Exp Brain Res (1997) 114:63–70 © Springer-Verlag 1997

RESEARCH ARTICLE

T. Prokop · M. Schubert · W. Berger

Visual influence on human locomotion

Modulation to changes in optic flow

Received: 10 April 1996 / Accepted: 30 September 1996

Abstract The effect of an optic flow pattern on human locomotion was studied in subjects walking on a self-driven treadmill. During walking an optic flow pattern was presented, which gave subjects the illusion of walking in a tunnel. Visual stimulation was achieved by a closed-loop system in which optic flow and treadmill velocity were automatically adjusted to the intended walking velocity (WV). Subjects were instructed to keep their WV constant. The presented optic flow velocity was sinusoidally varied relative to the WV with a cycle period of 2 min. The independent variable was the relative optic flow (rOF), ranging from −1, i.e., forward flow of equal velocity as the WV, and 3, i.e., backward flow 3 times faster than WV. All subjects were affected by rOF in a similar way. The results showed, firstly, an increase in stride-cycle variability that suggests a larger instability of the walking pattern than in treadmill walking without optic flow; and, secondly, a significant modulating effect of rOF on the self-chosen WV. Backward flow resulted in a decrease, whereas forward flow induced an increase of WV. Within the analyzed range, a linear relationship was found between rOF and WV. Thirdly, WV-related modulations in stride length (SL) and stride frequency (SF) were different from normal walking: whereas in the latter a change in WV is characterized by a stable linear relationship between SL and SF (i.e., an approximately constant SL to SF ratio), optic flow-induced changes in WV are closely related to a modulation of SL (i.e., a change of SL-SF ratio). Fourthly, this effect of rOF diminished by about 45% over the entire walking distance of 800 m. The results suggest that the adjustment of WV is the result of a summation of visual and leg-proprioceptive velocity informations. Visual information about ego-motion leads to an unintentional modulation of WV by affecting specifically the relationship between SL and SF. It is hypothesized that the space-related parameter (SL) is influenced by visually perceived motion information, whereas the temporal parameter (SF) remains stable. The adaptation over the entire walking distance suggests that a shift from visual to leg-proprioceptive control takes place.

Key words Vision · Locomotion · Optic Flow Adaptation · Human

T. Prokop (✉) · M. Schubert · W. Berger
Department of Clinical Neurology and Neurophysiology, University of Freiburg, Breisacherstr. 64, D-79106 Freiburg, Germany;
Tel.: +49-761-270-5361, Fax: +49-761-270-5390,
e-mail: prokop@nz11.ukl.uni-freiburg.de

Introduction

The importance of visual information in controlling locomotion is well documented. In the absence of visual information, it is impossible to make anticipatory modifications of the locomotor rhythm to avoid obstacles. When visual information is available, optic flow induced by locomotion (i.e., ego-motion) has to be distinguished in speed and direction from optic flow induced by object motion. The stabilizing/destabilizing effect of adequate and/or conflicting visual information on postural control in stationary subjects has been described already (Lishman and Lee 1973; Lee and Aronson 1974; Dichgans et al. 1976; Brandt et al. 1976; Forssberg and Nashner 1982; Bronstein 1986; Stoffregen et al. 1987). Recent experiments during a balancing motor task revealed a differential modulation of extensor and flexor muscles by an optic flow pattern (Dietz et al. 1994). Although similar effects due to optic flow should be evident in moving subjects, the requirements for static and dynamic equilibrium control differ (Winter 1991). During stance, postural control can be focused exclusively on the task of maintaining body equilibrium. Since body velocity is zero, absolute spatial coordinates are provided by the feet. These can be used as a reference to detect ego-motion (i.e., body-sway) and to distinguish the latter from object motion. In contrast, during locomotion the act of balancing has to be combined with the task of propelling the body forward. As the legs are lifted during the swing phase, the afferent (exteroceptive) input from the leg cannot provide absolute space coordinates, although velocity information is present via leg proprioceptors. In everyday walking the visual and proprioceptive information about ego-motion are concordant. Consequently, when the visual information about ego-motion is artificially changed in relation to walking velocity (WV), this will lead to the perception of a mismatch between "leg velocity" and "optic flow velocity," which, in turn, should lead to a correction in leg movements. Visual information either affects the balance component or the propelling component of the movement or both. Studies investigating the balance component of locomotion with conflicting visual information revealed a destabilizing effect by an increased variation of step-cycle parameters (Pailhouse et al. 1990) or even by sudden falls in infant walkers (Lishman and Lee 1973; Stoffregen et al. 1987; Schmuckler and Gibson 1989). In contrast, only a few reports exist concerning the influence of visual information upon the propelling component, and these are contradictory. Whereas Pailhous and coworkers (1990) found a small decrease in stride length (SL) combined with an increase in stride frequency (SF) caused by artificial optic flow in either direction, Konczak (1994) found a direction-specific effect: backward flow induced a decrease in WV, whereas forward flow induced an increase in WV. However, these results were based on the analysis of only a few successive strides, and changes in WV did not show a specific modulation of the relationship between SL/SF, which was described for visually guided walking (Zijlstra et al. 1995).

