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Max-Planck-Institut für Verhaltensphysiologie Seewiesen

Idiothetic Navigation in Gerbils and Humans

MARIE-LUISE MITTELSTAEDT and STEFAN GLASAUER

With 3 Figures

Abstract

This study investigates navigation in gerbils and humans with the aim of experimentally separating inertial form substratal and rotatory from linear components of the underlying system.

1. Gerbils are able to home unaided by external cues. By investigating this "idiothetic" performance on an arena rotating with constant velocity it is shown that the navigation system in fact uses rotatory as well as linear inertial information. Because the actual courses are intermediate between what is expected from purely inertial and purely substratal navigation, an additive cooperation between both mechanisms is most likely.

2. Experiments with humans allow conclusions on how the distance information in walking or passive transport under idiothetic conditions is gained. The distance indicated is larger than veridical if the proband walks at a slower than normal pace, but is smaller when walked faster. This relation reverses polarity in passive transport. Modelling these relations leads to the hypothesis that the processing structures themselves (rather than just the parameters) are different in the two cases.

3. The relevance of the results on distance processing for navigation is checked in a homing task featuring a triangular excursion, with varied conditions along the second leg (fast – slow; active – passive). Now the **angular** homing errors behaved as though the **linear** integration variable would indeed be subject to the same errors as those found above.

1. **Introduction**

Evidence is accumulating that mammals are able to home under experimental conditions designed to exclude all external cues (BERITOFF 1957; MITTELSTAEDT and MITTELSTAEDT 1980, 1982; POTEGAL 1982; MILLER et al. 1983; ETIENNE et al. 1985; for humans see chapter 3.1.). If the exclusion is perfect, this capability must be based on the integration and storage of the animal's own movement. Information about the latter (**idiothetic** information (MITTELSTAEDT and MITTELSTAEDT 1973)) could be gained in two basically different ways:

a) from sense organs like the vestibular system which measure the inertial forces elicited by the concomitant accelerations *(inertial idiothesis)*.

b) from those proprioceptors or efference copies whose signals are normally correlated with, and hence allow inferences about, the animal's course with respect to ground, air or water *(substratal idiothesis)*.

In either case, the rotatory components must be integrated over the linear components of the movement along the path in order to gain the location coordinates *(path integration)*.

The following study will investigate whether, and which type of, idiothesis plays a role in the navigation of gerbils and humans.

2. Homing in the gerbil

Gerbils are able to home by idiothesis from any place in a circular arena of 1.30 m diameter (MITTELSTAEDT and MITTELSTAEDT 1980, 1982). By rotating the arena with varying acceleration profiles it could be shown that the navigation mechanism does indeed use inertial information about **rotation**, and that its failures correlate quantitatively with those expected from the dynamics of the semicircular canals. On the other hand, in two pertinent paradigms, the animal appeared to be unable to reckon with **linear** acceleration.

However, in one of the two paradigms the gerbil was accelerated while it was sitting. Now, unlike the process which summates the rotations, the **path** integrator need not to be kept running when the location stays constant, and be better shut off then, to guard against the inevitable drift. In the second paradigm the entire arena was linearly shifted while the gerbil was in fact running. But there the acceleration profile may well have been outside the range the system can or does use.

We have therefore designed a third test paradigm the outcome of which should allow a definite decision. The paradigm lets the gerbil navigate under idiothetic conditions while the arena rotates at constant speed. The rationale is that, given perfect inertial navigation, the animal would orient with respect to **Newtonian space** rather than to the rotating surface.

If previously trained in a stationary arena, as indeed she was, to run straight ahead across the arena to find her young near the wall opposite her home, the gerbil would now run on a straight line with respect to the laboratory (Fig. 1a, dashed line), that is, the path on the arena would be curved in a sense opposite to that of the rotation of the apparatus (which was clockwise in all cases; see Fig 1a, solid lines). However, if navigating by substratal idiothesis, the gerbil would run on the same straight line with respect to the arena as in the stationary controls (Fig. 1b, solid line), whereas on a curved one with respect to the room (Fig. 1b, dashed lines). For an assumed constant forward velocity of the animal the course to be expected in either case may be computed for the arena velocity used (14.4; 28.8; 36.0 deg/sec).

The results (Fig. 1c) show that the gerbil's navigation system does in fact use both, rotatory as well as linear, inertial forces, though not to perfection. The actual courses appear to be intermediate ones between those expected under inertial idiothesis on the one hand and substratal idiothesis on the other. Hence, rather than forcing us to conclude that the inertial system is imperfect, the result points at an additive interaction of both mechanisms. This is all the more plausible because, in contrast to the situation in the test paradigm, they would be cooperative or complementary in all situations of normal life.

