Exp Brain Res (1999) 127:33–42

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RESEARCH ARTICLE

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The use of optical velocities for distance discrimination and reproduction during visually simulated self motion

Received: 3 June 1998 / Accepted: 15 February 1999

Abstract Successful navigation through an environment requires precise monitoring of direction and distance traveled (“path integration” or “dead reckoning”). Previous studies in blindfolded human subjects showed that velocity information arising from vestibular and somatosensory signals can be used to reproduce passive linear displacements. In these studies, visual information was excluded as sensory cue. Yet, in our everyday life, visual information is very important and usually dominates vestibular and somatosensory cues. In the present study, we investigated whether visual signals can be used to discriminate and reproduce simulated linear displacements. In a first set of experiments, subjects viewed two sequences of linear motion and were asked in a 2AFC task to judge whether the travel distance in the second sequence was larger or shorter than in the first. Displacements in either movement sequence could be forward (f) or backward (b). Subjects were very accurate in discriminating travel distances. Average error was less than 3% and did not depend on displacements being into the same (ff, bb) or opposite direction (fb, bf). In a second set of experiments, subjects had to reproduce a previously seen forward motion (passive condition), either in light or in darkness, i.e., with or without visual feedback. Passive displacements had different velocity profiles (constant, sinusoidal, complex) and speeds and were performed across a textured ground plane, a 2-D plane of dots or through a 3-D cloud of dots. With visual feedback, subjects reproduced distances accurately. Accuracy did not depend on the kind of velocity profile in the passive condition. Subjects tended to reproduce distance by replicating the velocity profile of the passive displacement. Finally, in the condition without visual feedback, subjects reproduced the shape of the velocity profile, but used much higher speeds, resulting in a substantial overshoot of travel distance. Our results show that visual, vestibular, and somatosensory signals are used for path integration, following a common strategy: the use of the velocity profile during self-motion.

Key words Path integration · Optic flow · Distance discrimination · Distance reproduction

Introduction

Successful navigation requires precise monitoring of the distance traveled, or “path integration”. It is well accepted that, in many species from insects to man, various self-generated or “idiothetic” signals (Mittelstaedt and Mittelstaedt 1973, 1980) are used in parallel to register active as well as passive self motion. Studies on insects (Wehner 1996; Wehner et al. 1996) have shown that, beside external cues (skylight compass), self-induced visual information (optic flow) is also used to accomplish the task of path integration (or “dead reckoning”) (Esch and Burns 1995; Ronacher and Wehner 1995; Srinivasan et al. 1996).

Vertebrates use inertial signals from the semicircular canals to monitor angular acceleration (Seguinot et al. 1993; Etienne et al. 1996; Israel et al. 1996; Sherry 1996), whereas otoliths are thought to play an important role in registering translational movements (Israel and Berthoz 1989; Israel et al. 1994). Even proprioception can be used to monitor active displacements, e.g., walking distance (Thomson 1980). Accuracy for walking towards a target is reduced under conditions of low visibility, however, demonstrating the importance of vision in this regard (Philbeck and Loomis 1997).

Previous studies in blindfolded human subjects have shown that vestibular and somatosensory signals can be used to reproduce passive linear displacements (Berthoz et al. 1995; Harris and Jenkin 1996; Israel et al. 1997). Although only asked to reproduce travel distances, it turned out that subjects tended to make use of parameters such as peak velocity, duration, and velocity profile of the passive displacement in order to correctly fulfill

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the task. Yet, this capability of reproducing travel distances was only successful for simple movements (triangular or trapezoidal velocity profiles) during the passive displacement. Subjects failed to reproduce distance correctly when more complex velocity profiles were applied.

In the above-mentioned studies, visual information was excluded as a sensory cue. Yet, in normal circumstances, vision is a potent source of information and often dominates over vestibular and somatosensory signals. A typical example is the illusion of self-motion perceived when sitting in a stationary train while a neighboring train starts moving (linear vection). Moreover, many studies in the past have shown the importance of visual information to detect one's own movement through space. Gibson (1950) first showed that optic flow, i.e., the visual motion experienced during self-motion, could be used to determine one's heading direction. Many studies thereafter have unveiled the capability of the visual system to extract heading direction (Warren and Hannon 1990; Royden et al. 1994; Van den Berg 1996). These studies pointed out the role of visual information for detecting and guiding the *direction* of movement. Here, we investigate the use of optic flow to determine *distance*.

Distance traveled could be estimated by using the duration and speed of the movement. In principle, the optic flow seen during linear self-movement cannot give absolute information about ego-speed, because it not only depends on the self-motion, but also on the distance of the visible objects from the observer. Without knowing these distances, it is only possible to extract combined information about distance and velocity, the "time-to-contact" or "tau" (Lee 1980) from the optic flow. However, it should be possible to compare two travel distances based on the optic flow, if both are performed in the same visual environment. In analogy to studies with blindfolded subjects that used only vestibular and proprioceptive information, we asked whether visual motion could be used to discriminate and reproduce simulated passive linear displacements.

Subjects were very accurate in discriminating travel distances with an average error of less than 3%. Reproduction of simulated displacements was accurate, too, given that visual feedback was available. Our results show that visual motion can be used for discriminating and reproducing travel distances. Vision complements vestibular and somatosensory signals in this regard. Utilization of all of these signals follows a common strategy: subjects rely on the velocity profile during (simulated) self-motion.

Materials and methods

Ten subjects (20–35 years old), with normal or corrected to normal vision, participated in the experiments. Subjects sat 57 cm in front of a tangent screen subtending 90° by 90°. Visual stimuli, generated by a Silicon Graphics workstation, were back-projected onto this tangent screen.

