

Take the Short Way Home

Ants meander on the outward leg of a foraging trip, but take a direct route home. To do this, they must navigate by dead reckoning, which requires the ability to measure the distance traveled. How ants actually measure the distance has remained obscure. By the simple experiment of lengthening or shortening the ants' legs, **Wittlinger *et al.*** (p. 1965) now show that the ants measure distance by counting their steps.



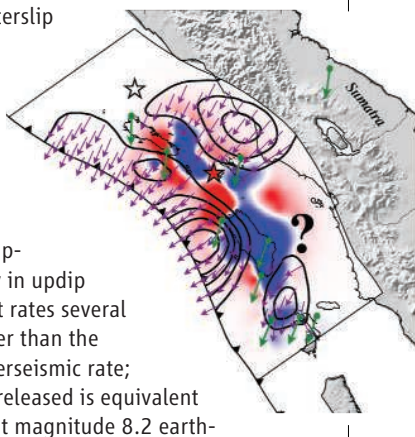
Precooling Climate

A sudden and large cooling episode occurred in the North Atlantic region approximately 8200 years ago (the "8.2 ky event") and punctuated the otherwise stable Holocene climate. **Ellison *et al.*** (p. 1929; see the news story by **Kerr**) present records of planktonic foraminifera from the subpolar North Atlantic Ocean which show that water in this region became colder and fresher more than 200 years before the 8.2 ky event. The 8.2 ky event was likely caused by meltwater discharge from the Laurentide Ice Sheet that began centuries before the major cooling episode and may have been related to changes in the strength of deep-ocean circulation.

Moving Slowly but Surely

Motion along faults is most commonly associated with earthquakes, but aseismic slip occurs as well. **Hsu *et al.*** (p. 1921) analyzed data from continuously recording global positioning satellite stations above and near the Sunda megathrust rupture region after the 28 March 2005 Nias-Simeulue earthquake off Sumatra.

Aseismic afterslip is still occurring on the subduction megathrust near the location of the 2005 rupture, mostly in updip direction, at rates several times greater than the average interseismic rate; the energy released is equivalent to a moment magnitude 8.2 earth-



quake. Bands of aftershocks are also seen, and their number scales with postseismic displacements, which indicates that most of the aftershocks are caused by the afterslip and not by the main shock.

Toward Plastics from Sugar

Because commercial chemicals often have petroleum as their ultimate source, there is great interest in the use of renewable sources such as biomass as alternative feedstocks. **Román-Leshkov *et al.*** (p. 1933) present an efficient route to 5-hydroxymethylfurfural, a furan derivative with strong potential for use in polyester synthesis, via the acid-catalyzed dehydration of fructose. They used a biphasic system in which the reaction occurred in an aqueous solution, with polar aprotic additives such as dimethylsulfoxide enhancing selectivity. The product was continuously extracted into a low-boiling organic phase. The system achieves >80% selectivity for the desired product at 90% fructose conversion.

A Companion for Ferrate

The rare example of iron in the +6 oxidation state is the ferrate ion, FeO_4^{2-} , and the extremely powerful oxidizing properties of this species has spurred a long search for additional hexavalent iron compounds. **Berry *et al.*** (p. 1937, published online 1 June) report that successive electrochemical oxidation and photolysis of an Fe(IV) azide complex yields an octahedrally coordinated

nitrido Fe(VI) compound that is stable at 77 kelvin. Spectroscopic characterization and supporting density functional theory are consistent with a diamagnetic ground state and an iron-nitrogen triple bond. Upon warming, the compound behaves as a three-electron oxidant.