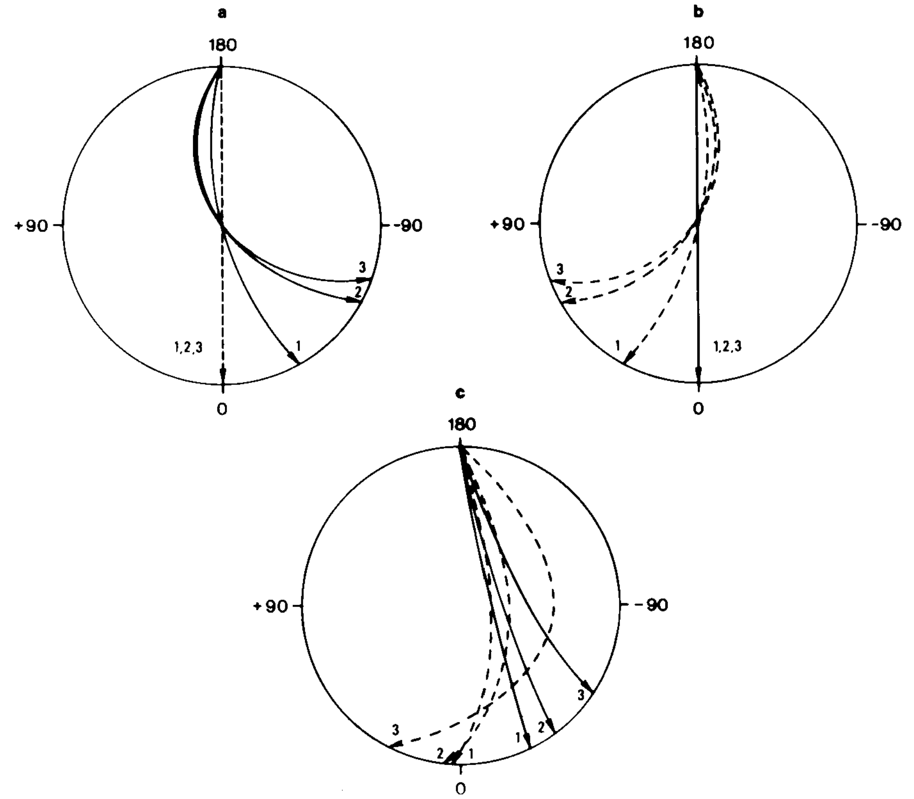

Fig. 1. Theoretical (a, b) and experimental (c) courses on an arena rotating clockwise at constant speed. The gerbil is previously trained to run from the nest (at 180) to pick up her young at the opposite wall (at 0) while the arena is stationary. Solid lines: courses traced on the arena; dashed lines: the same courses as seen from a stationary camera. a: expected courses at pure inertial navigation; b: expected courses at pure substratal navigation; c: experimental courses at 3 rotatory velocities of the arena ((1): 14.4°/s; (2): 28.8°/s; (3): 36.0°/s; means of 121 runs of 11 animals (1), 127 runs of 14 animals (2), 87 runs of 10 animals (3). The gerbil shows intermediate courses between those expected in a and b. Yet a young outside the arena, opposite the nest when the female leaves it, could be found in cases (1) and (2), whereas the young **on** the arena is missed.

3. Idiothetic navigation in humans

3.1. Theoretical prerequisites of inertial navigation

A mammal which is able to home by means of inertial idiothesis must possess an information processing structure connecting the rotatory with the linear acceleration sensors, e.g. those of the canals with those of the otoliths. The first mathematical model of how navigation could be achieved by such a connection has been developed by MAYNE (1974).

But that both organs must cooperate anyhow, in order to achieve the basic capabilities of angular orientation and postural control, follows from their physics, viz. from the inability of the otoliths to discriminate linear acceleration from gravity, and that of the canals to discriminate immobility from constant rotation.

The first mathematical model of such a cooperation, derived from experiments on fish (HOWLAND and HOWLAND 1962, HOWLAND 1968), was developed by HOWLAND (1971), followed by the models of ORMSBY (1974) and BORAH et al. (1988) on human orientation. When it turned out that all models mentioned failed to account for the well-known results of rotation about an earth-horizontal axis (LACKNER and GRAYBIEL 1978), a new model was developed by MITTELSTAEDT et al. (1989). This model may be worked out to serve as a basis for inertial navigation.

