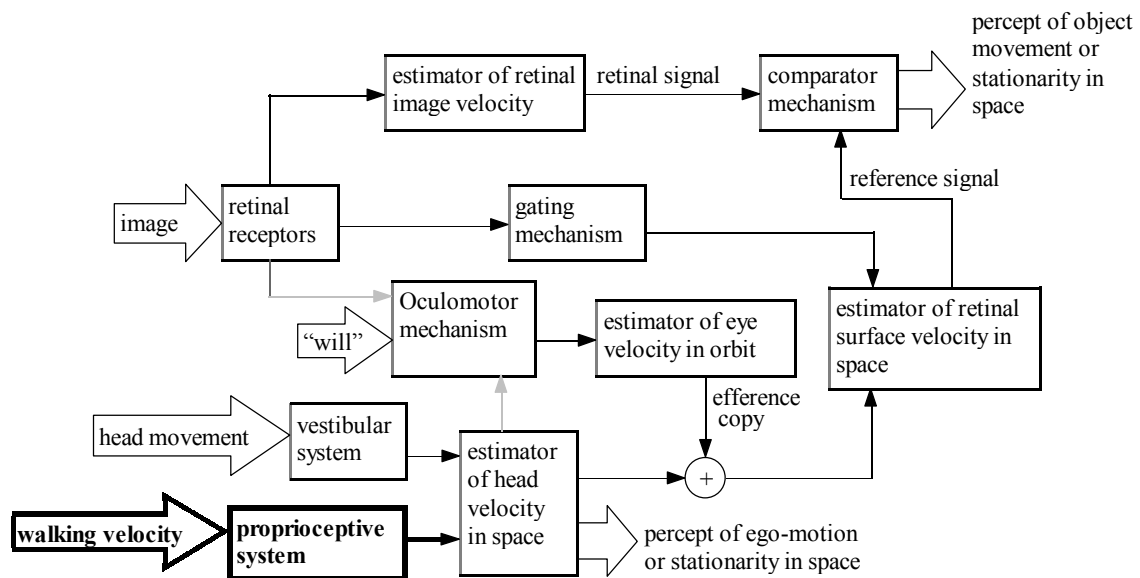


Figure 9. The modified inferential model (Wertheim, 1994) with proposed addition to enable application of the model to active self-motion such as walking (bold type). Grey lines denote pathways generating optokinetic and vestibular nystagmus.

Summary

The investigation was concerned with the relationships between the motor activity of walking and visual perception of optic flow velocity. A self-driven treadmill (i.e. one powered by the walker rather than a motor) was used, and systematic experimental comparisons were made to adjust this activity as closely as possible to natural overground walking. Increasing the tilt of a self-driven treadmill reduces a

component of the subjects' power output to values comparable to overground walking. Averaged over all subjects, walking velocities on a self-driven treadmill and overground are indistinguishable, though individual subjects may show differences. Gait parameters (i.e. stride frequency and length) are more similar to overground walking during self-driven treadmill walking than motor-driven treadmill walking. With the set-up used no effect of the gain of closed-loop optic flow (i.e. visual optic flow speed yoked to walking speed) upon walking velocity was seen. On the other hand, an effect of increasing walking velocity resulting in decreased perceived optic flow speed was consistently found for all subjects tested. Some subjects also displayed a possibly learned component resulting in veridicality at the subject's "normal" walking velocity. The observations can be described as a kind of *phenomenal regression*, the inability to decouple innate physical patterns from the perceptual outcome. The findings can be incorporated into a model of inferential self-motion perception (Wertheim, 1994), provided it is generalised to include active as well as passive self-motion.