A Small Director

Enzymes often achieve selectivity by aligning substrates in specific orientations through hydrogen bonding. **Das *et al.*** (p. 1941; see the Perspective by **Mas-Ballesté and Que**) show that even a small molecular catalyst can induce such alignment effects. They prepare a dimanganese complex with a carefully placed carboxylic acid (COOH) group in the ligand. Hydrogen bonding between this group and a substrate's carboxylic substituent leads to oxidation of a specific C-H bond on the other side of the substrate; modeling studies suggest that this oxidized site is oriented proximal to the manganese centers. Control experiments confirm that selectivity is lost when the COOH group is removed from the catalyst, or when acetic acid is added to disrupt the docking interaction.

Plant Productivity Benefits of High Carbon Dioxide Busted

Although rising CO_2 levels may reduce global crop yields through the effects of higher temperatures and decreased soil moisture, arguments have been made that direct fertilization effects will more than offset these losses. **Long *et al.*** (p. 1918; see the Perspective by **Schimel**) present a critical analysis of data on which the Intergovernmental Panel for Climate Change base their projections that elevated

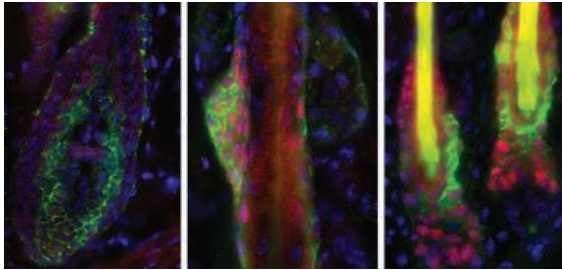
CO₂ will have a fertilizing effect. The original estimates came from experiments conducted in the 1980s in greenhouses and sheltered enclosures. More sobering figures are derived from open-field studies in which increased CO₂ levels enhanced crop yields ~50% less than in enclosure studies.

The Rise and Rise of Resistant Tuberculosis

Tuberculosis is spreading in a piggyback fashion along with infection by human immunodeficiency virus, with nearly 9 million cases estimated in 2003. Patients often do not complete the long treatment regimes, and thus help *Mycobacterium tuberculosis* develop antibiotic resistance. **Gagneux et al.** (p. 1944) show that rifampin-resistance mutations, such as *rpoB* S531L, have low fitness cost and are selected in patients during treatment and that these strains are the most prevalent in clinical isolates and more likely to spread in human populations.

Do As I Say, Not As I Do

The cycle of hair growth and replenishment depends on a steady reserve of stem cells in the hair follicle. As new cells are needed, progenitor cells give rise to differentiated cells. **Rhee et al.**



(p. 1946) now survey the transcriptional profile of progenitor cells to identify a gene that helps these cells generate differentiated daughters when needed but refrain from differentiating themselves. The gene encodes a transcription factor, *Lhx2*, already known for its effects in brain development and hematopoiesis.

Advancing Spring Migrations

Migratory birds, especially short-distance migrants, have advanced their spring arrival at their breeding grounds in response to climate change. **Jonzén et al.** (p. 1959) show that the timing of migration in long-distance migrants has advanced at least to the same extent as in short-distance migrants. Many long-distance migrant species wintering south of the Sahara desert are arriving in southern Europe progressively earlier. In Northern Europe, earlier arrival is not a simple effect of increased migration speed through Europe in response to increased temperature en route. Although improved foraging conditions across the African continent cannot be ruled out as an explanation, a more parsimonious hypothesis is an evolutionary change in the timing of migration in Africa.

Perfecting Proofreading

Most eukaryotic RNAs contain noncoding sequences (introns) that must be removed by messenger RNA (mRNA) splicing. The content of the mRNA can also be modified by alternative splicing where some coding sequences (exons) are removed. The signals (splice sites) in the RNA that mark the boundaries between introns and exons are short and degenerate, which raises the possibility that they could be misidentified by the splicing machinery and gross errors introduced into mRNA. **Mendes Soares et al.** (p. 1961; see the Perspective by **Kress and Guthrie**) now show that the protein DEK, previously implicated in autoimmunity and cancer, functions as part of a proofreading device for recognition of consensus 3'-AG splice sites by U2 auxiliary factor (U2AF). Phosphorylation of DEK promotes its binding to the U2AF35 subunit of U2AF, and this interaction minimizes the incorrect recognition of nonconsensus 3'-CG splice sites.

