Neuroscience Letters 462 (2009) 140–143

Contents lists available at ScienceDirect

Neuroscience Letters

journal homepage: www.elsevier.com/locate/neulet

Load affects human odometry for travelled distance but not straight-line distance

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ARTICLE INFO

Article history:
Received 28 April 2009
Received in revised form 17 June 2009
Accepted 1 July 2009

Keywords:
Distance perception
Idiothetic information
Path integration
Embodied perception
Human odometry

ABSTRACT

In a simple homing task with human participants, we disassociated the outbound distance travelled from the straight-line distance between home and target. Prior to the outbound journey, which involved a detour, participants were given one of two instructions concerning the inbound journey, which did not involve a detour: to walk the distance travelled or to walk to home. The inbound journey under each intention, made with eyes closed at a self-selected pace, was the measure of the perceived distance. We conducted two experiments that differed in whether or not the detour and target were visible during the outbound journey. In both experiments, we manipulated the load carried in the outbound journey (0% or 20% body weight) and the speed (fast or slow) of the outbound journey. The outcome of both experiments was that, indifferent to speed, participants perceived the distance travelled with load to be longer than that travelled without load, but perceived home's straight-line distance from target to be the same for both load conditions. Perceptions of travel distance and straight-line distance seem to be based on different information kinds and to refer to different animal–environment relations. In identifying neural mechanisms supportive of navigation, straight-line distance versus travelled distance may prove to be a productive distinction.

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A basic form of animal navigation is returning home (e.g., nest or hive), the place where most journeys begin. Awareness of home's location throughout the course of an outbound journey is attributed to a process of updating the home vector through the incremental integration of distance and direction, a process referred to as path integration. How path integration in mammals might be understood at a neural level is a prominent topic of contemporary neuroscience [2,7]. Its manifestation by non-mammals, most strikingly insects, suggests that the challenge posed by this higher-order perception-action capability is of wide scope but tractable [2].

With respect to the distance from home, it seems that the measurement is based primarily on information made available by the activity of locomotion itself, so-called idiothetic information [8]. For legged locomotion, non-visual idiothetic information about movement is available with respect to the surface of support and with respect to inertial space (the general background of resistance to acceleration). In Gibson's [3] classification of perceptual systems, the substrate variant of idiothetic information is detected by the haptic perceptual system and the inertial variant is detected by the basic orienting system (statocyst, vestibular organ). The substrate variant seems to be the primary basis for the non-visual ability of humans [12], dogs [13], fiddler crabs [15], and desert ants [14] to approximate, in their return journeys, the distances travelled from home.

In respect to the theory of animal odometry, it is commonly assumed that the outbound trip is measured through a variable associated with stepping. The leading candidate is the individual step size and the leading hypothesis about the odometer's nature is that it is a stride length integrator [15,18]. Typically, experimental tests of odometer hypotheses are conducted for the case in which outbound travel and inbound travel are constrained to linear paths. A more general case is outbound travel that is directionally variable, consisting of multiple segments, and inbound travel that is more direct, more linear (as would be characteristic, for example, of foraging followed by returning home; [18]). In such a case, the outbound distance travelled would be longer than the required inbound distance. By the stride integrator hypothesis, the animal's measure (perception) of distance travelled from home is not the animal's measure (perception) of the distance from home.

That the two distances may be related systematically is suggested by the experiments of Wohlgemuth et al. [19] with desert ants. The ground distance separating home from food was 5.2 m. Ants that travelled the outbound distance from home on a vertically corrugated surface, reproduced the ground distance on the inbound journey made on a flat surface, despite the fact that the path travelled on the corrugated surface was much longer (8.7 m). If, instead, the outbound travel was on the flat surface and inbound travel was

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doi:10.1016/j.neulet.2009.07.001

on the corrugated surface, then the ants covered the inbound distance on the corrugated surface that corresponded to 5.2 m on the ground surface. How might this equivalence of travelled and ground distances be achieved?

Wohlgemuth and colleagues conjectured that, in both outbound and inbound journeys on the corrugated surface, the ants perceived the ground distance by projecting their incremental path segments onto the horizontal and performing path integration within a virtual $x \times y$ planes. An alternative conjecture is that distance travelled from home and Euclidean distance from home are distinctly perceived but inter-convertible. For familiar places occluded at a given station point, children can readily distinguish Euclidean distances from the travel distances, and can produce either on request. Totally blind children, however, have difficulty distinguishing the two distances [1]. The orientation of a totally blind child to familiar surroundings is seemingly in terms of travel distances and not Euclidean distances. This travel-based environmental awareness, based on haptic and inertial variants of idiothetic information, suffices to allow the child to go to where he or she wishes to go. (Eventually, but at a pace slower than sighted children, the totally blind child develops the capability to exploit both distances in orienting to his or her familiar surroundings [1].)