Peripheral feedback from the legs can modify locomotor activity of the hypothesized central pattern generators (CPGs) in order to provide an appropriate movement according to external demands (Andersson et al. 1981; Dietz et al. 1995; for review, see Grillner 1981). Assuming that visual information is relevant in feedforward control of locomotion, optic flow should also be able to modify locomotor activity shown in terms of a modulation in three main components of locomotion, WV, SL, and SF. The aim of this study was to analyze the extent to which optic flow modulates WV and whether this modulation is the result of usually proportional changes of SL and SF or wether it is the result of a specific modulation of one of these parameters, as is already shown for voluntary visually guided walking (Zijlstra et al. 1995). The first assumption would favor an unspecific modulation, the latter a specific modulating effect of visual information on the hypothesized CPGs.

Materials and methods

General procedures and experimental design

After approval of the local ethical committee, ten healthy adults (mean age 25.0±3.6 years) participated in the study. Subjects walked on a self-driven treadmill. This was technically achieved by a closed-loop control system in which the measurement of subject's position on the treadmill was used to adjust the treadmill velocity according to subjects' chosen WV. The position was determined by a distance measurement (Headtracker ultrasonic system, Logitech) between a fixed emitter placed behind the treadmill and a receiver placed on the subject's back: when the subject tended to speed up or slow down, the measured distance increased or decreased and the computer control system accelerated or decelerated the treadmill in order to return the subject to the calibrated position. This apparatus thereby allowed the continuous monitoring of WV for an unlimited walking distance. During the experiment subjects walked a distance of about 800 m.

An optic flow pattern was projected onto a half-spherical screen located in front of the subject's head (radius of the screen, 0.9 m; distance to the subject's head at eye level, 1.2 m; aperture of the projecting lens, 180°). The design of the optic flow pattern was chosen to elicit the illusion of viewing a tunnel or a corridor, which could be moved independently in either direction along the subject's walking line (see also Fig. 1). In order to avoid undesired perception of the two-dimensional quality of the projected scene, subjects had to wear prism spectacles that occluded the borders of the screen and corrected for undesirable convergence and accomodation (prism angle 3.5°; divergence 1+ dioptre). Thus, when looking at the screen, the axes of the eyes were almost parallel, thereby increasing the virtual depth of the image and suggesting the far point to be at near-infinity. Subjects wore headphones with white noise in order to avoid auditory information about WV from the treadmill motor. Subjects were instructed to choose their preferred WV and to maintain it during the experiment. For calibration of the projector, the velocity of the optic flow pattern was

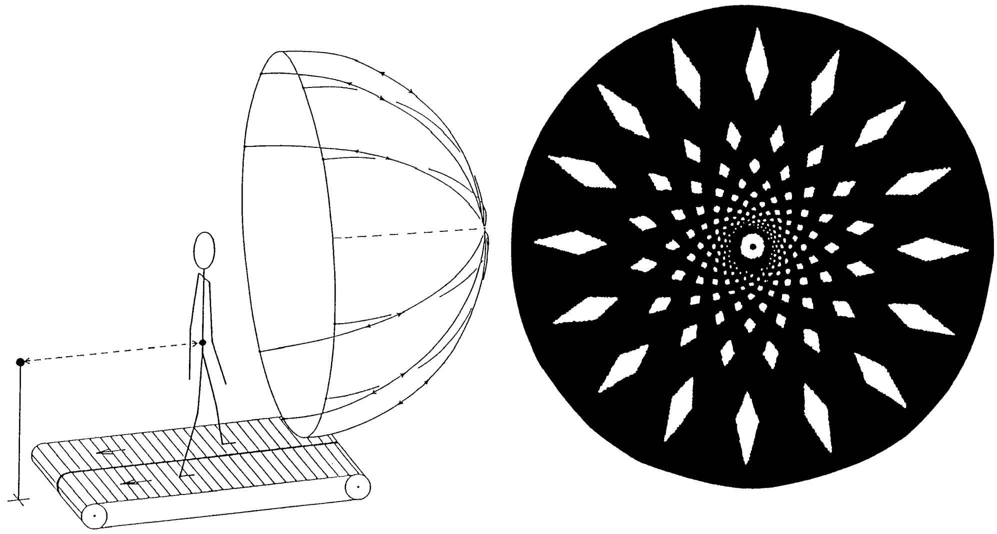

Fig. 1 Experimental design. *Left:* subject walking on the treadmill in front of a half-spherical screen. The treadmill velocity was controlled via distance measurement between the two points indicated. The visual pattern on the screen was moved along the *arrows*. *Right*: subject's view of the pattern, which was moved to evoke the illusion of motion along the line of walking

matched to be treadmill velocity. This was achieved by projecting the pattern onto the moving belt (at an eccentricity of 90°) and by adjusting the pattern to move as fast as the treadmill itself. Thus a locomotion-induced backward flow was generated similar to that perceived in a natural environment. The velocity of the flow pattern could then be modified in relation to WV by superimposing a computer-generated sine function (relative amplitude 2; duration 2 min; level of the mean 1). The resulting optic flow velocity was always related to WV and therefore called relative optic flow (rOF). The rOF as the independent variable was analyzed within the range of –1 to 3. An rOF of 1 represents the situation during normal walking, since WV and optic flow velocity are of the same magnitude and opposite (physiologically) in direction. However, when rOF is more than 1 subjects have the visual impression of being propelled faster than during normal walking; whereas, when rOF is less than 1, they have the visual impression of being propelled slower. The rOF of zero represents a stationary visual scene (i.e., walking on the treadmill without optic flow).