We Feel Your Pain

There is a widespread belief that empathy is a special human feature, or perhaps an exclusive ability of primates possessing theory of mind. **Langford et al.** (p. 1967; see the news story by **Miller**) performed a series of experiments with mice and observed that the mere observation of pain behavior in another mouse produces alterations in the pain behavior of the observer. Strikingly, these effects do not require genetic relationships between the observer and observed, but simply familiarity. The findings cannot be easily explained by stress, imitation, or conditioning, and may represent a nonprimate form of empathy.

CREDIT: RHEE ET AL.

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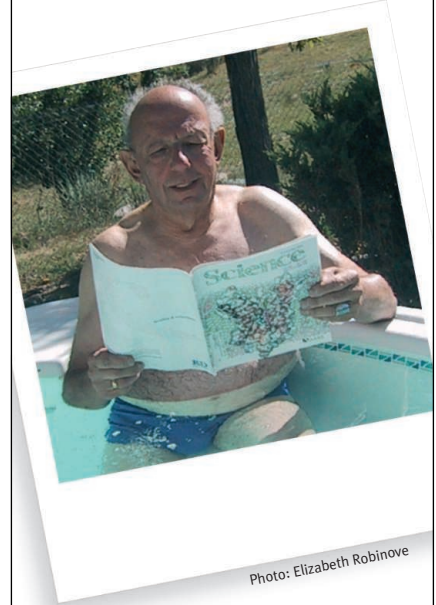


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Supporting Online Material

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Materials and Methods

Figs. S1 to S9
References and Notes

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The Ant Odometer: Stepping on Stilts and Stumps

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Desert ants, *Cataglyphis*, navigate in their vast desert habitat by path integration. They continuously integrate directions steered (as determined by their celestial compass) and distances traveled, gauged by as-yet-unknown mechanisms. Here we test the hypothesis that navigating ants measure distances traveled by using some kind of step integrator, or “step counter.” We manipulated the lengths of the legs and, hence, the stride lengths, in freely walking ants. Animals with elongated (“stilts”) or shortened legs (“stumps”) take larger or shorter strides, respectively, and concomitantly misgauge travel distance. Travel distance is overestimated by experimental animals walking on stilts and underestimated by animals walking on stumps.

Foraging Saharan desert ants, *Cataglyphis fortis*, use a mode of dead reckoning known as path integration (1, 2) to monitor their current position relative to the nest and to find their way home (3). This enables them to return on a direct route, rather than retracing the tortuous outbound journey performed when searching for food items in their flat desert habitat, which is often completely devoid of landmarks. The path integrator requires two kinds of input information: about directions steered, as obtained via the ant’s celestial compass (4), and about distance traveled, as gauged by the ant’s odometer.

The cues by which ants measure travel distance during locomotion have not yet been discovered. However, there are several promising hypotheses. The “energy hypothesis” posits that the (surplus) energy required for locomotion (as opposed to rest) is used to calculate travel distance. This hypothesis is of long standing in arthropod research (5), but is not applicable to the problem of the ant odometer, because ants assess their walking distances with great accuracy, irrespective of the load they carry (6). The “optic flow hypothesis” has been proven in honeybees, which integrate visual flow-field cues during their foraging flights to gauge flight distance (7, 8). In *Cataglyphis* ants, this mechanism plays a minor role, if it has any effect (9) (for further discussion of the optic flow hypothesis, see SOM). Even in complete darkness, on featureless platforms, or with the ventral halves of their eyes covered, the animals are still able to assess traveling distance correctly during

their homing runs (9, 10). Also, lateral optic flow does not have any influence at all on distance estimation (11). Considering the relatively constant locomotor speed of desert ants, a time-lapse integrator might function to measure walking distance—although this possibility has been refuted in slightly different experimental contexts (12). Thus, ants appear to rely primarily on idiothetic cues, most probably derived from the movements of their legs (13). Although this step integrator or “pedometer” hypothesis was initially proposed as early as 1904 (14), it has remained untested. Here, we examine whether or not ants with manipulated leg lengths, walking on stilts or on stumps, exhibit changes in their stride lengths and, consequently, misgauge their travel distance during homebound runs.