Distance discrimination

In a first set of experiments, subjects were shown two sequences of linear motion across a textured ground plane, as shown in Fig. 1. Displacements could be forward-forward (ff), forward-backward (fb), backward-forward (bf), or backward-backward (bb). The simulated height of the observer was 1.6 m above ground level. The simulated visibility, i.e., the maximum visible distance that the subject could see from any point on the plane, was 30 m. Scene details beyond this point were not displayed on the screen. Each trial consisted of two movement sequences, with different or equal movement direction. This resulted in the four sequences described above (ff, fb, bf, or bb). The first movement always had a fixed duration (2 s) and speed (2 m/s), leading to a travel distance of 4 m. In the second movement, speed and duration were independently varied between 0.5 and 1.5 times the original value. The travel distance of the second movement thus ranged from (0.5*2 s)*(0.5*2 m/s)=1 m (distance ratio: traveled distance 2nd movement/traveled distance 1st movement = 0.25) to (1.5*2 s)*(1.5*2 m/s)=9 m (distance ratio = 2.25). Subjects were asked in a 2AFC task whether the distance traveled in the second sequence was longer or shorter than distance in the first sequence. Each subject performed 50 trials.

In a second set of discrimination experiments, subjects saw trials mimicking movement through a 3D cloud of dots rather than across a textured plane. As before, the first sequence always simulated the same movement (duration: 2 s; speed: 3 m/s), while speed and duration of the second movement varied independently between 0.5 and 1.5 times the original value. In addition, visibility, i.e., the maximum visible distance at which the rendering of the

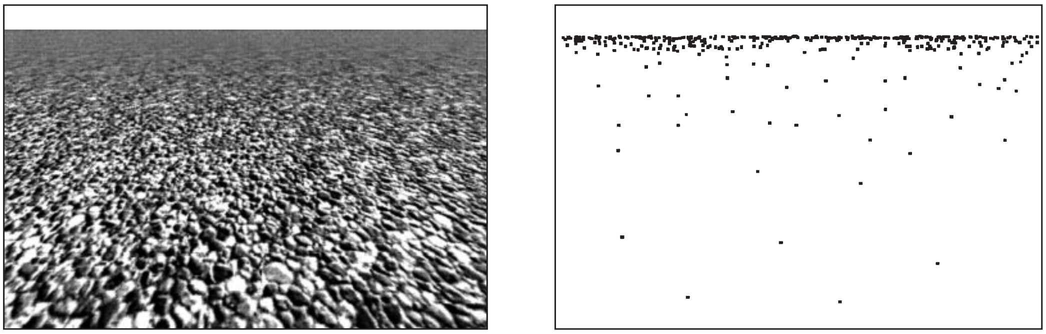


Fig. 1 Two examples of the stimuli employed in the experiments. The *left panel* shows a rendered image of the textured ground plane. This stimulus was generated by defining the four spatial corner-points of a large plane made up of textured elements. The *right panel* depicts an image of the 2-D plane of random dots, as used in our experiments. For the latter stimulus, the density of the dots increases towards the horizon. In addition, a 3-D cloud of dots was used in some experiments

environment was truncated, was varied between the first and the second movement. Subjects were not aware of this variation, since the distribution of dots in space was re-generated before each movement. In the first movement, maximum visible distance was always 20 m. In the second movement, it varied between 10 and 30 m in steps of 5 m.

The number of visible dots in the two successive movements was adjusted so that it was always the same at the beginning of each movement. Dots were placed at equidistant intervals along the lines of sight of the observer at the beginning of the movement. Depending on the visibility, the intervals were chosen wider or smaller, such that the total number of dots was constant. The distribution was then randomized by adding a small random offset to each point. This arrangement guaranteed a homogenous distribution of dots for all depths at the beginning of the movement. However, it is important to note that the dot density somewhat decreased during the movement, i.e., the number of points that entered the field of view at its most distal end was smaller than the number of points that left the field of view as they passed the observer.

In order to quantify the ability of subjects to discriminate the travel distances, we determined the point of subjective equivalence (PSE), i.e., the distance ratio for which the second distance was estimated as being equivalent to the first. To do so, responses (“longer”=1; “shorter”=0) were plotted against the distance ratio and fit by the following sigmoidal function:

$$f(x) = \frac{1}{1+e^{ax+b}}$$

The PSE is reached for f(x)=0.5 (with x=distance ratio) and, therefore, is given by the equation ax+b=0, leading to x=–b/a. The PSE was determined for each subject under each of the four conditions (ff, fb, bf, bb).

Distance reproduction

After subjects had accomplished the distance discrimination task, they were asked in a second set of experiments to actively reproduce (active condition) the distance of a previously viewed, passive linear forward movement (passive condition). The two conditions simulated movement across a textured ground plane, across a 2-D dot-plane, or through a 3-D cloud of dots. Subjects controlled the speed of their own simulated movement in the active condition by increasing or decreasing pressure applied to an isometric force detector (SpaceBall 3003, Spacetec, IMC). Subjects indicated the end of their movement by a “button press”. The first movement (passive) always lasted 5 s, speed varied randomly between 1 and 5 m/s in steps of 1 m/s. In different blocks of trials, the passive movement had constant, sinusoidal, or complex velocity profiles. In case of sinusoidal velocity profiles, the velocities mentioned above (1 m/s–5 m/s) indicate the peak velocities. Complex velocity profiles consisted of a collection of several short sequences of different length and with different speeds. A random process generated speed and duration of the individual sequences. The only instruction given to the subjects was to reproduce the travel distance of the passive displacement in the active condition. Subjects were allowed to become familiar with the use of the SpaceBall prior to data recording.