Recording methods

The separate treadmill belts for each leg were placed over a force-measuring system (Kistler), so that the force exerted on each belt could be determined. This was taken for calculation of spatiotemporal parameters: stride-cycle duration (T_c), and duration of support (T_{sup}), swing (T_{swi}), and double support (T_{bip}) of the right and left leg. As in the dark the lateral sway was enhanced in all subjects, sometimes the left leg was placed on the right belt and vice versa, so that not all strides could be correctly determined by the force-measuring system. To determine spatiotemporal parameters for these strides, subjects wore a specially designed shoe on the right foot, which contained circuit breakers to determine heel strike and toe-off. The treadmill velocity, the velocity of the visual flow pattern, and the position of the subject in an anterior or posterior direction on the belt were also recorded.

Data analysis

Spatiotemporal and velocity recordings were amplified (floating-input amplifier, bandwidth 3–1000 Hz; sensitivity 2 mV/V) and via an analog-digital converter transferred on-line to a computer system (IBM compatible 486/60), sampled at 500 Hz.

The data were analyzed off-line as follows: the onset of the force signal was used as a trigger for selecting successive stride-cycles. WV, optic flow velocity, T_c, T_{sup}, T_{swi}, and T_{bip} were then calculated for each stride. The ratio between WV and optic flow velocity was calculated for each stride to create the independent variable rOF. Strides with similar rOF were taken together to the nearest 0.25 unit, resulting in group means for the respective parameters. The following calculations were made:

1. For the evaluation of the stability of stride-cycle events the mean variability of T_{sup}, SL, and SF for each rOF was calculated according to the equation CoVar=(SD/mean)×100.
2. To quantify the visual influence, linear regression functions were individually calculated versus rOF for WV, SL, and SF.
3. A linear regression function of the ratio SL to SF against the WV observed during different rOF was calculated.
4. Stride-cycle parametes T_{sup}, T_{swi}, and T_{bip} were expressed as relative stride-cycle events to the respective T_c, and linear regression functions were calculated against WV.
5. To evaluate the amount of attenuation, strides during the 1st, 2nd, 3rd, and 4th cycle of the sinusoidally changing rOF were analyzed separately.
6. As strides of equal rOF could either be recorded during a period of increasing or decreasing rOF (due to the sinusoidal change of rOF) both periods were analyzed separately. Statistical analysis (calculation of means, SDs, *t*-tests, correlation coefficients, and regression functions) was performed using an SPSS/PC package and EXCEL v5.0.

Results

After a short training period, all subjects were able to perform free walking on the treadmill over a distance of about 800 m. All subjects reported the impression of walking in a tunnel within the training period (approximately 1 min). When optic flow was artificially changed, all subjects were aware of these changes in speed and direction. Despite interindividual differences in the absolute values, all subjects were influenced in a similar way and rOF had similar modulating effects on the stride-cycle parameters.

Stride-cycle variability

The stability of the walking pattern is shown in Table 1 by the mean variability of T_{sup}, SL, and SF from all subjects while walking with different rOF. No significant differences could be detected in the variability with respect to differences in rOF. However, the overall variability was significantly increased compared with that during treadmill walking at a given speed without optic flow (Zijlstra and Dietz 1995). The variability observed by these authors was 2.4% at a WV of 0.5 m/s and 1.1% at a WV of 2 m/s.

Walking velocity, stride length, and stride frequency

Figure 2 shows an example of a single subject: the WV is plotted against the successive strides during the experimental run. The solid line represents rOF, calculated for each stride. The computer-generated sine function of rOF can be seen. The dots show the actual WV in the successive strides. Although the subjects were asked to keep WV constant, the following changes were observed: during an increase in rOF, the WV decreased and, vice versa, during a decrease in rOF, the WV increased.

Figure 3 shows the modulation of SL and SF due to rOF. Data from the same subject were plotted against the successive strides. The solid line again indicates rOF in

Table 1 The mean variability of duration of support (T_{sup}), stride length (*SL*), and stride frequency (*SF*) for each relative optic flow (*rOF*) calculated as a measure of the stability of the walking pattern according to the formula: CoVar=(SD/mean)×100. None of the analyzed parameters showed a tendency to change with changing rOF

rOF	SD		
	T_{sup}	SL	SF
–1	4.45	7.09	3.72
0	6.50	7.44	4.49
1	5.64	7.32	4.25
2	6.04	7.98	3.83
3	5.93	9.38	4.81