The ants were trained to walk from their nest entrance to a feeder, over a distance of 10 m and in a linear alloy channel (Fig. 1, top). After at least 1 day of training, the animals were caught at the feeding site and transferred to a test channel, aligned parallel to the training channel (Fig. 1, bottom). Once transferred into this test channel, the ants performed their homebound

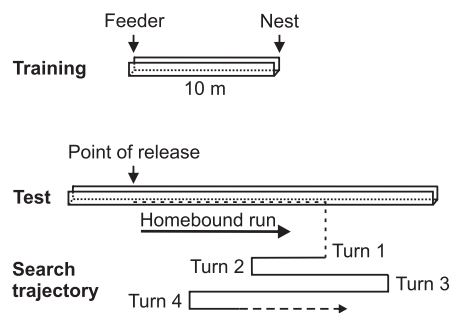


Fig. 1. Schematic diagram of channel layout, as well as training and testing procedures applied in *Cataglyphis* foragers (not drawn to scale).

runs, and we recorded the point at which the ants switched from their straight and steady return path to their characteristic nest-searching behavior. This point is marked by a 180° U-turn (15), followed by a run pacing back and forth around the anticipated location of the nest entrance. Details of the experimental procedure are given in (16).

Ants that had reached the feeder on a foraging trip through the training channel were caught and subjected to experimental manipulation. To increase stride length on the animals’ homebound runs, their legs were splinted and extended with pig bristles glued to the tibia and tarsus, as illustrated in Fig. 2 (stilts). To decrease stride length, the legs were shortened by severing the tarsomeres in the middle of the tibia segment (Fig. 2, stumps). Operated animals were supplied with a food item and transferred to the test channel, with the food item in their mandibles (“test 1”). These ants started determined homeward runs, and when they had covered the assumed distance to the nest, they switched to the nest-searching behavior outlined above. The ants walking back homeward on stilts clearly overshot [15.30 m, interquartile range (IQR) = 3.24 m, $n = 25$], whereas ants with shortened legs undershot (5.75 m, IQR = 1.81 m, $n = 25$) with regard to their normal homing distance (10.20 m, IQR = 2.40 m, $n = 25$) (Fig. 3A). There are statistically significant

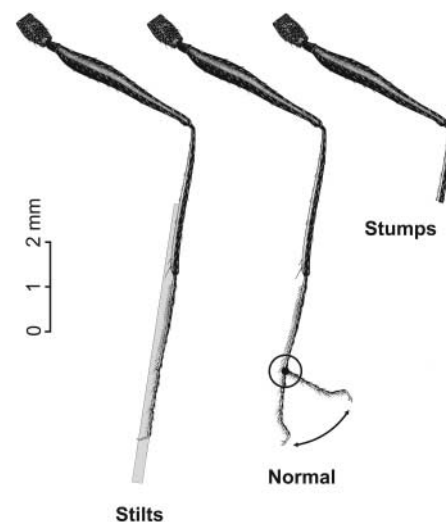


Fig. 2. Manipulation of ant legs as performed in the present study. In stilts, attached pig bristles elongated the legs; second, normal unmodified legs, with approximate range of tarsus movement indicated; third, shortened legs (stumps). The right hind leg is shown from anterior [see figure 1 in (18)].

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differences ($P \leq 0.001$, Kruskal-Wallis test) among these groups.