In order to gain constraints on and critical tests for this model we need navigation experiments with human subjects. The extant literature, which we cannot review here, offers only a few studies which were undertaken with the explicit objective to probe the involvement of the vestibular system (LIEBIG (1933); WORCHEL (1952); BERITOFF (1957)). Yet because the inputs of the vestibular system have not been systematically varied, definite decisions are not possible. It is necessary, then, to design paradigms which allow to separate, in the performances under study, rotatory from translatory inputs as well as inertial from substratal ones.

3.2. Processing of linear information

In our first paradigm the proband (S) tries to reproduce an originally seen distance when blindfolded and earphoned with white noise a) by walking to the imagined goal and b) by indicating it during passive transport.

In a long hallway the distance of 10 meters from the starting point is marked by a cardboard square fastened 2 m above ground. After inspection of the marker the S is blindfolded and asked to stop below the imagined goal. Five classes of velocity from very slow to very fast, according to the S's standard, are selected by the experimenter.

In test b) the S is moved at corresponding velocities while standing on a low trolley and asked to signal when passing the goal. The trolley is either moved smoothly, or rhythmically to imitate walking. The velocity applied, the distance indicated and the number of steps are measured (in the case of passive transport, position and acceleration data were recorded on-line by computer).

In most Ss, the distance indicated turned out to depend on (mean) velocity. In a) the S overshoots the mark at slow, undershoots it at fast velocity, and is best at what the S considers her/his normal pace. In b) this relation reverses polarity, undershooting at fast, overshooting at slow velocity (Fig. 2).

The data cannot be explained by a procedure such as counting steps or stopping after a constant time. If instead it is based on an idiothetic **velocity** signal, the distance must be derived by temporal integration. Hence either the original signal or the integration is non-veridical.

Let us assume that a "leaky" integrator is initially loaded like a capacitor by the reference value which codes the seen distance. Assume further that the gain factor (see appendix) is adjusted such that, by the combined effect of the velocity integration and the leakage, the load is zero at the right distance when the S's