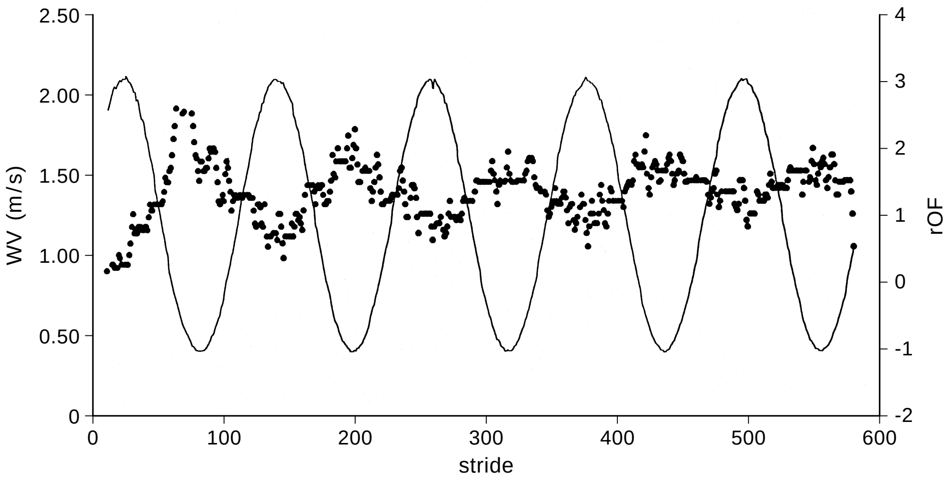

Fig. 2 An individual experimental run. Walking velocity (*WV; dotted line*), scaled on the left *y*-axis, plotted against the successive strides. The right *y*-axis indicates the relative optic flow (*rOF; solid line*) during the respective stride

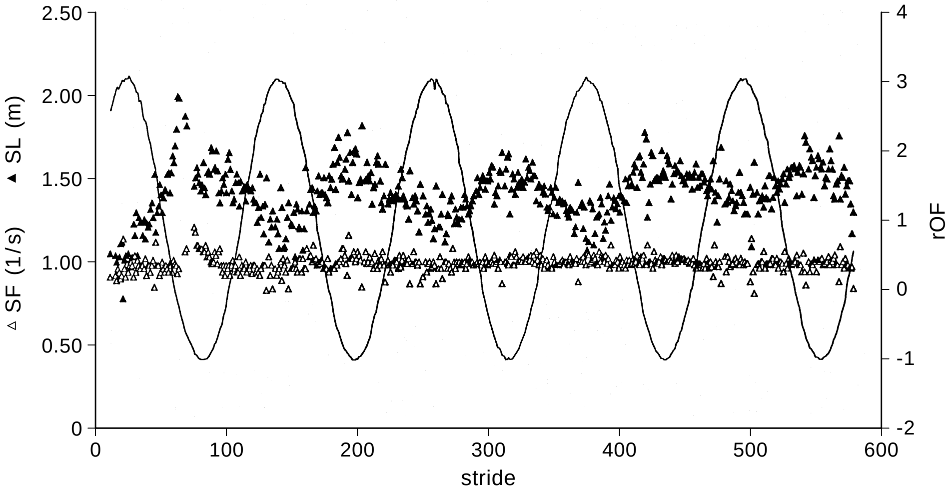

Fig. 3 An experimental run (same subject as in Fig. 2): stride length (*SL; filled triangles*) and stride frequency (*SF; open triangles*) plotted against the successive strides. The right *y*-axis indicates the rOF (*solid line*) during the respective stride

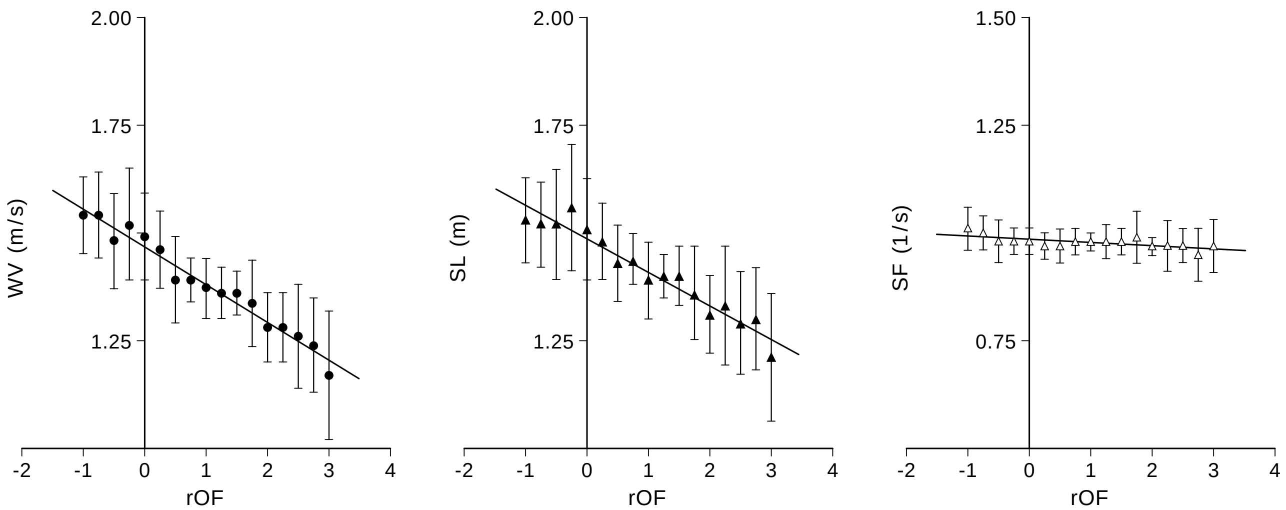

Fig. 4 The data of Fig. 2 and 3 are now plotted against rOF. Group means and SDs for each parameter were calculated by bins of 0.25 (arbitrary units of rOF). The dependency of WV (*left*), SL (*middle*), and SF (*right)* can be described by linear regression functions

the respective stride. The changes in WV shown in Fig. 2 were largely due to changes in SL, whereas SF was negligibly modulated by the rOF. In Fig. 4, WV, SL, and SF from the same subject as in Figs. 2 and 3 were now expressed in relation to rOF. Strides of equal rOF were sorted into bins (see Materials and methods). Figure 4, (left), shows a clear dependency of WV on rOF, which is