The modified and tested ants were put back into their nest and were tested again when they turned up at the feeder during one of the following days (“test 2”). Having already performed their outbound runs to the feeder on stilts or stumps, these animals exhibited homing runs almost identical to those of normal, unmodified ants (Fig. 3B). Ants walking on stilts (stilts, $n = 25$) searched for the nest at 10.55 m (IQR = 1.45 m) distance from the release point and ants with shortened legs at 10.25 m (IQR = 1.76 m) (stumps, $n = 25$). No significant differences were observed between these groups or with regard to unmodified animals (above, 10.20 m).

These results support the hypothesis that desert ants use a pedometer for distance measurement, or a step integrator [loosely speaking, a step counter, although the ants most probably do not literally count (17)]. According to the pedometer hypothesis, ants that have traveled to the feeder on normal legs and have had their leg length modified at the feeder should cover a different distance on their homebound journey. This is because the same number of strides made during the outbound travel, as registered by the step integrator, should presumably carry them over longer (stilts) or shorter (stumps) distances, respectively. And later, on reemerging from the nest with their legs still modified, the number of strides will be the same again for outbound and inbound travel (although different from the situation with normal legs in both cases). No

such straightforward interpretation is possible for any of the competing hypotheses.

This interpretation rests on the assumption, however, that stride length is indeed altered by the manipulation of leg length, roughly in proportion to the imposed length changes. Thus, a quantitative assessment of the (manipulated) ants’ stride lengths and their relation to walking distances is also necessary. It was impossible to count the ants’ strides during experiments (for instance, by filming the complete outbound and homebound journeys on high-speed video). Instead, stride lengths were determined in a different set of animals, both normal and manipulated, in a small pen erected on the desert floor. As in most animals, stride length in normal *Cataglyphis* depends on at least two parameters. The first is leg length and, thus, body size, as body morphology is isomorphic in *Cataglyphis fortis* workers (18). That is, larger ants take correspondingly longer strides. The second is walking speed. The faster an ant runs, the larger are the strides it takes (19–21). Normalization of homebound travel distances with regard to both body size and walking speed is thus required for a quantitative interpretation of the above experiments. High-speed video recordings of running ants were analyzed to determine the actual changes in stride lengths caused by the stilts and stumps manipulations described above. Walking speeds were determined in the above experimental animals by the time required for uninterrupted straight segments of homebound travel (and confirmed on the high-speed movies in a different set of animals).

To derive a quantitative prediction of how far the manipulated ants would have to run on their homebound journey, based on the pedometer hypothesis, the experimental data were first normalized with regard to body size. That is, relative stride lengths with regard to body dimensions were calculated to eliminate effects of size variation. Second, the actual stride lengths were determined in normal and manipulated ants. Ants walking on stilts took significantly longer strides ($P < 0.01$, t test; 14.8 mm, SD = ± 2.5 mm, or +13.9%) than did normal animals (13.0 mm, SD = ± 1.98 mm), and ants on stumps made significantly shorter strides ($P < 0.001$; 8.6 mm, SD = ± 1.73 mm, or –33.2%). These values were then used to derive a prediction for the respective undershoot or overshoot of manipulated ants, based on the assumption that distance is measured by a step integrator, that is, that the ants took the same number of strides during their outbound journey to the feeder and when returning to the nest on manipulated legs (hatched boxes in Fig. 3A). The predicted values show that there is general agreement between the predicted and observed homebound travel distances in manipulated ants, further corroborating the step integrator hypothesis.

However, there are some differences (significant in stilts, $P = 0.015$; not significant in stumps, $P = 0.125$; Mann-Whitney rank sum test) between the observed and the predicted homebound travel distances. Impairment of the ants by the preparation procedures cannot account for these effects. Any serious impairment would tend to shorten the ants’ homebound runs. The animals walking on stilts clearly traveled for much longer distances than the normal controls, however, and they did so with apparently normal vigor. Indeed, experimentally modified ants were observed to stilt or stump through their habitat on successful foraging trips several times a day and for many days thereafter (see movie S1 in SOM).