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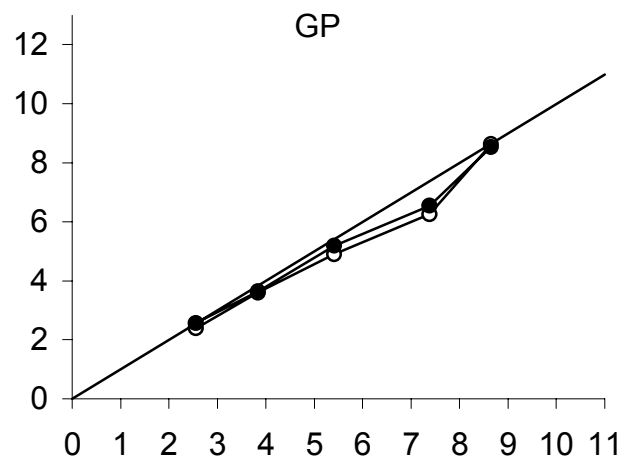
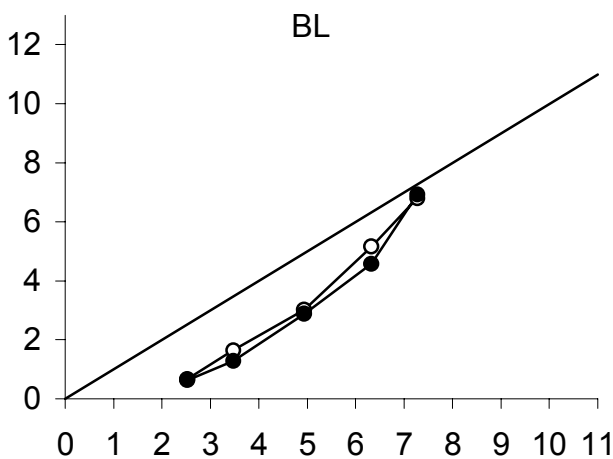
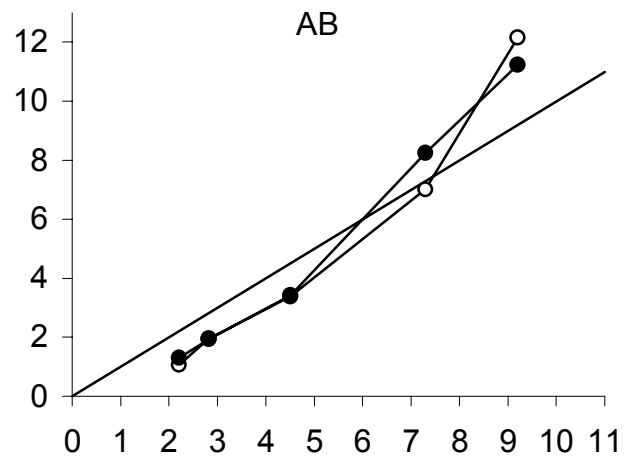
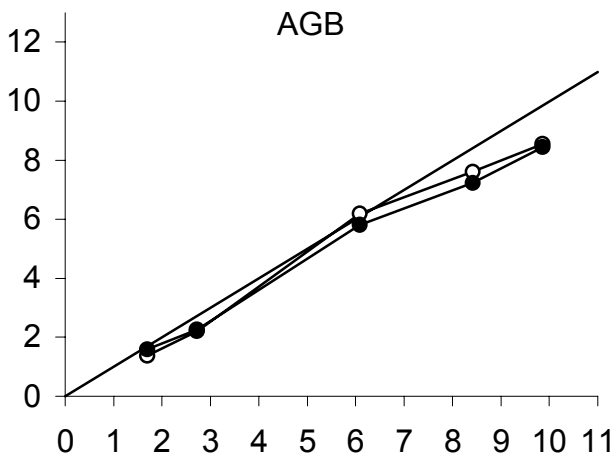
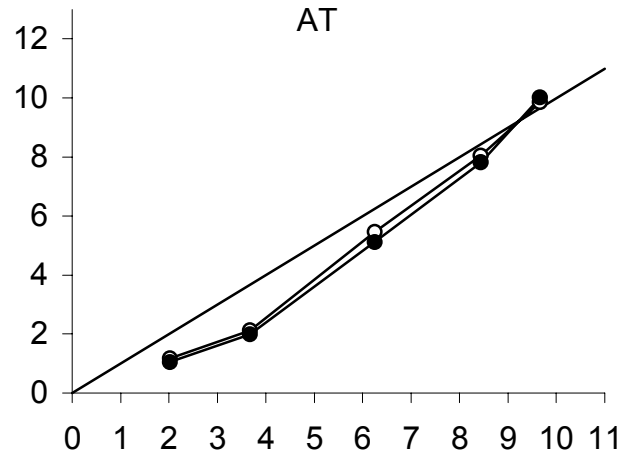
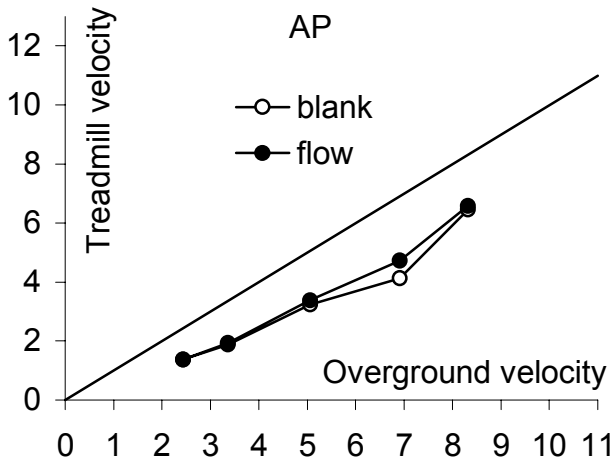
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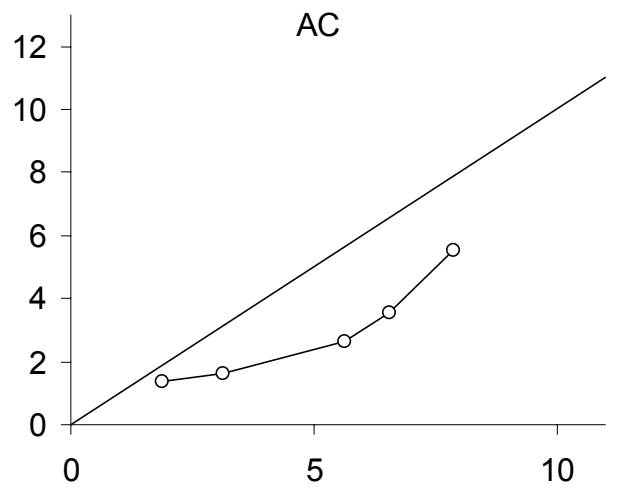