Table 2 Quantification of the influence of rOF on walking velocity (*WV*), stride length (SL), and stride frequency (SF) given by the values *a* and *b* of the linear regression functions: each subject separately and mean and SDs of all subjects. *b* represents the value for WV, SL and SF during a stationary optic scene (rOF=0), whereas *a* is the "amount of change" (slope) per unit of rOF. *r* indicates the correlation coefficient of each linear regression function and *P* the level of significance (* *P*<0.01; ** *P*<0.001)

a rOF+*b* Subject	WV				SL				SF			
	a(m/s)	*b* (m/s)	*r*	*P*	*a*(m)	*b*(m)	*r*	*P*	*a*(1/s)	*b*(1/s)	*r*	*P*
1	–0.086	1.47	–0.98	**	–0.077	1.49	–0.97	**	–0.0073	0.99	–0.69	*
2	–0.020	1.31	–0.77	**	–0.017	1.45	–0.77	**	–0.034	0.91	–0.54	ns
3	–0.060	1.25	–0.89	**	–0.052	1.34	–0.89	**	–0.0085	0.93	–0.78	**
4	–0.034	1.27	–0.94	**	–0.030	1.44	–0.86	**	–0.0044	0.88	–0.64	*
5	–0.019	1.12	–0.86	**	–0.015	1.19	–0.79	*	–0.0034	0.93	–0.62	*
6	–0.084	1.35	–0.94	**	–0.066	1.50	–0.91	*	–0.0176	0.90	–0.90	**
7	–0.039	1.31	–0.71	**	–0.037	1.26	–0.71	*	–0.0025	1.04	–0.54	*
8	–0.017	0.96	–0.75	**	–0.012	1.13	–0.61	*	–0.0053	0.84	–0.63	*
9	–0.039	1.36	–0.89	**	–0.027	1.32	–0.85	**	–0.0104	1.03	–0.84	**
10	–0.036	1.28	–0.88	**	–0.029	1.32	–0.65	*	–0.0052	0.98	–0.46	ns
Mean ±SD	–0.043 ±0.024	1.27 ±0.13	–0.86 ±0.08	**	–0.036 ±0.021	1.34 ±0.12	–0.80 ±0.11	**	–0.0068 ±0.0043	0.94 ±0.06	–0.66 ±0.13	*

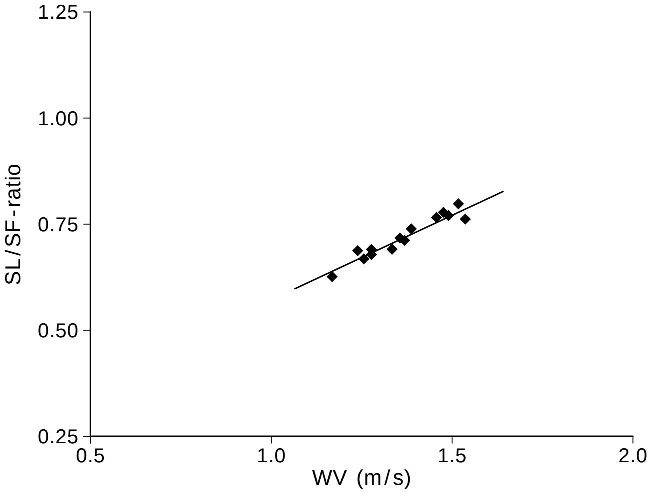

Fig. 5 Dependence of SL and SF on WV and rOF: *x*-axis, WV; *y*-axis, the ratio of SL to SF. A single data point represents the mean value of all strides recorded during a specific rOF. An increase in WV due to rOF results in an increase in the relation SL to SF

Table 3 Quantification of the influence of WV on the ratio SL to SF given by the values *a* of the linear regression function SL to SF ratio=*a* WV+*b*: each subject separately and mean and SDs of all subjects. Value *a* represents the "amount of change" (slope) per unit of rOF; *r* indicates the correlation coefficient of each linear regression function and *P* the level of significance (* *P*<0.01; ** *P*<0.001) (*b*, the hypothetic SL to SF ratio during stance, is not shown)