The differences between observed and predicted homing distances may be attributable, though, to altered walking speeds in the manipulated ants. In fact, normal ants traveled at an average 0.31 m/s, and ants walking on stumps averaged 0.14 m/s, a value in good agreement with their shortened legs and stride lengths (see similarity of predicted and experimentally determined homing distances in Fig. 3A). Ants on stilts however, rather than walking at increased speeds, were also slightly slower than normal animals, walking at an average 0.29 m/s. This was presumably due to the added load of glue and pig bristles on their legs. As noted above, changed walking speeds are associated with correspondingly altered stride lengths, which would appear to explain the unexpectedly short prediction value in Fig. 3A (top hatched box). We thus corrected this prediction with the established relations between walking speed and stride length (19, 20). We assumed as a first approximation (and conservatively, when con-

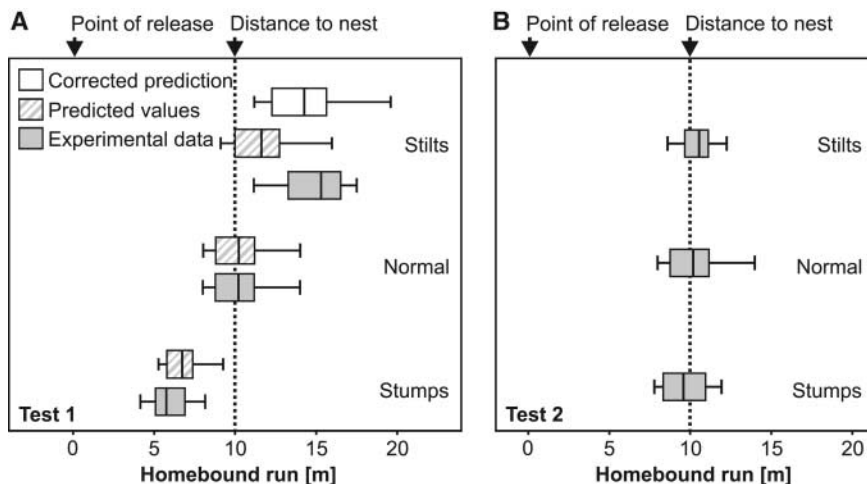


Fig. 3. Homing distances of experimental ants, tested immediately after the lengths of their legs had been modified at the feeding site. (A) Leg lengths were normal during the outbound journey but manipulated during the homebound run, resulting in different homing distances. (B) Ants tested after reemerging from the nest after previous manipulation. In this situation, leg lengths were equal, although manipulated, during outbound and homebound runs. Box plots show median values of the homing distances recorded in $n = 25$ ants per experiment (as well as IQRs, box margins, and 5th and 95th percentiles, whiskers). Median values of the initial six turning points of an ant’s nest-search behavior were considered as the centers of search, indicating homing distance. The hatched box plots in (A) illustrate the centers of search as predicted from the high-speed video analyses of stride lengths in normal and manipulated animals. The open box represents the prediction corrected for slow walking speed. Details in text.

sidering the actually imposed changes in leg length) that ants might run by as much faster on stilts as they ran slower on stumps (0.48 m/s, a value regularly observed in highly motivated normal ants and almost reached by the fastest ants on stilts). This procedure indeed yields a value that is not significantly different from the observed homing distances in ants on stilts (open box in Fig. 3, A; 14.25 m, IQR = 3.35 m), thus confirming the consistency of our data with the step integrator hypothesis.

The slower speeds of the ants walking on stilts further rule out the only alternative explanation of our homing distance data (Fig. 3A, solid boxes). In principle, a step integrator and a time-lapse integrator would both yield the same homing distances, even in ants with manipulated leg and stride lengths, if only the ants kept their stride frequencies constant [or in normal ants, walking speed—which in fact they almost do under normal conditions (19, 20)]. Constant stride frequency would result in a change in walking speed in proportion to altered stride length and a resulting difference in homing distance during a set (outbound) travel time. This assumption is evidently

not correct, though, given the walking speeds of the experimental animals.

