prove to have cognate membrane chaperones that facilitate their folding/assembly and prevent their aggregation in the ER. This view is supported by evidence suggesting that calnexin may act as a 'membrane chaperone' during the folding and assembly of the polytopic proteolipid protein, in this case specifically recognising misfolded or misassembled transmembrane domains [13].

In other cases, specialised ER components may actively promote the export of polytopic proteins from the ER as originally suggested for Shr3p [10,11]. For example, the ER membrane component DRiP78 regulates the export of the dopamine D1 receptor [14], while a 39 kDa receptor-associated protein facilitates the passage of various members of the LDL-receptor family through the secretory pathway [15]. Doubtless, many other 'membrane chaperones' await discovery, both in the ER and in other membrane systems.

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Ant Navigation: Reading Geometrical Signposts

Ants often travel along complex pheromone trail systems between their nest and foraging areas. A new and surprising discovery is that Pharaoh's ants can work out from the geometry of individual branch points on the trail whether they are heading towards or away from the nest.

Thomas S. Collett and David Waxman

Imagine walking through a complicated cave system in the dark to reach an underground lake, guided only by a rope left by previous explorers. You trip and let go of the rope. When you manage to find the rope again, how can you be sure that you are facing in the same direction as before? Ants of many species can encounter similar problems when following pheromone trails between their nest and foraging area, should they mistakenly wander away from the trail, or should the trail have small gaps. Lengths of trail, like rope, carry no obvious directional labels [1]. One solution to the ant's problem, though correct, no longer seems exciting: ants can know their direction of travel along a trail from external compass cues, such as the sun or the Earth's magnetic field. Jackson *et al.* [2] have recently given this problem new interest. They have discovered that Pharaoh's ants can use a subtle and unexpected cue to monitor their direction of travel.

Suppose that the guide rope consists of short lengths knotted together with the ends tied so that both ends of each knot point in the same direction along the rope. If all the lengths are tied the same way, then each knot gives a directional signal, which you could use to check your direction along the rope. Jackson *et al*. [2] point out that a geometrical cue of this sort is inherent in the tree-like geometry of an ant's trail. A path rooted in the nest divides in a sequence of Y junctions. An ant has no need of a bird's eye view of the resulting dendritic structure to deduce its heading within the tree, as the polarity of the trail is to be seen at almost every fork (Figure 1). The angle between each arm and the trunk (~150°) is usually more than twice as large as the angle between the arms (just less than 60°). If an ant can measure, or merely distinguish, these angles, the fork can serve as a signpost pointing homewards or foodwards.

In Pharaoh's ants, a trail network typically extends for 10 m from the nest. The trail is shorter if food is very abundant around the nest and longer when food is scarce there. The record trail length for this tiny, 2 mm ant is an impressive 50 metres.

An outgoing forager, reaching a fork from the trunk of the Y, has a choice between two arms, both of

Figure 1. A pheromone trail with forks made by Pharaoh's ants.

The trail was imaged by having ants walk over smoked glass. The scale can be gauged from the 2 mm size of an ant. We thank Duncan Jackson for letting us use his photograph. Copyright Duncan Jackson.

which point in directions that are no more than 30° away from the ant's current direction of travel. Similarly, an ant on the way home need only turn through the same small angle to continue down the trunk. It would know, if it had mistakenly selected the other arm because it would have turned through 120°. Thus, one benefit of constructing forks with this geometry is that ants moving in the correct direction up or down the tree need only turn through small angles at each fork, and ants returning home need never select the wrong branch.

A series of neat observations led Jackson *et al*. [2] to conclude that Pharaoh's ants can recognise which way the forks are pointing, and that foodbound and homebound ants exploit the information in different ways, with foodbound ants using it to check that they are moving away from the nest and homebound ants doing the reverse. In an initial experiment, returning or outgoing foragers were placed part way along an empty, but natural, trail. Some ants by chance set off in the right direction and most of these ants continued in that direction either to the nest or to food. In contrast about 70% of the ants that happened to start off the wrong way did reverse direction. As in this situation there may be additional compass cues, the important point to note is that most corrections were made at or within 1 cm of a fork.

The correction was not always made at the first fork the ant encountered, which is consistent with later experiments using single forks, in which ants corrected their direction on about 45% of trials. From the numbers given by Jackson *et al*. [2], we can get an idea of the efficiency with which ants use trail forks. Suppose that half of the ants joining a trail move initially in the right direction, then, after encountering a single fork, approximately 70% will be moving in the correct direction.

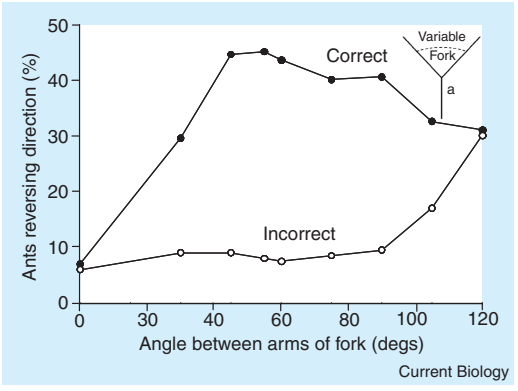

Figure 2. Choices made by individual ants when travelling over an artificially constructed fork.

When the angle between the arms lies within the range 40° to 90°, ants change direction if moving the wrong way on about 45% of trials and on less than 10% of trials if moving in the correct direction. For larger angles, these differences become smaller. With an angle between the arms of 120° ants reverse direction on about 30% of trials, whether the ants are in a nest bound or a food bound motivational state. Redrawn from [2].