Subject	*a*(m×s)	*r*	*P*
1	0.39	0.95	**
2	0.23	0.72	*
3	0.34	0.88	**
4	0.38	0.75	**
5	0.22	0.53	*
6	0.25	0.77	**
7	0.42	0.96	**
8	0.11	0.23	ns
9	0.18	0.78	**
10	0.29	0.64	*
Mean ±SD	0.28 ±0.09	0.72 ±0.20	**

primarily due to changes in SL and not in SF (Fig. 4 middle and right). To quantify the influence of rOF, linear regression functions for these parameters are shown in Table 2: in the upper part data are shown for each subject separately and in the lower part as group means and SDs of all subjects. A quantitative analysis of the influence of rOF is given by the respective values *a* and *b* for each linear regression function:

$$X = a \text{ rOF} + b$$

where *X* is the analyzed parameter (WV, SL, and SF), *b* the value during a stationary optical scene (rOF=0), and *a* the "amount of change" (slope) per unit of rOF. For example, in the first subject, WV was 1.47 m/s for strides during a stationary optic scene and decreased by 0.086 m/s (5.9%) when rOF increased by 1 unit. Over the analyzed range of 4 units of rOF the mean change in WV for all subjects was at about 0.17 m/s (13.3%). We found that 0.14 m/s (10.4%) were due to changes in SL and only 0.03 m/s (2.9%) resulted from changes in SF.

Figure 5 shows the SL to SF ratio for a single subject when WV was modulated by rOF. The single points represent the SL to SF ratio expressed as mean values for strides of equal rOF. With increasing WV a clear increase in the ratio can be seen. This modulation was found in all subjects, as shown by linear regression functions in Table 3.

When analyzing the relationship between T_{sup} and WV in our paradigm, a similar relationship could be observed as was described for walking under visual constraints (Zijlstra et al. 1995). To allow for a direct comparison, calculations were made for the step length instead of SL. The linear regression function for the relationship between T_{sup} and WV found in that study (T_{sup}=–16.1·(step length)+74.6; r=0.98, P<0.001) was

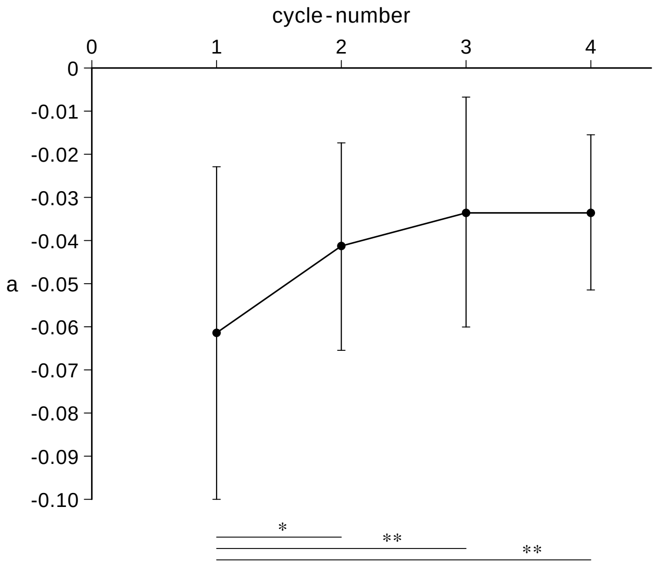

Fig. 6 Comparison of the influence of rOF on the WV during the 1st, 2nd, 3rd, 4th cycle of the sinusoidally changing rOF:Means and standard deviations of value *a* of the regression function WV=*a* rOF+*b* are shown for all subjects. Levels of significance: * $P<0.05$; ** $P<0.001$; paired *t*-test

quite similar to our findings (T_{sup}=–17.2·(step length)+ 68.0; r=0.74, $P<0.001$).

Time-related adaptation

Figure 6 shows a comparison of the modulation of WV induced by rOF over 4 cycles of the sinusoidally changing rOF. Means and SDs of the value *a* (slope) of the regression function: WV=*a* rOF+*b* from all subjects are shown for the different cycles. It can be seen that the modulation of WV induced by rOF attenuation significantly over time and reached a constant level after 3 cycles. Whereas during the 1st cycle the WV decreased by 0.061 m/s±0.038/unit of rOF, the modulation during the 2nd, 3rd, and 4th cycle was 0.041 m/s±0.024, 0.033 m/s±0.026, and 0.033±0.018, respectively, which corresponds to an attenuation of 32.5%, 45.6%, and 45.7%.

Strides of equal rOF could either be recorded during a period of increasing or decreasing rOF. The comparison of both periods revealed no difference in WV, SL, and SF, and therefore the data are not shown.

Discussion

The aim of this work was to study the influence of an optic flow pattern on locomotion. The main result indicates that optic flow modulates WV. This effect is due to a modulation in SL and it is attenuated over time.

From animal experimental work it is known that optic flow can trigger locomotion or induce a modulation of locomotion velocity (Davis and Ayers 1972). In running gerbils an optic flow rectilinear to the self displacement has a systematic effect on locomotion velocity (Sun et al. 1992). In humans the influence of optic flow on the perception of ego-motion has been described (Larish and Flach 1990), and during stance visual information is known to have an influence on the subjects' performance of postural control: a stabilizing one when appropriate (Dichgans et al. 1976; Paulus et al. 1989) and a destabilizing one when conflicting (Berthoz et al. 1975; Nashner and Berthoz 1978; Bronstein 1986; Dietz et al. 1994; Dijkstra et al. 1994). It was expected that artificial optic flow should affect human locomotion. This influence could either concern the balance or the propelling component of the movement.