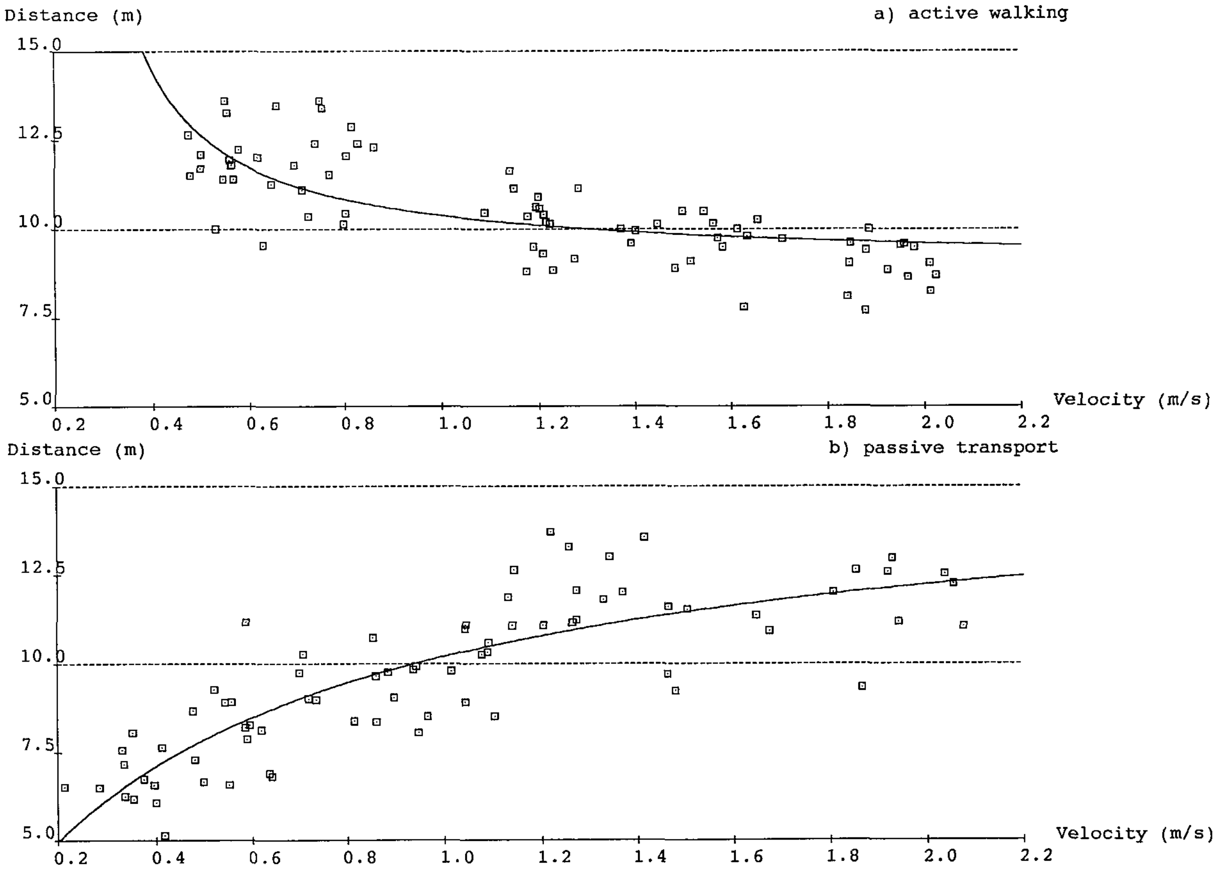

Fig. 2. Linear motion experiments in a blindfolded human subject (S), who was told to a) walk to a previously seen goal (distance 10 m) and b) indicate during passive transport when reaching it. Squares: distance indicated by the S. Solid lines: least square fits to two models described in chapters 3.2 and 4 (time constants of the proposed integrators: 34.8 ± 3.3 s (a) and 12.4 ± 1.6 s (b)). The distance indicated depends on the mean velocity of the walk (a) or transport (b).

velocity is normal. Such a processing structure would yield the data of b), of passive transport. If, alternatively, the leaky integrator would start from zero, and loaded by velocity integration **until** the reference is reached, again with the gain factor adjusted to the normal pace, the data of a), of active walking, would result.

Fits of these two cases to the data (Fig. 2) yield very different values for the time constants of the leakage. This makes it likely that, rather than merely the parameter values, the processing structures themselves are different in the two cases. A definite decision, also concerning a possible difference between smooth and rhythmic motion, demands further experiments, such as with variation of distance, or walking on a conveyor belt. Further insight might be gained from more detailed analyses of yet existing data of walks with varied head position and varied step width, as well as from homing experiments.

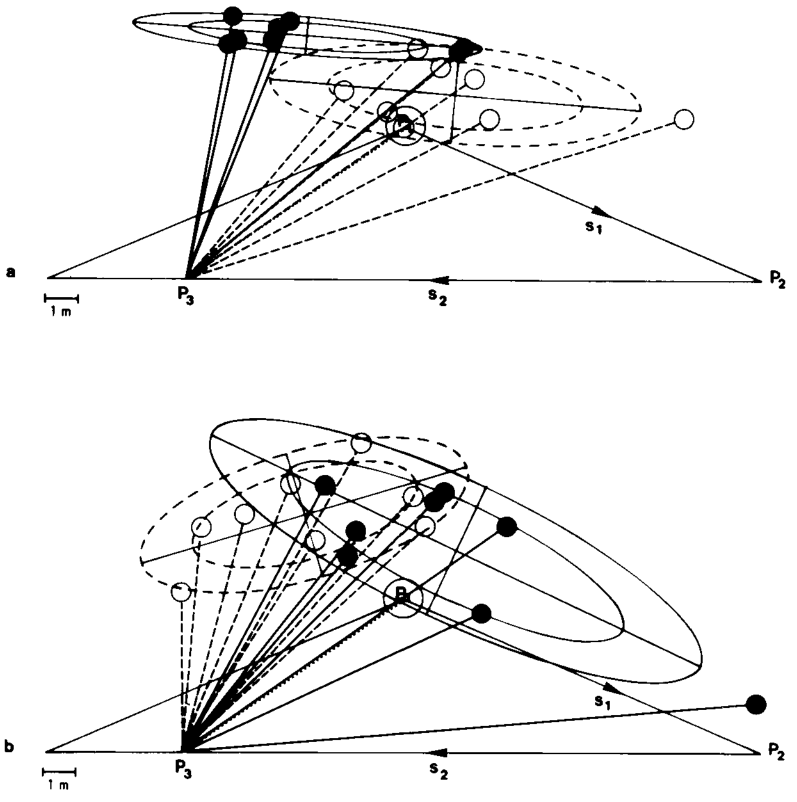

Fig. 3. Homing experiments in blindfolded human subjects (Ss), who were led at normal pace from P_1 to P_2 and then at variable velocity to P_3. Dots (slow velocity from P_2 to P_3) and circles (fast velocity from P_2 to P_3) are stops of return walks from P_3 to imagined P_1 (at normal pace). a: active, b: passive transport from P_2 to P_3. Fast velocities 1.68 m/s (a) and 1.55 m/s (b); slow velocities 0.61 m/s (a) and 0.47 m/s (b). Data from 8 Ss, 1 run per S, 99% and 95% confidence ellipses (BATSCHELET 1982). Differences between slow and fast means are significantly different from zero ($p < 0.001$ in a, $p < 0.05$ in b).