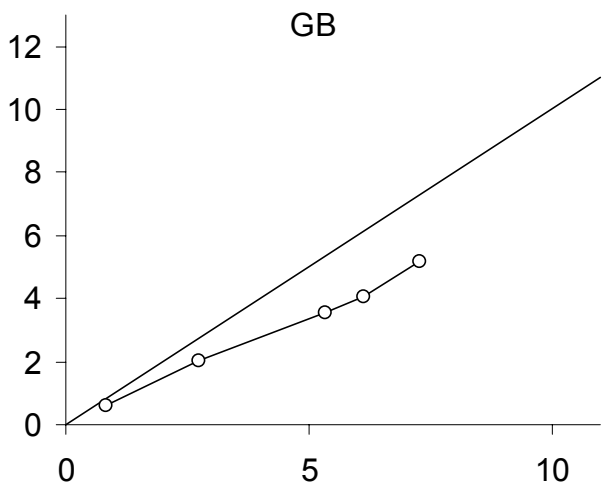
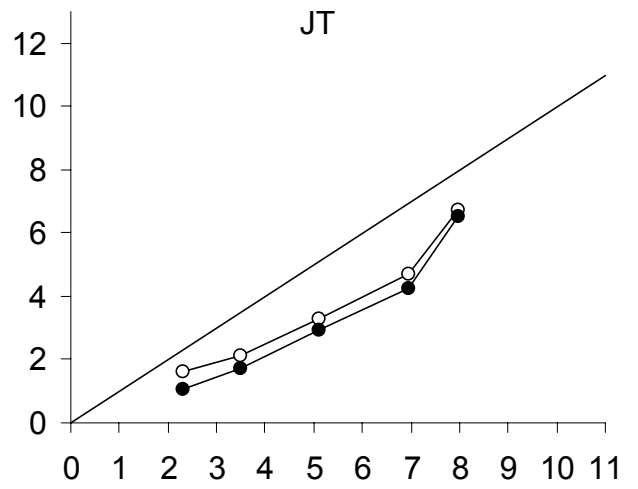
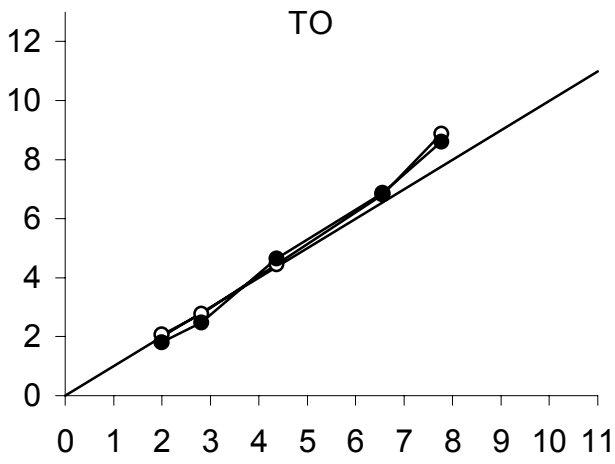
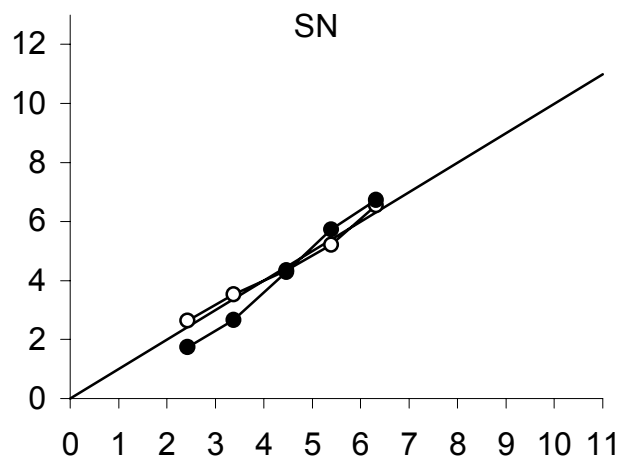
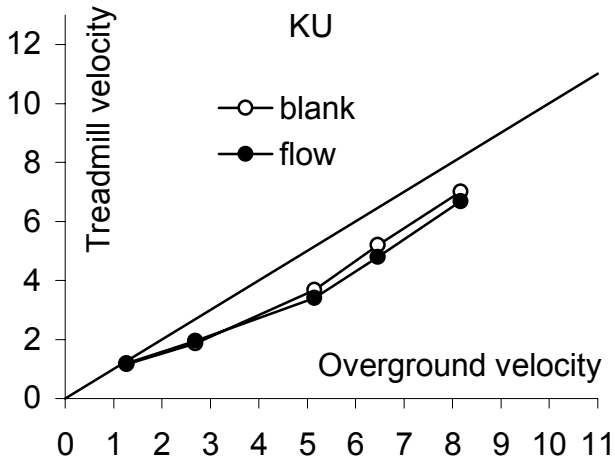
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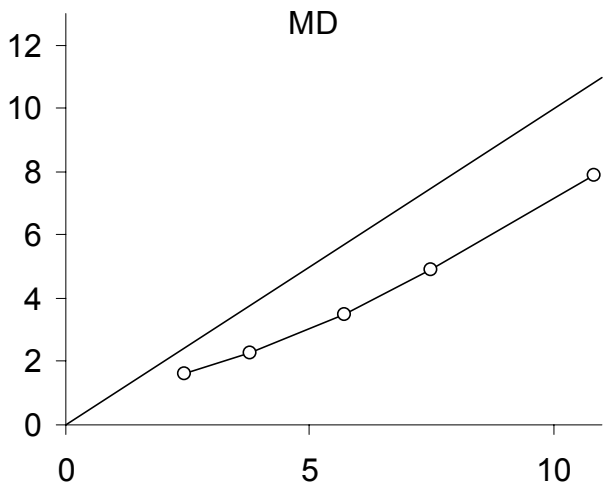
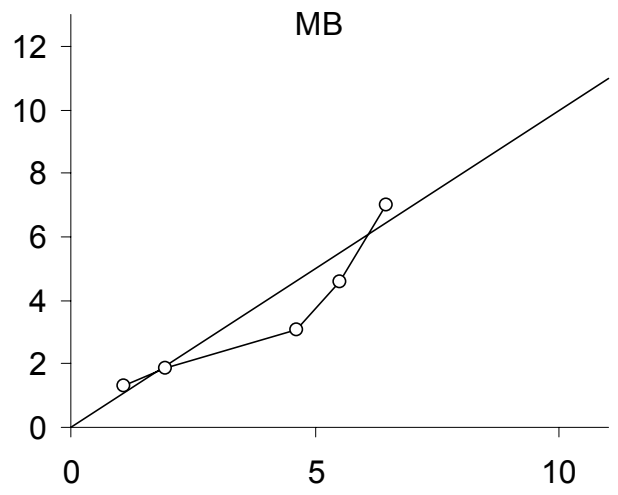