Balance control

From developmental studies it is known that infant walkers have substantial difficulties in maintaining equilibrium (Bril and Brenière 1989), especially with conflicting visual information (Stroffregen 1987; Schmuckler and Gibson 1989). In contrast to this, in the present experiment adults were able to walk without major equilibrium problems for about 10 min corresponding to a walking distance of about 800 m. Nevertheless the variability of stride-cycle events was increased compared with that during treadmill walking at the same speed without optic flow (Zijlstra and Dietz 1995), indicating a decreased stability of the walking pattern due to the artificial change in optic flow. However, the stride-cycle variability was not different with respect to different levels of rOF. It is therefore suggested that also in adults artificial optic flow leads to a decrease in the stability of the walking pattern, but to a smaller extent than in children. However, within the analyzed range of rOF, there was no direction-specific and velocity-specific influence of rOF on the stability of the walking pattern, at least when the change in rOF was brought about slowy. Our results are in line with earlier findings by Pailhous and Bonnard (1992), who found no difference in the stability of the walking pattern comparing normal walking (physiological optic flow while walking overground) with treadmill walking (no optic flow, while walking on a treadmill). This result can now be extended to the range of rOF analyzed here.

Propelling control

The present experiment showed that rOF induced a modulation in WV. Backward flow led to a decrease in WV, whereas forward flow led to an increase in WV. Within the analyzed range of rOF the effect on the WV can be described by a linear negative regression function. This is in contrast to recent experiments of Masson and Pailhous (1994). They reported no influence of optic flow on WV, SL, and SF in an experiment, where the optic flow was generated by stripes on a self-driven treadmill. The stripes were perpendicular to the walking direction and their temporal frequency was sinusoidally modulated by changing their frequency edge. A comparision of both studies is difficult for methodological reasons, since the proportion of the visual field covered by the flow pattern, a different cycle-period, the different changes in rOF, and the use of a fixation-point in our paradigm could explain the discrepant findings. Obviously our stimulus was stronger – quasi more realistic – consequently uncovering mechanisms provided by nature. Our results prove the systematic influence of optic flow on locomotion. In line with our results, Konczak (1994) reported an influence of optic flow on WV during overground walking. Backward flow induced a decrease, whereas forward flow induced an increase in WV. However, these results were based on the analysis of only a few successive strides and the velocity of the optic flow was 0.6 m/s in either direction and not related to subjects' WV. Konczak argued, that "subjects attempted to match their own walking speed to the velocity of the visual moving scenes." If so, this should have led to problems in the performance of subjects in our paradigm. As the velocity of the optic flow was always related to the WV – and therefore called rOF – the only congruent situation to achieve this goal would be during a rOF of 1 and during standing, since otherwise the optic flow velocity would be too fast or too slow compared with the WV. However, no subject slowed down to a standstill or tried backward walking during forward flow. The influence of rOF on WV was rather continuous over the whole range and can be described by a linear regression function. In other words, no turning point in the behavior can be seen over the analyzed range of rOF, suggesting that (1) velocities are perceived relative to each other and that (2) no absolute spatial reference is provided during locomotion. We therefore favor the hypothesis that the subjects' strategy to keep their WV constant (which was the required task) lies more in a weighting of the information coming from different afferent sources and in a striving for reduction of mismatch when these sources of information are conflicting. An artificial increase in backward flow generates a higher retinal image velocity than the locomotion-induced backward flow. Subjects' visual perception "of walking faster than they actually do" therefore leads to a decrease in their WV. The leg-proprioceptive and the visual velocity information both contribute to the impression of WV, and velocities are perceived relative to each other. A quantification of the visual contribution to the velocity perception could, in our experiment, directly be deduced from the linear regression function for WV. It is, with 4.3 cm/s (±2.4 cm/s) per unit of rOF, rather small, but nevertheless highly significant, as shown by the respective r and P values (see Table 2). However, this visual influence adapted over time (within approximately 8 min) by about 45%, indicating a shift back toward a more propriocptive control. This is in line with experiments of Bronstein (1986) on visually evoked postural responses during standing, which showed an attenuation within four trials.

An important findings of this study is the fact that the modulation of WV to rOF is mainly the result of a modulation in SL without a modulation in SF. During normal walking the walking pattern is characterized by a modulation in both SL and SF, resulting in a stable linear relationship between SL and SF. A recent study by Zijlstra et al. (1995), analyzing voluntary and involuntary modulation when walking to external cues, showed an analogous modulation to a spatial constraint: subjects showed no modulation in SF when they were asked at different WV to step on stripes fixed on the floor at different widths. Contrary to normal walking, the latter study indicated that SF was kept constant during a task where SL had to be voluntarily chosen according to spatial cues. This result of a voluntary modulation observed in their study can therefore also be extended to that of an involuntary modulation due to rOF. It is argued that during locomotion visually induced modulation in general might induce a modulation of SL, the spatial component of the leg movement, whereas SF, the temporal component, remains constant. Proprioceptive feedback from the legs is known to specifically modify locomotor activity on a spinal level (central pattern generator, CPG) in order to provide an appropriate movement according to external demands (Andersson et al. 1981; Grillner 1981). However, it remains unclear whether the characteristics of supraspinal, e.g., visual, influence consist of a nonspecific or a specific modifying effect on the drive of lower level CPGs. The influence of rOF on the leg-movement characteristics in our study favors a specific supraspinal effect. It is hypothesized that the space-related parameter (SL) is modified by visually perceived motion information, whereas the temporal parameter (SF) remains stable. The visual information might therefore specifically interact with space-related factors in the drive of the CPGs.