In a last experimental series, subjects were asked in an analogue paradigm to reproduce previously seen passive displacements without visual feedback. Again, the first (passive) trial simulated a movement across a textured ground plane. 500 ms after this movement had stopped, the tangent screen turned black. Then subjects had to use the SpaceBall to simulate an equidistant displacement, but without any visual control of their performance. Again, the passive (visible) movement had either a constant, sinusoidal, or complex velocity profile, and subjects had to indicate the end of their own (invisible) simulated movement by a “button press”. All subjects in this last experimental series had gained experience in using the SpaceBall while participating in the previous series of experiments.

Results

Distance discrimination – ground plane

Subjects were very accurate in discriminating travel distances across a textured ground plane. For each subject, we determined the point of subjective equivalence (PSE) in each of the four movement conditions concerning the first and second part of the trial: forward-forward (ff), forward-backward (fb), backward-forward (bf), or backward-backward (bb). As shown in Fig. 2, the smallest error was found for the ff condition (0.32%). Average error was smaller than 3%. Error values were not significantly different in the four conditions (Kruskal-Wallis ANOVA, 3 *DF*, *H*=1.14, *P*=0.767). Table 1 shows the PSE values of the 10 subjects in the four experimental conditions.

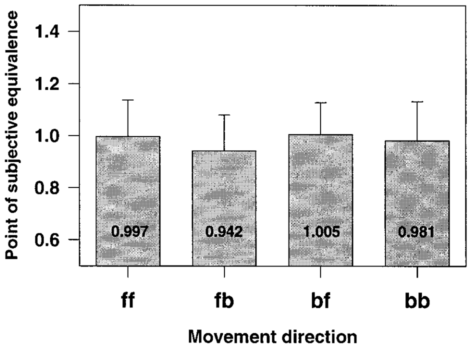


Fig. 2 Point of subjective equivalence for travel distances across a textured ground plane. The four *bars* indicate the means (±SD) for the four possible combinations of displacements. *ff* (forward-forward) and *bb* (backward-backward) indicate equally directed movements, whereas *fb* (forward-backward) and *bf* (backward-forward) indicate differently directed movements

Table 1 Points of subjective equivalence for movement across a ground plane. Displacements were into the same direction (*ff* forward-forward, *bb* backward-backward) or into opposite directions (*fb* forward-backward, *bf* backward-forward). *Initials* indicate individual subjects

Displacement	CF	KZ	MM	MR	MW	SH	UC	UN	WL	WZ
ff	1.074	0.853	1.019	1.015	1.025	0.929	0.864	1.288	0.814	1.087
fb	0.979	0.730	0.926	0.895	0.790	0.967	1.110	1.160	0.827	1.036
bf	1.011	1.009	0.949	1.013	1.019	0.840	1.056	1.276	0.837	1.040
bb	1.026	0.962	1.025	0.984	0.896	0.813	0.826	1.327	0.870	1.085

Distance discrimination – cloud of dots

In the above experiment, subjects were very accurate in discriminating travel distances from visual motion. However, the optic flow field experienced during ego-motion is, in principle, not sufficient to unambiguously provide absolute ego-speed or true travel distance. Optical velocities scale with distance from the observer. Thus, without the knowledge of the distances in the environment, or "scene layout", only relative speed can be obtained from the optic flow.

In a second set of experiments, we varied the scene layout in order to test the dependence of the judgments of travel distance on the distribution of distances of objects in the environment. Yet, this difference in scene layout had to go unnoticed by the subjects, since they otherwise might have tried to correct for it. Therefore, distribution of dots in space was varied before each movement, not allowing for any estimation of visible distance.

Movement through a three-dimensional cloud of random dots was simulated. In this case, the distance of each individual element from the observer was randomized within a certain overall distance range. This distance range was given by the visibility, i.e., the maximum visible distance of the observer. Only points of the cloud that were closer to the observer than this maximal visible distance were drawn on the screen. In order to test for the influence of the distance range on the perceived travel distance, we varied the distance range between the first and the second movement. During the first movement, maximum visible distance was always 20 m. Maximum visible distance during the second displacement varied from trial to trial between 10 m and 30 m. Since the distribution of dots in space was always much greater than the maximal visible distance, new distant points appeared during the movement, while near points passed the observer.

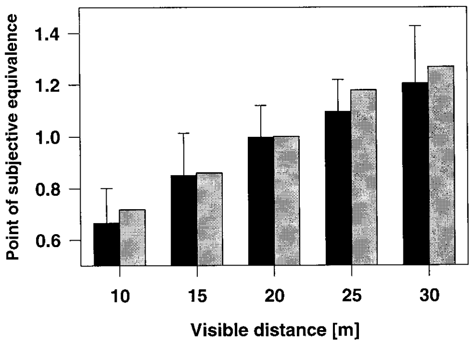


Fig. 3 Point of subjective equivalence (PSE) for travel distances with different visible depths. For movements through a 3-D cloud of dots, judgments of traveled distance were strongly influenced by the visible depth during the second movement sequence. Bars in *black* indicate PSE averages across subjects (mean ±SD). Bars in *light gray* indicate the expected values if the average dot speed in the display was used

Variation of maximum viewing distance had a highly significant influence on the subject's estimation of traveled distances (Kruskal-Wallis ANOVA, 4 *DF*, H=30.9, P<0.0001). Figure 3 shows the mean values of the PSEs in this condition, individual values for all subjects are shown in Table 2. A PSE value of almost exactly one (0.997) was obtained when the visible distance during the second movement equaled the one from the first movement, i.e., when it was 20 m.