3.3. Combined processing of linear and angular information

It has been shown (BLES et al. 1984) that humans can estimate full rotations, with idiosyncratic errors, by means of inertial as well as substratal idiothesis. In our own experiments (which will not be detailed her) estimated angle turned out to depend on rotatory velocity after active as well as passive rotations. Intent on testing the relations revealed above in combining linear with angular inputs, we therefore kept the latter constant while varying the former in a series of homing experiments.

In a circular hall, which offered a flat smooth surface of 26 m in diameter, the S, again blindfolded and earphoned, was led on a triangular course by gently touching the shoulders from behind (see Fig. 3). In each run the S started from the tip P_1 of the isosceles triangle of Fig. 3 at a self-adopted "normal" velocity, was made to stop at P_2, asked to turn right, and again stopped when facing P_3. The S, instructed to use various velocities as in the runs of chapter 3.2, was then led from P_2 to P_3, and stopped there. (Alternatively, as in chapter 3.2, the S was rhythmically moved on a trolley from P_2 to P_3.) After the stop at P_3 the S was instructed to walk back to the start at normal pace, without any guidance, and stop there.

The results are shown in Fig. 3. When walking slower than normally (Fig. 3a), the Ss, witness the average homing direction, behaved as if they had underestimated the distance P_2-P_3, and overestimated it at a faster pace. At passive transport this relation reversed polarity, just as in the experiments of the preceding chapter. This confirms the theoretically expected role of the linear component in the navigation process.

The mean homing distance on the other hand, as shown by the confidence ellipses, is clearly longer than the correct one. On average the Ss behave as if the guided turn at P_2 is underestimated and/or the free turn at P_3 is overestimated.

A detailed analysis of these relations must await further experimentation. But already the present evidence shows that the fundamentals of idiothetic navigation, including those of inertial idiothesis, are operative in man.

4. Mathematical Appendix

The Laplace transfer function of a leaky integrator can be written as

$$\frac{\tau}{1 + s * \tau} \tag{1}$$

where τ is the time constant and s the complex frequency.
Let us assume constant velocity during motion, that is a velocity step v as integration input. Then the response of the integrator can be expressed as

$$X(s) = \frac{\tau}{1 + s * \tau} * K * \frac{v}{s} \tag{2}$$

where K is the gain factor, or, depending on time t as

$$x(t) = K * \tau * v * (1 - e^{-t/\tau}) \tag{3}$$

which is then the linear displacement x computed by our leaky integration. A correct integration would lead to the correct distance

$$d(t) = v * t \tag{4}$$

The condition of reaching the reference distance x_r is simply

$$x(t) = x_r\,. \tag{5}$$

The true distance covered when equation (5) is fukfilled can be obtained from equation (4) after computation of t from equations (3) and (5) as

$$d(\mathrm{v}) = -\tau * \mathrm{v} * \ln\left(1 - \frac{x_r}{K * \tau * \mathrm{v}}\right) \tag{6}$$

which was used to fit the experimental data of active walking (see Fig. 2a).

When loading the integrator with the reference distance x_r before starting, we can write the response as the following transfer function

$$X(s) = \frac{\tau}{1 + s * \tau} * \left(K * \frac{\mathrm{v}}{s} - x_r\right) \tag{7}$$

or, depending on time t as

$$x(t) = K * \tau * \mathrm{v} * (1 - \mathrm{e}^{-t/\tau}) - x_r * \mathrm{e}^{-t/\tau} \tag{8}$$

similar to equations (2) and (3). Now our condition of reaching the distance x_r is

$$x(t) = 0 \tag{9}$$

and the true distance covered depending on v (from equations (4), (8), (9)) becomes

$$d(\mathrm{v}) = \tau * \mathrm{v} * \ln\left(1 + \frac{x_r}{K * \tau * \mathrm{v}}\right). \tag{10}$$

This equation was used to fit the data of passive movement (Fig. 2b). In this case we simply assumed, that the first integration converting linear acceleration to velocity is correct.

As can be seen from equations (5) and (10), there is no way to separate the gain factor K from the reference value x_r chosen by the S. But we can suppose, that the time constant should be the same when varying the distance to be covered, and test the model with this assumption.

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Author's address: Dr. MARIE-LUISE MITTELSTAEDT, Max-Planck-Institut für Verhaltensphysiologie, D-W-8130 Seewiesen, Post Starnberg, FRG.