Future studies will have to address the mechanism of the proposed step integrator, for example, whether it actually registers steps by means of proprioceptors, or whether it integrates activity of a walking pattern generator, and to what extent sensory feedback regarding stride length and walking performance is considered.

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Social Modulation of Pain as Evidence for Empathy in Mice

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Empathy is thought to be unique to higher primates, possibly to humans alone. We report the modulation of pain sensitivity in mice produced solely by exposure to their cagemates, but not to strangers, in pain. Mice tested in dyads and given an identical noxious stimulus displayed increased pain behaviors with statistically greater co-occurrence, effects dependent on visual observation. When familiar mice were given noxious stimuli of different intensities, their pain behavior was influenced by their neighbor's status bidirectionally. Finally, observation of a cagemate in pain altered pain sensitivity of an entirely different modality, suggesting that nociceptive mechanisms in general are sensitized.

Although most consider true empathy to be an exclusive ability of higher primates, empathy may be a phylogenetically continuous phenomenon with subclasses such as “emotional contagion” well within the reach of all mammals (1). However, there is little evidence for adult-adult empathy outside of primates. In rats (2) and pigeons (3), the pain-related distress of a conspecific can serve as a conditioning stimulus. Rats produced operant responses to terminate the distress of a conspecific (4), but this might be better explained by arousal than altruism (5). One theory of human empathy postulates “physiological linkage” between empathizing individuals (6).

In one study, empathic accuracy for negative emotion was highest in those dyads featuring high levels of time synchrony of autonomic measures (7). We hypothesized that if empathy does indeed exist in mice, the real-time observation of pain in one mouse might affect the responses of its conspecifics to painful stimuli.

We first used a sensitive nociceptive assay, the reflexive 0.9% acetic acid abdominal constriction (“writhing”) test. We placed mice singly within transparent Plexiglas cylinders to observe writhing behavior. For comparison, we placed two same-sex mice within each cylinder and injected either one or both mice. In the “both writhing” (BW) condition, each mouse observed the other in pain; in the “one writhing” (OW) condition, the injected mouse observed an uninjected counterpart. BW mice displayed significantly more pain behavior than isolated mice, but only when their counterparts

were cagemates (Fig. 1A). The hyperalgesia was marginally enhanced in same-sex siblings living together, but a separate experiment confirmed that close genetic relatedness was not required (fig. S1). Writhing behavior in BW dyads co-occurred in time at levels significantly exceeding those expected by chance (Fig. 1B) and significantly more so in cagemate pairs than stranger pairs. The hyperalgesia and behavior co-occurrence developed over 14 to 21 days of being housed together (Fig. 1, C and D). In general, observed behaviors other than writhing were similar across all conditions (figs. S2 and S3), although evidence suggested higher levels of anxiety or stress produced by the noxious stimulus in stranger pairs relative to cagemates (fig. S4). Because the observed effects on pain behavior were higher in cagemates, stress is not a likely mediator.

When strangers were tested in dyads, a significant decrease in writhing behavior was observed in the OW condition compared to that observed in isolation (Fig. 1A). The inhibition was entirely specific to males (fig. S5) and is likely due to distraction or social stress-induced analgesia.

These findings imply the communication of pain from one mouse to another. To determine the transmitting sensory modality, we blocked sensory inputs individually, by placing physical barriers to sight and/or touch or by rendering mice anosmic or deaf (8). The only manipulation that significantly abolished the BW/OW hyperalgesia was a visual blockade using an opaque Plexiglas barrier (Fig. 2A). [Despite their albinism, the CD-1 mice used in these studies display no deficits in visually dependent behavioral tasks (9).] The opaque barrier also

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The Ant Odometer: Stepping on Stilts and Stumps

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Movie S1

Supporting Online Materials

Methods details

Both training and test channels were 7 cm wide, and channel walls were 7 cm high, such that the ants experienced a restricted, strip-like view of the sky of approximately 53° to read the skylight pattern and compass information. Channel walls were painted with matt grey varnish to provide a featureless and even environment, and the channel floor was coated with fine grey sand to provide traction for walking.