Use of optical velocities in distance discrimination

An influence of maximum viewing distance would be expected if the distribution of optical velocities across the visual field determined the performance of the subjects, i.e., if travel distance was estimated from the velocity distribution of the optic flow field. One hypothesis might be that subjects use the average velocity across the entire movement field, which they determine from the velocity distribution. The perceived travel distance would then scale with the ratio between the average speed in the first and the second movement. We compared the experimental data with this prediction. To do so we computed the average optical velocity of visible dots in the display, taking into account the decreasing dot density over time. The estimate of perceived travel distance, based on average velocity, almost perfectly matched the behavioral data (Fig. 3). Thus, we conclude that subjects mainly relied on the average optical velocity in the display in order to estimate their displacement.

Distance reproduction – textured ground plane

Subjects reproduced distances quite accurately for all velocity profiles (Fig. 4). The left panel in Fig. 4 depicts results for a linear passive displacement with constant speed across a ground plane. The slope of the regression

Table 2 Points of subjective equivalence for a forward-forward movement through a 3D cloud of dots with variable visible distances during the second displacement. *Initials* indicate individual subjects

Visible distance [m]	CF	KZ	MM	MR	MW	SH	UC	UN	WL	WZ
10	0.550	0.555	0.513	0.691	0.562	0.732	0.963	0.755	0.696	0.646
15	0.809	0.665	0.980	0.972	0.680	0.843	0.867	1.196	0.756	0.735
20	1.058	0.907	1.050	1.018	0.934	0.968	0.902	1.301	0.922	0.910
25	1.235	1.038	1.334	1.063	1.166	0.942	1.032	1.149	1.018	0.968
30	1.425	1.166	1.631	1.091	1.318	0.928	0.971	1.353	1.048	1.115

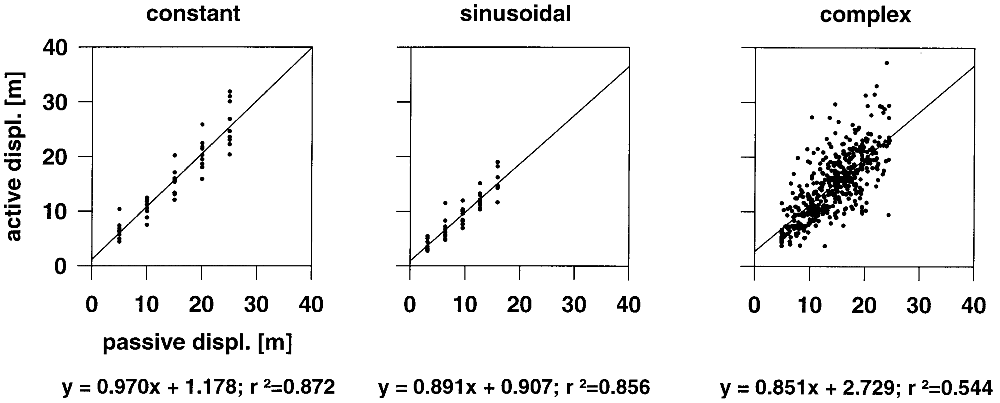


Fig. 4 Reproduction of previously seen displacements. The three panels show the distances reproduced by the subjects after simulated passive displacements across a textured ground plane. Velocity profiles in the passive condition were constant (*left panel*), sinusoidal (*middle panel*), or complex, i.e., a randomized sequence of constant speeds (*right panel*). Each *dot* represents average values from 50 trials from individual subjects (*left and middle panel*) or results from individual trials (*right panel*)

line (statistical model: y=ax+b, a=0.97, n=45, r^2=0.872, P<0.0001) is nearly 1.0. The intercept is at b=1.178 m, i.e., active displacements were usually too long, leading to a constant overshoot. The same is true for the sinusoidal velocity profile (middle panel). However, here the initial overshoot (b=0.907) is combined with a general tendency to undershoot at larger distances (a=0.891). Thus, the regression model (n=45; r^2=0.856, P<0.0001) predicts an accurate behavior for a passive displacement of 8.3 m. For smaller passive displacements, subjects would overshoot, whereas they would undershoot the required distance for passive displacements beyond this value.

Even passive displacements with complex velocity profiles (see Materials and methods for details) could be reproduced quite accurately (Fig. 4, right panel). Yet, underestimation of small and overestimation of large travel distances were more pronounced in this experimental condition. The intercept of the regression line increased to b=2.729, whereas the slope declined to a value of a=0.851. The linear regression model could be applied with high significance (n=489, P<0.0001).

Although subjects were only required to reproduce travel distance, they tended to increase the velocity in the active condition when the velocity in the passive condition was increased (Kruskal-Wallis ANOVA: P<0.0001). This was true for displacements with constant as well as sinusoidal velocity profiles, as shown in Fig. 5. Peak velocities were always higher in the active condition.