With respect to the experiments of Wohlgemuth and colleagues, it could be argued that their experimental conditions specified the ant's task as "report distance *as the crow flies*". One could imagine different experimental conditions that would have specified the ant's task as "report travelled distance". Here we report two experiments using human participants under conditions designed to compare these two tasks. In each experiment the participant, on any given trial, walked from home to a target situated at a straight-line distance (as the crow flies) between 4 and 23 m from home. The outbound journey was along an indirect path—a detour—from home to target, and the detour, by definition, was longer than the straight-line distance from home to target. The inbound journey was walking from the target in the direction of home with eyes closed. The relation of travelled to straight-line distances is depicted in Fig. 1a.

The specification of "report the straight-line distance" and "report travelled distance" was achieved by instruction given prior to the outbound journey. Simply, participants were told to match their inbound walk (a) to the straight-line distance between home and target or (b) to the detour distance actually travelled between home and target. It was expected, of course, that instruction (b) would result in longer inbound journeys than instruction (a). At issue was whether the two kinds of distance measures would respond differently to manipulations of the outbound locomotion. In both experiments participants made the outbound journey at a faster or slower pace and with or without a load that increased body weight by 20%. In both experiments the inbound journey was made with eyes closed at the participant's own pace and (approximately) own body weight.

In Experiment 1, participants were able to see the detour and target during the outbound journey but not detour, target *and* home. They could therefore visually control their outbound journey to the target but could not visually inspect the spatial separation of target from home. The visual restriction was achieved through special headgear, namely, a baseball cap with a "blinder" attached to the right side. Home was to the right of the outbound journey.

Twenty University of Connecticut students (10 male, 10 female) participated. They received credits as part of a requirement for an Introductory Psychology class. The experiment was conducted outdoors on a grassy area devoid of fixed sound sources. All participants gave their consent in accordance with the University of Connecticut's Internal Review Board's regulations for studies with human participants.

There were 35 trials, with each trial starting at a new home site. Twenty-four randomized experimental trials were used to manipulate the pace (fast, slow), distance (6, 12, 18 m), and load (0%, 20%) of outbound travel and the instructions (walk the straight-line distance, walk the travelled distance) for inbound travel. Each participant completed one trial in every possible crossing of these conditions. The additional 11 trials, not included in the experimental analysis (so called filler trials), were interleaved with the 6, 12 and 18 m trials using randomly assigned distances of 4, 9, 15, 21 and 23 m. These extra trials guarded against the participants coming to recognize there were only three experimental distances. Five practice trials preceded the experiment using distances of 5, 8, 13, 17 and 21 m. All preceding distances are the straight-line distances from home to target. The derivation of the detour distance (effectively, travel distance) from home to target for a given straight-line distance from home to target is shown in Fig. 1a. The experiment lasted roughly 90 min including rest breaks. At the end of the experiment participants were debriefed.

Load was manipulated by means of a backpack fitted with a detachable weight system that allowed the added weight to be adjusted individually to a common position (center of back) and magnitude (20% body weight). Absent the weight system the backpack (plus computer, see below) increased body weight by less than 5%.

A portable electrogoniometer (Biometrics, Gwent, UK) attached to upper and lower segments of the right leg measured knee flexion and extension. It was connected to a computer in the backpack that digitized the analogue output of the electrogoniometer with a sampling frequency of 50 Hz. The movement time series from the right knee was used to calculate the number of steps made in the outbound and inbound journeys. A rotary pedometer, wheeled by

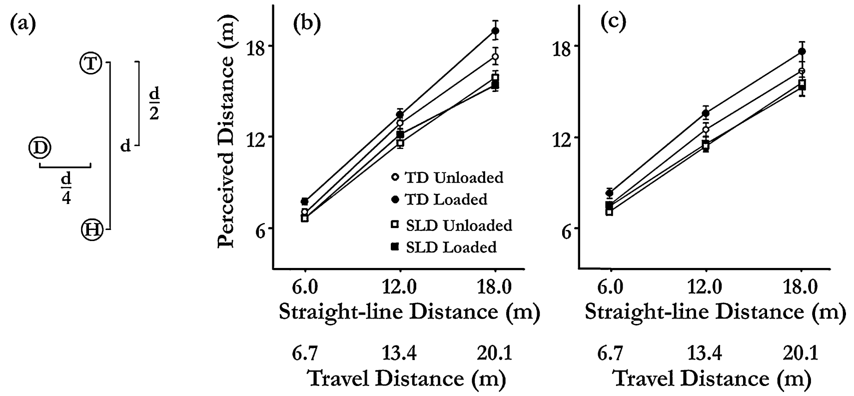

Fig. 1. Panel (a) shows relation between straight-line distance (d) from home (H) to target (T), and travelled distance from H to T around detour (D). Panels (b and c) show perceived straight-line distance (SLD) and perceived travelled distance (TD) as a function of load in Experiment 1 and Experiment 2, respectively.

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