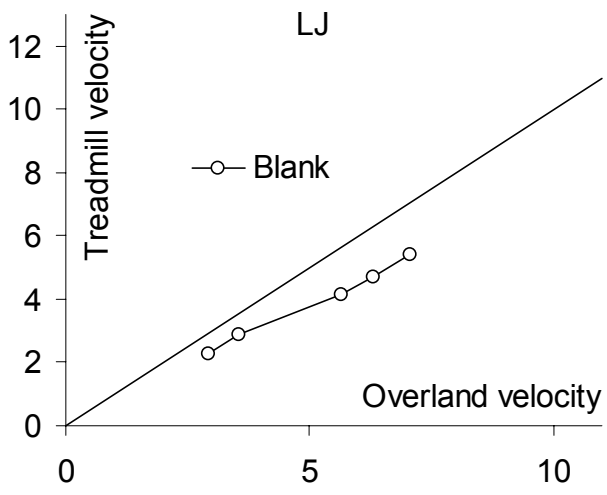
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Appendix 1

Comparison of overground and treadmill walking with and without optic flow. The straight line on each graph represents the walking velocity on the treadmill that would be equal to the overground walking velocity. Thus if treadmill walking was faster than overground walking it appears above the line. Five subjective walking velocities were used for each subject. See figure 3 for average of all subjects.

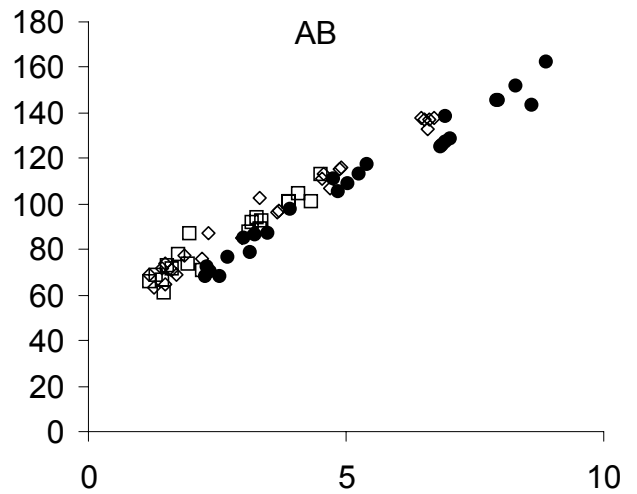
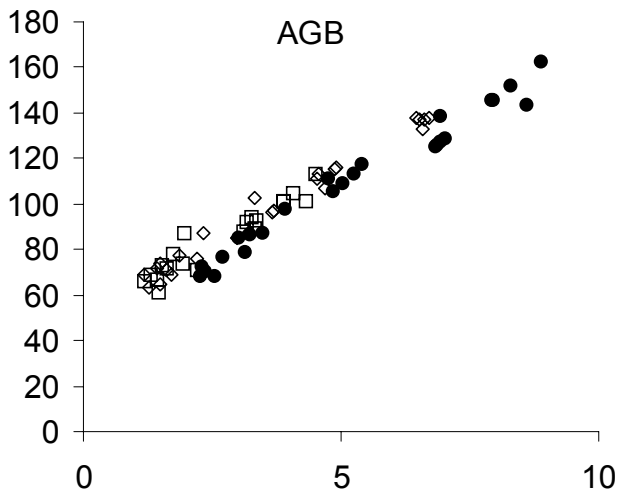
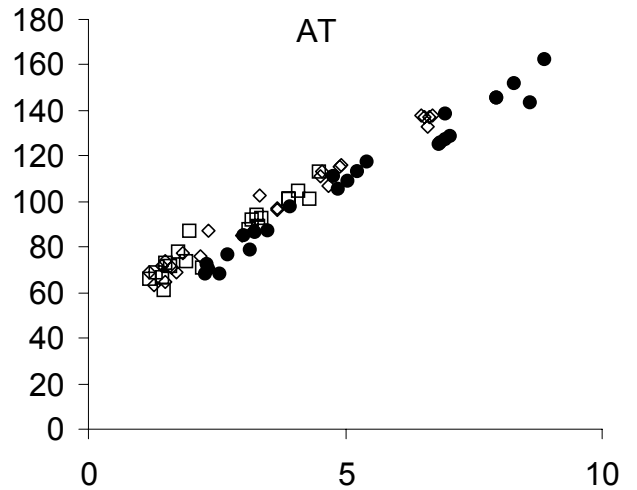
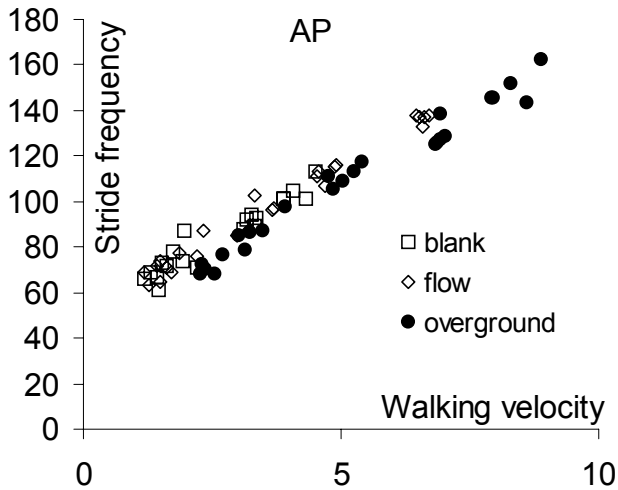


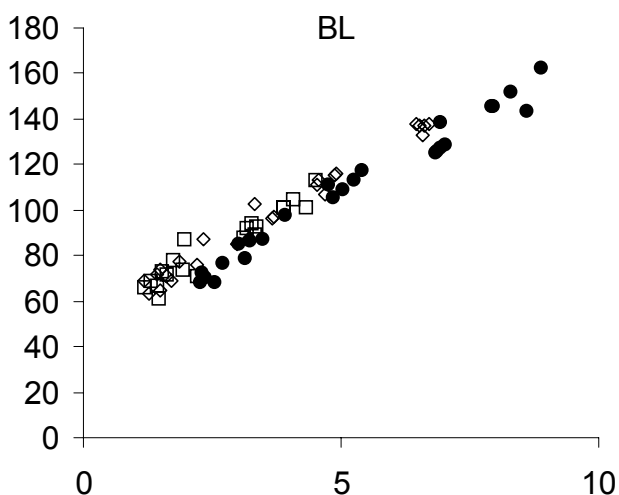