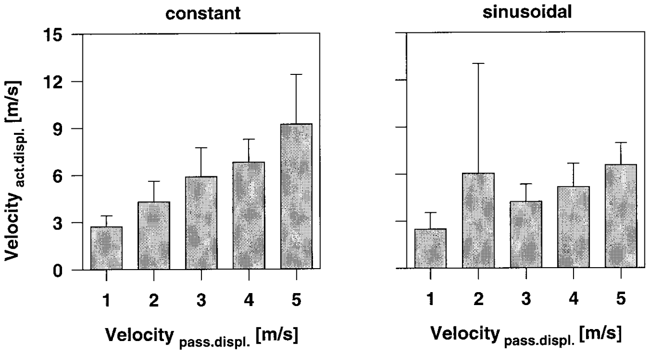
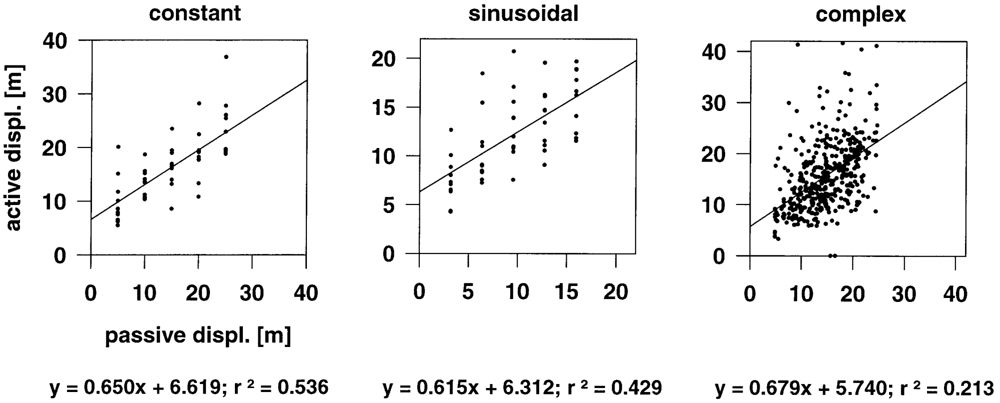


Fig. 5 Peak velocity during distance reproduction. The two panels plot peak velocity in the active condition as a function of the peak velocity in the passive condition. For both velocity profiles (constant and sinusoidal), subjects increased peak velocity in the active condition, in accordance with an increase in the passive condition

Distance reproduction – random dots

In this experiment, subjects were asked to reproduce previously seen displacements through a three-dimensional cloud of dots or across a plane of random dots. Data for movement through a 3-D cloud of dots are shown in Fig. 6. An increase of reproduced distance with an increase of passive displacements is apparent. Performance was less accurate than for movements across a ground plane (compare Fig. 4). The slopes of the regression lines were always smaller than 1.0. Interestingly, an almost constant overshoot of about 6.0 m was observed in all three experimental conditions (constant, sinusoidal, complex).

In this experimental condition, the density of dots had not been constant throughout the trial. Instead, the density declined continuously during the trial (see Materials and methods for details). We therefore decided to run a second set of experiments with constant dot density. Dots were positioned in a cubic array at equidistant intervals with small randomized offsets. Velocities were always constant with speeds of 1, 3, 5, 7, and 9 m/s. Results for this second set of trials are shown in the left panel of Fig. 7. In this condition, the slope of the regression line reached the ideal value of 1.0 (the actual value was a=1.001). However, consistent with the findings from the first set of trials, subjects again overshot the required distance by a constant value of about 6.0 m. Performance was better for movements across a 2D plane of dots, as shown in the right panel of Fig. 7. A constant overshoot of about 2 m was accompanied by an increasing accuracy for larger displacement, indicated by a slope of the regression line of a=1.059.

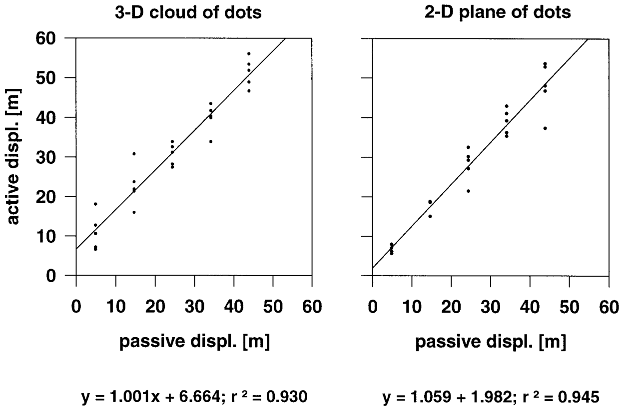


y = 0.650x + 6.619; r ² = 0.536

y = 0.615x + 6.312; r ² = 0.429

y = 0.679x + 5.740; r ² = 0.213

Fig. 6 Reproduction of previously seen displacements through a 3-D cloud of dots. The three panels show the performance of subjects reproducing displacements through a 3-D cloud of dots. As in Fig. 4, velocity profiles in the passive condition were constant (*left panel*), sinusoidal (*middle panel*), or complex (*right panel*). Note that ordinate and abscissa have the same scale in individual panels, but are differently scaled between panels. For more details, see legend of Fig. 4



y = 1.001x + 6.664; r ² = 0.930

y = 1.059 + 1.982; r ² = 0.945

Fig. 7 Reproduction of previously seen displacements through a 3-D cloud of dots and across a 2-D plane of dots. The *left panel* shows the performance of subjects reproducing displacements through a modified 3-D cloud of dots (see text for details). The *right panel* depicts performance for displacements across a 2-D plane of random dots. Velocity profiles in the passive condition were always constant

Distance reproduction without visual feedback

In a final set of experiments, subjects were asked to reproduce a previously seen displacement in darkness, i.e., without visual feedback. The passive displacement across a textured ground plane had constant, sinusoidal, or complex velocity profiles. The initial displacement always lasted 5 s, and maximum speed was between 1 and 5 m/s with a step size of 1 m/s.

