Reversing ants navigate successfully despite going backwards

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Scampering across the salt pans of Tunisia on their spindly legs, desert ants (*Cataglyphis fortis*) have a single-minded mission: locate food and get it back to the nest. Normally, individual raiders bear a tasty morsel in their mandibles and navigate home along the most direct return route, regardless of how tortuous the outbound journey was.

However, their determination is often tested to the extreme when the robust animals stumble upon a particularly large piece of food - such as a dead spider or locust. Undaunted, the scavenger simply drags the feast backwards: "They are really awesome", chuckles Matthias Wittlinger from the University of Ulm, Germany. However, how do the insects navigate while reversing? "All the cues are from the other direction", says Wittlinger.

Puzzled, Wittlinger and his colleagues Verena Wahl and Sarah Pfeffer travelled to their field site in the Tunisian desert to try to find out how the ants locate home while reversing with a heavy load. They publish their discovery that reversing ants are as good at navigating as ants that are walking forward and that the animals must somehow measure the length of each stride that they take, in order to keep track of their location, in *Journal of Experimental Biology*.

Having tempted ants from their nest with a nearby pile of alluring biscuit crumbs, the scientists first set the enthusiastic foragers a challenge to find out if they could still navigate in reverse. Abducting individuals as they arrived at the feeder, the trio transported the ants to a long metal

channel lying parallel to the direction that they would return home and presented them with a colossal biscuit crumb, weighing 10 times more than the ant itself: "They say, "Wow, there is a large food item, let's get home'", chuckles Wittlinger. While filming the ants as they heaved the large lunch, the team quickly realised that they were onto something unexpected. Instead of weaving rhythmically from side to side as they would if they were using their normal tripod gait - always keeping three legs in contact with the ground as the other three swing forward - the ants' overall movement appeared less coordinated; they were not simply reversing their normal forward walking pattern. And when the ant reached the point at which they would expect to locate home in the metal channel, they performed a U-turn, indicating that they knew how far they had travelled, despite moving backwards. Their odometer was functioning regardless of their erratic walking style. Amazed, Wittlinger and Pfeffer began dissecting the fine details of the ants' reversing technique.

Pfeffer filmed the ants with a high-speed camera at 500 frames s?1, and saw that the reversing ants walked at about the same step rate as when they moved forward, about 10 strides s?1. However, she says, "Each leg was acting on its own", adding that they had completely done away with the conventional three-legged walk. She also noticed that they had increased their contact with the ground, "They do it by faster swings and they often use leg combinations where more than three legs have ground contact to increase their static stability' she says. Wittlinger adds, 'we have been trying for years to make them walk in a non-tripod way", in the hope of learning how they measure distances; now he had the perfect opportunity.

"There are a couple of hypotheses of how a stride integrator [odometer] would work", he says. "One is that they would use an efferent copy of the motor signals [and sum the signals to calculate a distance], and the other one would be that they actually use each single stride and measure

each stride amplitude, or the length of the stride or the swing". Because the ants were able to determine precisely how far they had travelled, even though each leg was moving individually, Wittlinger says, "The data suggest it is the second hypothesis".

But Wittlinger and Pfeffer were still none the wiser about how the reversing ants managed to navigate when all of the visual and odour cues that they use to locate home were in the wrong position. "We painted a white grid onto the desert floor and then we released the ant with a large food crumb [and] it walked towards the fictive nest site", says Wittlinger, who manually tracked the ant's progress with Pfeffer. However, the duo was surprised that the reversing ant periodically put down its cargo and began searching in a loop, before returning to the morsel and resuming its homeward journey. "We think that this behaviour probably helps the ant to orientate. The early search loops are normally very short and often directed to the fictive nest site, and probably they scan the panorama searching for some cue", says Pfeffer.

So plucky Cataglyphis desert ants are able to navigate successfully while reversing, and now Wittlinger and Pfeffer are keen to learn more about how the animals use information gleaned during reconnaissance when they discard their precious cargo while reversing home.

More information: Pfeffer, S.E., Wahl, V. and Wittlinger, M. (2016). How to find home backwards? Locomotion and inter-leg coordination during rearward walking of Cataglyphis fortis desert ants. J. Exp. Biol. 216, 2110-2118. DOI: 10.1242/jeb.137778

Pfeffer, S.E. and Wittlinger, M. (2016). How to find home backwards? Navigation during rearward homing of Cataglyphis fortis desert ants. *J. Exp. Biol*. 216, 2119-2126, DOI: 10.1242/jeb.137786

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