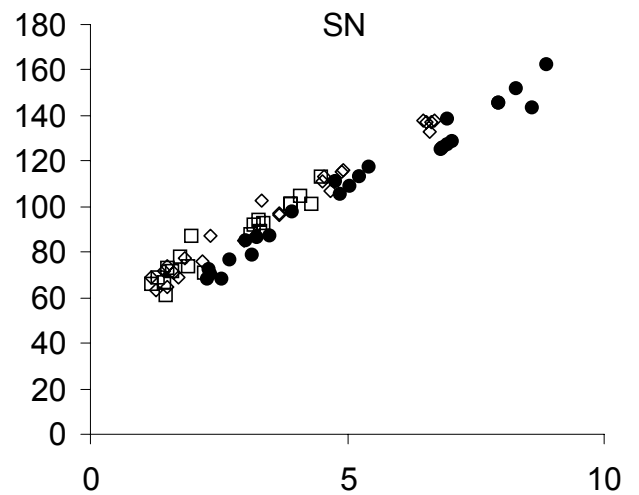
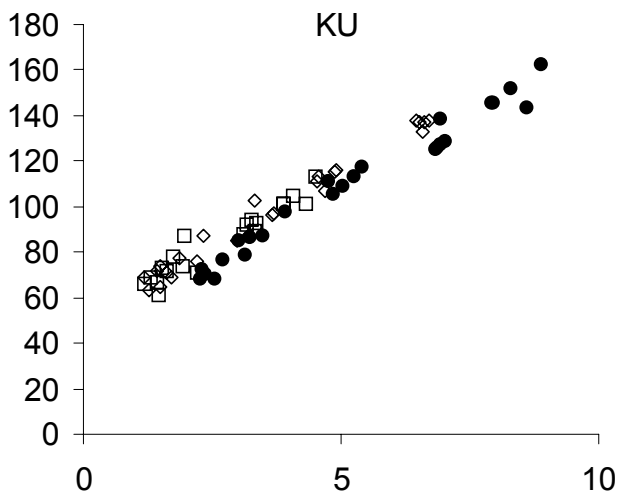
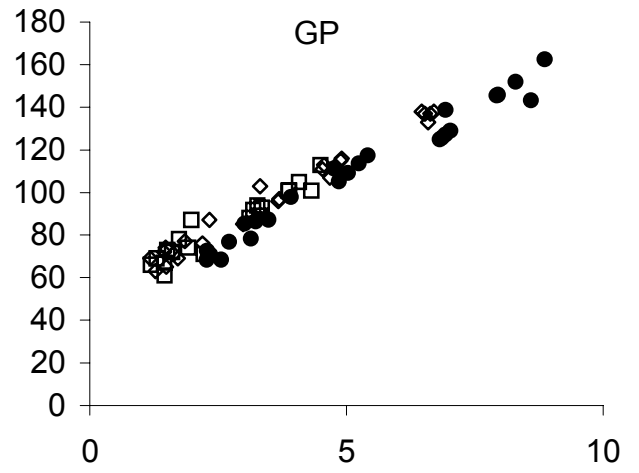
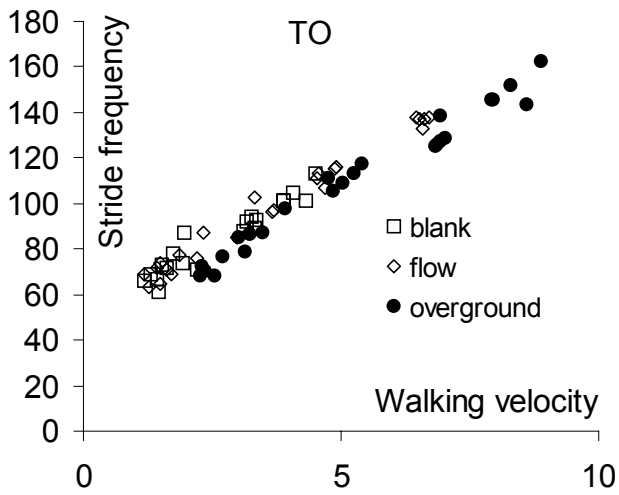




Appendix 2

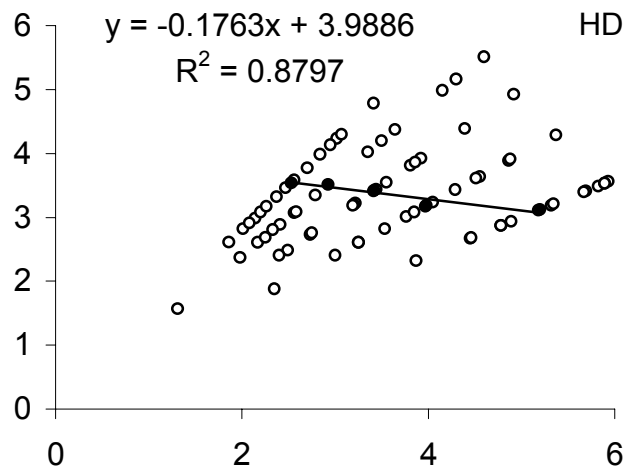
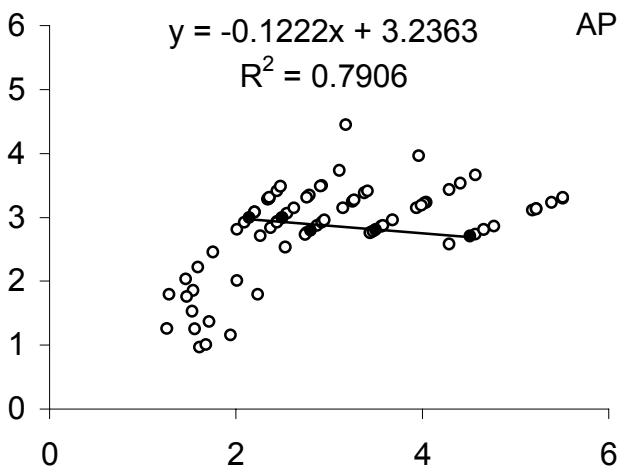
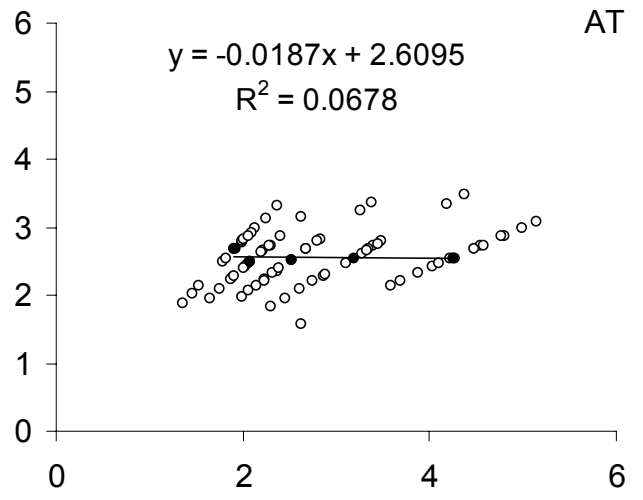
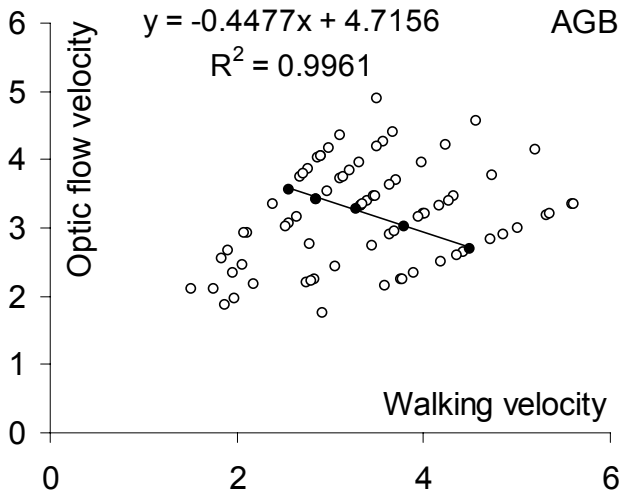
During trials in which subjects walked at five subjective velocities on three walking surfaces: overground, treadmill with optic flow and treadmill without optic flow, stride frequency was also calculated from variations in the walking velocity during treadmill trials or manually during overground trials. No difference between walking surfaces is evident though this may in part be due to noise in the treadmill stride frequency. In all cases, stride frequency is plotted against walking velocity for individual subjects.





Appendix 3

See Fig. 6 for explanation. White: individual trials, black: averages at a particular gain.



Appendix 4

See Fig. 7 for explanation. White: individual trials, black: averages for each subjective walking velocity.