In this condition, subjects showed very large overshoots. Yet, a clear correlation of the distances in the active and passive condition was observed, i.e., an increase in travel distance in the passive condition was accompanied by an increase of displacement in the active condition, as shown in Fig. 8. The left and middle panels depict results for displacements with constant and sinusoidally modulated speed in the passive condition. The right panel depicts the results for the complex movement. A significant dependence (linear regression: $P<0.05$) was observed in all three experimental conditions. As can be seen in Fig. 8, performance was much better in the constant and sinusoidal condition than in the complex condition.

Even in this experimental condition with no visual feedback, subjects often increased their maximum speed following an increase of speed in the first movement (Fig. 9). This tendency, however, was only significant for displacements with constant speed (left panel, linear regression: $P<0.01$) and not for displacements with sinusoidal velocity profiles (right panel, $P>0.3$).

Use of optical velocities in distance reproduction

In order to test for the strategies used by individual subjects to replicate travel distances, we compared the velocity profiles in the active with those in the respective passive displacements. For this, we normalized all active displacements with respect to their duration. This normalization procedure allowed trials to be averaged in order to obtain a subject's "standard response profile". This response profile was qualitatively and quantitatively compared with the respective passive condition. Qualitative estimation was accomplished by classification of responses into one of three categories: constant, sinusoidal, unclassifiable (Table 3). These classifications were checked quantitatively by fitting each response profile with a trapezoid and using the parameters of the fit to distinguish constant from sinusoidal velocity profiles. Using a trapezoid allowed fitting both constant and sinusoidal velocity profiles for the following reason: each movement in the active condition started and ended with a velocity value of zero. Thus, even if subjects performed an almost "ideal" distance reproduction with constant velocity, their velocity profiles had to contain acceleration and deceleration phases. Thus, even almost ideal constant velocity profiles could be approximated better by a trapezoid than by a constant function. A sinusoidal velocity profile can also be approximated by a trapezoid. However, compared with the constant velocity profile, it should result in a much smaller slope of the flank of the trapezoid and a smaller value for the height of the trapezoid. Based on these measures (slope and height of the approximated trapezoid), response profiles could be classified as constant or sinusoidal.

A total of 60 response profiles had to be classified (ten subjects, six experimental conditions). In 63%

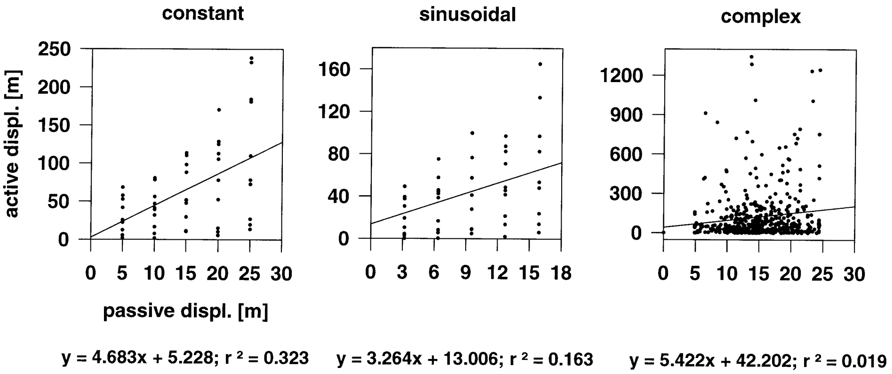


Fig. 8 Reproduction of displacements without visual feedback. The three panels depict performances of subjects for reproduction of previously seen displacements with constant (*left*), sinusoidal (*middle*), and complex (*right*) velocity profiles. Note that ordinate and abscissa have the same scale in individual panels, but are differently scaled between panels. For more details, see legend of Fig. 4

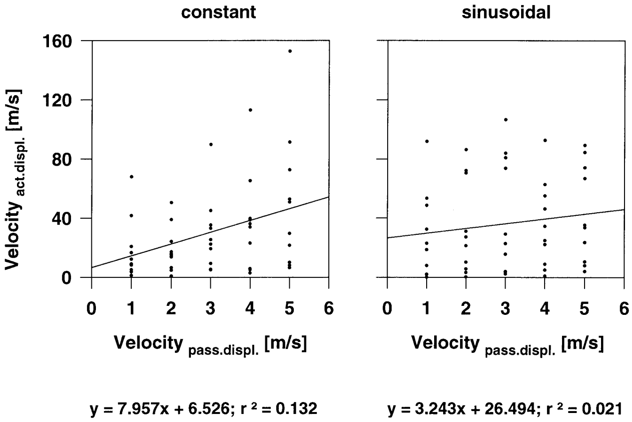


Fig. 9 Peak velocity during distance reproduction without visual feedback. The two panels reveal an increase of the peak velocity in the active condition, in accordance with an increase of the peak velocity in the passive condition, but the increase was statistically significant only in the constant speed condition

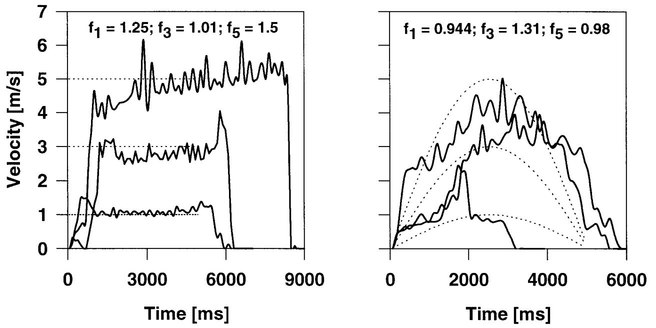


Fig. 10 Velocity profiles during distance reproduction. The two panels show sample traces for two subjects reproducing displacements with constant (*left*) and sinusoidally modulated speeds (*right*). As can be seen in both panels, subjects almost exactly replicated the structure of the previously seen displacement. Yet, durations of passive and active displacements were sometimes different, resulting in mismatches of travel distances in the two conditions, indicated by the distance ratio, *f*