In the later experiments the possible use of external directional cues was eliminated. Artificial trails, each with a single Y junction, were constructed out of straight lengths of trail. To make the artificial trails, ants were first encouraged to walk from their nest to a feeder across a sheet of paper. The paper with pheromone trails laid by the ants was then cut into strips to provide test trails on which individual ants were run. Because the pheromone trails decay quite rapidly, data could only be collected for about 20 minutes after the trail had been laid.

Directional changes on a straight artificial trail were relatively infrequent, however the trail was oriented. In relation to the original direction of the trail as laid by the ants, the reversals made by outgoing or returning ants were as likely to be wrong as right, so confirming the absence of any intrinsic trail polarity and the lack of use of compass cues.

When the artificial trail included a single Y junction with normal angles between branches, fed ants travelling in the wrong direction tended to correct their path at the fork by returning back along the trunk of the Y, while unfed ants moving the wrong way turned back at the fork and walked down one of the arms. Reversals of direction, when going the wrong way, were made on about 45% of trials, whereas directional changes when going the right way were seen on no more than 5% of trials.

To show that ants based these decisions on the geometry of the fork, forks were constructed with different angles between the arms. The ants' adaptive behaviour gradually broke down as the angle between the arms was increased. Ants chose randomly when all three angles were 120° and the Y junction was unpolarised (Figure 2).

How do ants decide on the fork's polarity? The fact that homeward and foodbound ants are equally confused by equiangular forks [2] suggests that ants must in some way measure at least two angles at the fork and base their decision on

both. For instance, an ant might first walk just beyond the fork being sure to turn through a small angle to do so, and then turn in the opposite direction to measure its angle with respect to the remaining branch. If that angle is small the ant is heading away from the nest and if it is large the ant is going home.

In whatever way the measurement is made, it requires some effort, raising the question: under what conditions do ants bother to assess the geometry of a fork? Do they do it at every fork that they notice, or only when they are in a state of uncertainty, after joining a trail, or when they are confused after interacting with other ants that they meet on a busy trail? Testing ants individually on more complex artificial trails, which contain several forks with opposite polarities, may give an answer.

Meanwhile, the current findings of Jackson *et al*. [2] give an intriguing glimpse into the sophisticated decision-making of individual Pharoah's ants. The arthropod mental toolkit appears to comprise an amazing array of special purpose devices that operate automatically in particular behavioural circumstances. Although the adaptive decision making of ants often depends on group interactions, the behaviour of Pharaoh's ants stresses that social intelligence is underpinned by smart individual behaviour. This leaves us with a final question. By what mechanism are the 60° forks formed? Are they the result of a directional decision made by an individual ant when it first leaves a trail to make a new branch, or do the forks become increasingly well formed when travelled by many ants?

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Evolution of Cooperation: Does Selfishness Restraint Lie within?

Traditional models of how cooperative strategies succeed in evolution have largely focused on social interactions among individuals and selection acting at kin and group levels. A recent study at the genetic level suggests that cooperation may also be promoted by the evolution of gene–trait relationships that limit the range of possible cheating mechanisms that can evolve.

Gregory J. Velicer

The evolutionary conundrum presented by cooperative behavior is well known. Cooperative traits are costly to express and are thus open to exploitation. Selfish individuals can defect from cooperation and benefit from the social contributions of others without reciprocating themselves. Such 'cheaters' can thus threaten the stability of cooperative systems.

Selfish social strategies are not limited to mammals with complex behavioral plasticity, such as ourselves [1]. Cheating is also common in social insects and in microbes with relatively hard-wired social traits. For example, some insect queens, known as social parasites, steal workers from the colonies of other queens and use them to raise their own offspring [2]. In bacteria, selfish individuals can cheat by failing to make beneficial extra-cellular compounds that are produced by cooperative neighbors [3].

Yet despite the common occurrence of cheating, cooperative systems such as genomes, multi-cellular organisms and animal societies have succeeded many times throughout evolutionary history. Such cooperative success requires mechanisms that limit the frequency and/or intensity of selfish behavior [4]. In the absence of restraint, cheaters destabilize cooperation and can even cause whole populations to go extinct when cooperation is required for survival [5]. How then is cheating restrained?

Previous studies of cheater limitation have focused primarily on social interactions among individuals and natural selection acting on kin networks [6] and spatial groups [7]. For example, cooperation might be promoted by preferential cooperation with kin [6,8], behavioral reciprocity (where cooperative and selfish acts are returned in kind) [9], policing (where cheaters are recognized and punished) [10] or purifying colonization (where only cooperators found new social groups) [11].

It has recently been proposed that cheating might also be restrained at the genetic level within potential cheats themselves [11,12]. The complexity of gene–trait relationships presents the opportunity to genetically short-circuit the appearance of successful cheaters. The most direct way to accomplish this would be to make mutations that cause defection from cooperation intrinsically harmful to fitness ('intrinsic defector inferiority') [11]. Such fruitless defection could be accomplished by linkage of a gene for a costly cooperative trait to a distinct trait important to evolutionary fitness.

Recent work by Foster *et al.* [12] on a defector mutant of the cooperative slime mold *Dictyostelium discoideum* has revealed an interesting case of a pleiotropic linkage that causes defector inferiority. *D. discoideum* is well known for its ability to undergo social development during starvation to form