Acknowledgements The authors wish to thank W. Zijlstra for critical reading, F. Pfister for hard- and software adaptation to the experimental demands and O. Meyer-Hamme and U. Römmelt for technical assistance. This work was supported by the Deutsche Forschungsgemeinschaft (Be 936/5-1), the Bundesministerium für Forschung and Technologie (grant 01KL9402) wo W.B., and the Swiss National Science Foundation (grant 31–33567.92) to V.D.

References

Andersson O, Forssberg H, Grillner S, Wallen P (1981) Peripheral feedback mechanisms acting on the central pattern generators for locomotion in fish and cat. Can J Physiol Pharmacol 59:713–726

Berthoz A, Pavard B, Young LR (1975) Perception of linear horizontal self-motion induced by peripheral vision (linearvection) basic characteristics and visual-vestibular interactions. Exp Brain Res 23:471–489

Brandt T, Wenzel D, Dichgans J (1976) Visual stabilization of free stance in infants: a sign of maturity (author's translation from German). Arch Psychiatr Nervenkr 223:1–13

Bril B, Brenière Y (1989) Steady-state velocity and temporal structure of gait during the first six months of autonomous walking. Hum Mov Sci 8:99–122

Bronstein AM (1986) Suppression of visually evoked postural responses. Exp Brain Res 63:655–658

Davis WJ, Ayers JL (1972) Locomotion: control by positive-feedback optokinetic responses. Science 177:183–185

Dichgans J, Mauritz KH, Allum JH, Brandt T (1976) Postural sway in normals and atactic patients: analysis of the stabilizing and destabilizing effects of vision. Agressologie 17:15–24

Dietz V, Schubert M, Discher M, Trippel M (1994) Influence of visuoproprioceptive mismatch on postural adjustments. Gait Posture 2:147–155

Dietz V, Colombo G, Jensen L, Baumgartner L (1995) Locomotor capacity of spinal cord in paraplegic patients. Ann Neurol 37:574–582

Dijkstra TM, Schöner G, Gielen CC (1994) Temporal stability of the action-perception cycle for postural control in a moving visual environment. Exp Brain Res 97:477–486

Forssberg H, Nashner LM (1982) Ontogenetic development of postural control in man: adaptation to altered support and visual conditions during stance. J Neurosci 2:545–552

Grillner S (1981) Control of locomotion in bipeds, sect 1, tetrapods and fish. In: Brookhards M, Mountcastle VB (eds) Motor control. (Handbook of physiology, sect 1, The nervous system, vol 2, part). Am Physiol Soc, Washington DC, pp 1179–1235

Konczak J (1994) Effects of optic flow on the kinematics of human gait: a comparison of young and older adults. J Mot Behav 26:225–236

Larish JF, Flach JM (1990) Sources of optical information useful for perception of speed of rectilinear self-motion. J Exp Psychol Hum Percept Perform 16:295–302

Lee DN, Aronson E (1974) Visual proprioceptive control of standing in human infants. Percept Psychophys 15:529–532

Lishman JR, Lee DN (1973) The autonomy of visual kinaesthesis. Perception 2:287–294

Masson G, Pailhous J (1994) Modulations of the optical flow did not induce locomotor pattern fluctuations in treadmill walking in man. Percept Mot Skills 78:755–767

Nashner L, Berthoz A (1978) Visual contribution to rapid motor responses during postural control. Brain Res 150:403–407

Pailhous J, Bonnard M (1992) Steady-state fluctuations of human walking. Behav Brain Res 47:181–190

Pailhous J, Ferrandez AM, Fluckiger M, Baumberger B (1990) Unintentional modulations of human gait by optical flow. Behav Brain Res 38:275–281

Paulus W, Straube A, Krafczyk S, Brandt T (1989) Differential effects of retinal target displacement, changing size and changing disparity in the control of anterior/posterior and lateral body sway. Exp Brain Res 78:243–252

Schmuckler MA, Gibson EJ (1989) The effect of imposed optical flow on guided locomotion in young walkers. Br J Dev Psychol 7:193–206

Stroffregen TA (1987) Use of central and peripheral optical flow in stance and locomotion in young walkers. Third International Conference: Event perceptions and action (1985, Uppsala, Sweden). Perception 16:113–119

Stoffregen TA, Schmuckler MA, Gibson EJ (1987) Use of central and peripheral optical flow in stance and locomotion in young walkers. Perception 16:113–119

Sun HJ, Carey DP, Goodale MA (1992) A mammalian model of optic-flow utilization in the control of locomotion. Exp Brain Res 91:171–175

Winter DA (1991) The biomechanis and motor control of human gait: normal, elderly and pathological. University of Waterloo Press, Waterloo, IA

Zijlstra W, Dietz V (1995) Adaptability of the human stride cycle during split-belt walking. Gait Posture 3:250–257

Zijlstra W, Rutgers AWF, Hof AL, Werden TW (1995) Voluntary and involuntary adaptation of walking to temporal and spatial contraints. Gait Posture 3:13–18