Table 3 Velocity profiles used by the subjects in different experimental conditions (*Plane* textured ground plane, *Cloud* 3D cloud of dots, *Plane/Dark* textured ground plane without visual control). *Const* indicates a constant velocity profile, whereas *sin* indicates a sinusoidal velocity profile used by the subjects and as judged by visual inspection and curve fitting. Response profiles which did not fit in any category (-) were considered as not matching the velocity profile in the passive condition. *Initials* indicate individual subjects

	Plane constant	Cloud constant	Plane/Dark constant	Plane sinus	Cloud sinus	Plane/Dark sinus
CF	Const	Const	Const	Const	Const	Sin
KZ	Const	Const	Const	Sin	–	–
MM	Const	Const	Const	Const	Const	Const
MR	Const	Const	–	Sin	–	Sin
MW	Const	Const	Const	Sin	Sin	Sin
SH	–	–	–	–	–	–
UC	Const	Const	Const	Const	Const	Const
UN	–	Const	Const	Sin	Sin	Const
WL	Const	Const	Const	Sin	Sin	Sin
WZ	Const	–	–	Sin	Sin	Sin
Velocity profiles						
Equivalent	8/10	8/10	7/10	6/10	4/10	5/10
Different	0/10	0/10	0/10	3/10	3/10	3/10
Not Classifiable	2/10	2/10	3/10	1/10	3/10	2/10

(38/60) of the cases, subjects' response profiles matched the velocity profile of the previously seen passive displacement. In 15% (9/60) of the cases, subjects used constant velocity profile in order to reproduce a passive sinusoidal displacement. In the remaining 22% (13/60) of the cases, response profiles were not classifiable as being either constant or sinusoidal. Looking for the performance of individual subjects revealed the following: one subject (SH) never made use of the previously seen velocity profile and used some other strategy. Two subjects (MM and UC) always used constant speed displacements to fulfill the required task.

An example in which the subject reproduced displacements across a ground plane (with visual feedback) by reproducing the velocity profile is shown in Fig. 10. The left panel depicts three results for a constant velocity

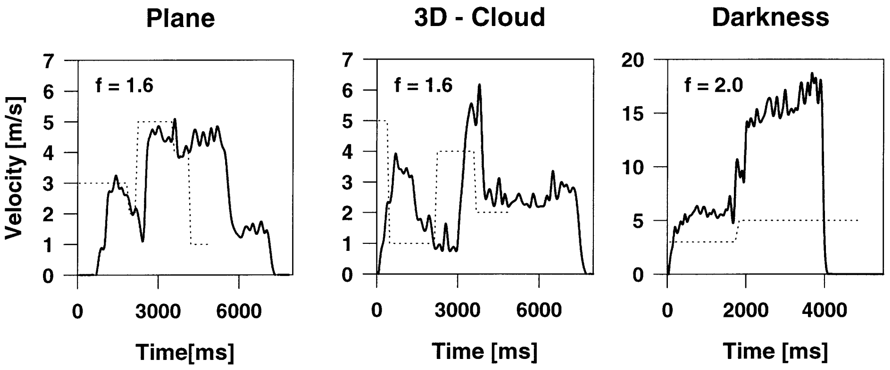


Fig. 11 Velocity profiles during reproduction of complex displacements. The three panels show sample traces for complex displacements across a textured ground plane (*left*), through a 3-D cloud of dots (*middle*), and across a textured plane without visual feedback (*right*). The *solid lines* in each panel indicate the subjects' performance in the active conditions, while the *dotted lines* show the velocity profiles in the passive conditions. As can be seen in all three panels, subjects qualitatively replicated the velocity profile of the previously seen displacement. Yet, differences in duration and peak velocity between passive and active displacements resulted in differences of travel distances in the two conditions, indicated by the distance ratio, *f*

movement with speeds of 1, 3, and 5 m/s, indicated by the dotted lines. The thick lines indicate the velocity profiles (unfiltered raw data) produced by the subject in these three cases. This velocity profile is an almost exact reproduction of the speed seen in the previous displacement. Movement duration was reproduced less well. Normalized distance ratios *f* (= reproduced distance/simulated distance) for the different displacements with different speeds are shown in the top part of the figure. A value of *f*=1.0 would indicate a perfect reproduction of distance, whereas a value of *f*=2.0, for instance, would indicate an overshoot of two times the original distance. Indices indicate the respective speeds. The right panel depicts results for displacements with sinusoidal velocity profile for another subject. Again, three displacements with different maximum speeds are shown along with the subject's behavior. Clearly displacements are reproduced by mimicking the velocity profile accompanied by adjusting the maximum speed to that of the previously seen movement.

Subjects also applied the same strategy of reproducing velocity profiles to "complex" displacements, as shown in Fig. 11, although reproduction of speed values is poorer than with visual feedback (Fig. 10). The three panels depict results for movement across a plane (left), through a 3D cloud of dots (middle), and across a textured ground plane in "darkness", i.e., without visual feedback (right). *f* values again indicate the normalized reproduced distance in the different conditions.

Discussion

Our results show that visual motion can be used for discriminating and reproducing travel distances. Vision complements vestibular and somatosensory signals in this regard. Utilization of all of these signals follows a common strategy: subjects rely on the velocity profile during (simulated) self-motion.