We had carefully chosen the fine grey sand that covered the floor of the test and training channels explicitly to avoid optic flow cues. Sandblasting sand with grain sizes ranging from 0.2 to 0.4mm was used. Assuming an optical divergence angle of 5° in the ventral hemisphere of the *Cataglyphis* eye (*S1*), and an eye-substrate distance of 5 mm for the smallest normal ants, the largest sand grains are still well below the ant's optical resolution (about 0.9 mm; note that according to Shannon's Information Theory criterion one needs one receptor in between two resolvable points; see, e.g. review in (*S2*). This is a worst-case scenario since most of the ant's ventral visual field is much farther away from the floor than the eye-substrate distance [compare (*S3*)]. Finally, the contrast provided by the below-resolution-threshold ground floor (i.e., the light-reflection difference between the centres of the grain particles and the boundaries between adjacent particles) was so low that even an above-resolution-threshold graininess would certainly not have provided the ants with sufficient optical ground heterogeneity.

For each experimental situation—stilts, stumps, and normal controls—the respective ants were marked with a particular colour, such that every animal participated in only one experiment, and each individual was successively run through control, test 1, and test 2 (below).

To extend the legs, pig bristles were glued to the legs with cyanacrylate adhesive (superglue) and extended beyond the tarsal claws for about another 1 mm. Already the leg splint itself would have increased stride length by causing the animals to “tiptoe” on their tarsi. This is, since the tarsal segments, except the most proximal one (the basitarsus), are quite flexible and normally touch the substrate during walking (compare “Normal” in Fig. 2). Legs were shortened by simply clipping the tibiae at the desired place with a pair of minute scissors.

Each manipulated ant was put into a small container, together with an assortment of food items. Only when the ant accepted one of the food items (usually a biscuit crumb)—indicative of a predominant motivation to carry the booty home (*S4*)—was it placed into the test channel. Having covered their assumed homing distance, the ants switched to a search pacing up and down the test channel, with the search centred on the assumed nest position. We took the initial six turns of each search to calculate homing distance, as the median value. Each ant was tested twice, first, right after the experimental manipulation (test 1), and second, after having re-emerged from the nest and visited the feeder again (test 2).

High-speed video recordings were made with a Redlake Motionscope, with a frame rate of 250 per second. Stride lengths were evaluated in frame-by-frame analysis on a computer monitor, aided by Redlake software. Stride lengths were determined for left and right middle legs as the distances between subsequent foot falls (*S5*).

SOM Text

Discussion of optic flow cues

As mentioned in the main text, it has been established previously that optic flow also plays a role in ant odometry, at least flow in the ventral visual field. However, this contribution is small indeed. The data provided by Ronacher and Wehner (S6) allow a quantitative judgment of this contribution of optic flow. The training distance in these experiments was 10 m. In one particular experimental situation, 26 m homing distance would have been expected if optic flow were the only mechanism used in ant odometry. Actual homing distance was, however, only 11.24 m. The overshoot was thus 1.24 m, compared to 16 m expectation. This amounts to a little less than 8% contribution of the optic flow mechanism to the *Cataglyphis* odometer. And this contribution was observed with strong visual contrast in the ventral visual field, while under low contrast conditions (as in our experiments) the use of all visual cues is inevitably reduced.

References

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Movie S1. An experimental ant walking on stilts filmed in its typical desert habitat to demonstrate how the animals are able to walk accurately and trouble-free with these modified legs (walking speed ca. 0.25 m/s). The reproduction is in slow motion, $\times 0.5$.