Our experiments were designed in analogy to previous experiments on blindfolded subjects, who were passively displaced on a mobile robot and who had to reproduce this displacement (Berthoz et al. 1995; Israel et al. 1997). The only sensory cues available in these experiments were vestibular and proprioceptive signals. In our experiments, displacements were only simulated, i.e., vestibular and proprioceptive input were excluded as sensory information. The only available sensory cue was vision. Yet, it turned out that subjects in both experimental paradigms relied on velocity profiles for the reproduction of the previously experienced passive displacement.

Distance discrimination

Subjects were very accurate in discriminating travel distances, with an overall error of less than 3%. Performance was good regardless of whether displacements were forward or backward.

In our reproduction experiments, subjects clearly relied on optical speed as a cue to perceived travel distance. This utilization of optical flow for estimating displacements is not only found in humans, but also in insects (Esch and Burns 1995; Ronacher and Wehner 1995; Srinivasan et al. 1996). Yet, it is known that velocity derived from optical flow can only be judged up to a scaling factor (Lee 1980). The relative angular speed of objects during forward movements changes with their distance from the observer. Thus, information about forward speed is only available when the distances of the environmental objects are known. If cues to the depth layout of the scene such as, e.g., objects of known size or information about the height of the observer above ground level are not available, subjects can only rely on retinal image velocities. In order to carry out the given task, they have to equate these retinal velocities in the two movement sequences under the assumption that the environment in both sequences was the same. This assumption was violated in a second set of experiments, which was designed to investigate how the different parts of the visual scene contribute to the estimate of speed of self-motion, i.e., what strategy subjects used to determine their speed. In this paradigm, visible depth varied in randomized order in the second movement, but not in the first. This variation was performed without the subjects' knowledge. If subjects assumed a constant layout of the environment throughout all trials, they should have produce predictable errors. This was indeed observed. The errors can be used to determine how subjects use the distribution of optical speeds in the visual scene. The results suggested that subjects use the average speed of the visual motion seen during the movement.

The range effect, complex velocity profiles, and displacements without visual feedback

In all of our experiments under "full vision", a range effect was observed. Subjects overshot small displacements and undershot large displacements. This is in good agreement with previous studies on blindfolded subjects using real displacements. In these studies, subjects either had to walk towards a previously seen target (Rieser et al. 1990) or they had to estimate or reproduce passive displacements on a rotational chair, a sled, or a mobile robot (Israel and Berthoz 1989; Berthoz et al. 1995; Israel et al. 1996, 1997).

In the experiments of Israel and coworkers, subjects were unable to reproduce complex velocity profiles, i.e., profiles including many different accelerations and decelerations within a single displacement. In our experiments, however, subjects accomplished this task. Performance was almost as good as in "easier" trials with constant or sinusoidal velocity profiles. Even in this complex task, subjects tended to reproduce the previously seen velocity profile. It can thus be argued that the different sensory qualities are used in the same manner, i.e., by reproducing velocity profiles. However, vision in this circumstance is superior to vestibular information, which does not allow blindfolded subjects to dissociate between a deceleration of a forward movement and an acceleration of a backward movement.

Performance without visual feedback was much lower. This was caused by a tremendous overshoot of reproduced speed, while subjects still tried to replicate the velocity profile. This is very different from the result of Israel and co-workers. It might be related to a difference in the experimental setup concerning the control of speed. In Israel's experiments, the robot had a maximum speed, which was also in the range of those applied in the passive displacements. In our experiments, however, speed of displacement had virtually no upper limit. Furthermore, the isometric force detector (SpaceBall) has a strongly progressive transfer characteristic. This caused small increases of force to lead to a much larger increase in speed, while equal decreases in force led to smaller decreases in speed. Under visual feedback, this was easy to control for. In the absence of visual feedback, this could likely have caused the observed overshoots.

Distance reproduction and the role of vision in the process of path integration

Path integration requires estimating travel distances and changes in direction or orientation. Much research on path integration has been performed in insects. This is also true for the role of vision in path integration. Insects are known to integrate angular and linear components of their movements utilizing a sun compass, as well as other kinds of visual information (Esch and Burns 1995, 1996; Srinivasan et al. 1996; Wehner 1996; Wehner et al. 1996). Ants measure the rotational component of their self-motion by measuring skylight information rather than by using idiothetic signals (Wehner 1994). For translational displacements, two different strategies are used: optical flow and snapshots of the visual scene. As shown by Ronacher and Wehner (1995), foraging ants rely on the speed of the underlying terrain to control their own speed and, therefore, estimate their homing distance. Manipulating the relative speed between the walking ants and a moveable pattern seen by the ants through a transparent platform influenced the ant's traveled homing distances. Foraging honeybees also use visual motion to estimate the distance to a food source (Esch and Burns 1995; Srinivasan et al. 1996).

Studies with humans in virtual environments indicate multiple ways to use visual information for navigation and path integration. Visual snapshots of identifiable places, static visual distance cues, and visual motion are used (Peruch et al. 1997; Gillner and Mallot 1998; Witmer and Kline 1998). Our results are consistent with this. They suggest that visual motion can be used to estimate the distance between two positions along a traveled path, which might also be useful in tasks of navigation and path integration. Recently, it was shown that perceived ego-speed is influenced by contrast and spatial frequency of the viewed scene (Distler and Bülthoff 1996; Snowden et al. 1998). It remains to be seen whether these factors likewise influence judgements of travel distance from visual motion.

Acknowledgements We thank Andrea Borgard and Harald Frenz for their help with the experiments. This was work was supported by the Deutsche Forschungsgemeinschaft (LA 952/1 and SFB 509) and the Human Frontier Science Program (RG71/96B).

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