And that is how the desert locust lost its memory

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A solitary male desert locust (left) facing a gregarious male (right) of the same species. Solitary locusts rely on camouflage to elude their predators. In the swarming gregarious phase, locusts feed on toxic plants to make themselves unpalatable, and develop bright yellow warning colours to advertise this to predators. Credit: Tom Fayle, University of Cambridge.

The desert locust (a type of grasshopper), much like Dr Jekyll/Mr Hyde, goes from being an innocuous solitary-living individual to become a voracious gregarious animal that destroys everything on its path (and back). These two very different "personas" are remarkable adaptations of a single genome to distinct environments. But apparently, this flexibility is even more impressive says Patricio Simōes, Jeremy Niven and Swidbert Ott from the Champalimaud Neuroscience Programme, the Instituto Gulbenkian de Ciência in Portugal and the University of Cambridge, as they reveal that the locust' solitarious and gregarious forms also have different memory and learning abilities to suit the needs of the two life stages.

The work, out in *Current Biology*, looked into the mechanism that allowed gregarious locusts to change their diet surprisingly fast – just a few hours after solitarious locusts are crowded they are eating toxic plants which they previously avoided because of bad taste. To Simões and colleagues' surprise it was found that this was due to an incapacity by newly gregarious locusts to acquire negative/aversive memories, that made them on encountering toxic plants see these as appetitive. Although gregarious animals later recover this capacity, their diet is not affected because at this point the food taste is no longer an important deciding factor. In fact, in a swarm of millions of individuals competing for little food, taste is probably the least essential criteria. The research provides new insights on how the environment can affect gene expression, and on insects' extraordinaire adaptability. Most importantly, to understand better how the desert locust adapts is to get a step closer to find a way to stop the swarms that every year endanger as much as 10% of the world food resources.

Locusts in the wild tend to live solitary lives until it rains and enough food becomes available to trigger their multiplication. Then, as their numbers increase, food exhaustion and physical contact with other locusts as result of their crowding, triggers a cascade of metabolic and behavioural changes that lead to their transformation into the gregarious form that goes to form the swarms. These solitarious and gregarious forms are so distinct in aspect, behaviour and even physiology that were once thought to be even different species in an impressive show of adaptability.

But if this plasticity in response to the environment (in this case population density) is remarkable, what is even more impressive is how fast it all occurs with new behaviour present after only 4 hours of crowding. The changes in diet were particular puzzling to scientists since food is a crucial survival tool and an adaptation to the animal's specific life story and ecology. Although the new diet improved the survival chances of the animal in the swarm by increasing the range of food available and its protection against predators (toxic plants make locusts unpalatable), how could such major adaptation occur in just a few hours?

To try to answer this Simōes and colleagues exploited the locust's ability to associate an odour with a reward – which in the wild allows it to make quick food choices - to study the memory and learning abilities of its three stages/forms - solitarious, gregarious and transiens (an intermediate stage, when locusts only just started to aggregate but already show the behaviours of gregarious animals).

They used a protocol similar to the one in Pavlov's dog experiments (where a dog is conditioned to associate a bell with being fed) using vanilla (the locusts' favourite) and lemon odours. But in this case the locusts were taught to link a vanilla odour with unpalatable nicotine food (so with a negative/ aversive stimulus), or, instead, lemon with a nutritious diet (positive stimulus). Since locusts prefer the smell of vanilla to lemon, if after training they chose lemon the conditioning had been successful.

What the researchers found was truly curious - while solitarious and gregarious locusts had no problem gaining negative memories (so being conditioned to link vanilla to the unpalatable diet), although it took much longer to gregarious animals, transiens locusts could not do it. In contrast, all 3 stages gained without problems the positive/appetitive memories (to link the lemon odour to nutritious food).

On the other hand, if the animals were first trained, then crowded and only after tested, crowding had no effect on (old) memories, whether these were positive or negative.

This showed that during the locusts' initial period of gregarization/crowding (transiens form) the animals can not acquire new negative memories. While both solitarious and gregarious locusts can do it, they seem, nevertheless, to use different learning mechanisms, as revealed by the different times it takes them to gain the aversive memory (4 hours for solitarious locusts and 24 hours for the gregarious). These are interesting results but they still did not explain how the gregarious animals changed their diet so fast.

So next Simōes and colleagues used hyoscyamine - a toxic alkaloid substance present in plants of the locust's natural habitat that are avoided by solitarious forms (because of their bad taste) but eaten by gregarious and transiens forms. The idea was to see how these preferences would now affect the locusts' training.

To start the animals were taught to associate vanilla with hyoscyamine, but this time while solitarious locusts learned to avoid vanilla – so gained the negative memory - neither transiens nor gregarious locusts could do it. In fact, to these two forms hyoscyamine seemed to even be neutral or appetitive. While this was clearly advantageous when in a swarm, how could a previously negative stimulus become suddenly a positive one? Since crowding blocks new negative memories could the old negative memory be simply replaced by a positive one?

To test for this possibility the researchers used a slightly different protocol - solitarious locusts were trained to associate hyoscyamine, not with a vanilla, but with the lemon odour. The idea being that since locusts normally chose vanilla, they will only go for lemon if hyoscyamine has a strong appetitive value. After training animals were divided into two groups - one half was kept in a cage, the other half crowded- , and after 4 hours trained again and tested. So all locusts are double trained, but only half are crowded between the two training episodes. Remarkably, now the majority of transiens locusts (so those that have been crowded) chose lemon over vanilla, in comparison with only one third of solitarious, non-crowded, locusts showing that they in fact see hyoscyamine as appetitive.

These results show is that even if crowding cannot eliminate a previous memory, by temporarily blocking new aversive memories, it permits an update of it when locusts are re-exposed to the toxic plants. This capacity to override previous memories, which only occurs during the initial stages of gregarization/crowding, is crucial for survival in the swarm because with increasing numbers of individuals also raises not only competition for food but also exposure to predators.

The reason why later gregarious locusts continue to eat toxic plants despite being able to gain aversive memories lies in their learning mechanism. In fact, while solitarious locusts acquire aversive memories in about 4 hours, most probably through a taste-controlled mechanism, gregarious animals take 24 hours to show a reaction (and transiens never do). This suggest that the gregarious' learning mechanism is post-ingestive, and most probably dependent on food toxicity instead of taste. Transiens locusts appear to have none of these two mechanisms since they simply do not acquire new negative memories, suggesting that they are even more resilient to toxicity than gregarious.

Simões and colleagues' research shows for the first time how the same animal can adapt its learning and memory abilities to suit different life stages in a remarkable show of insects' survival skills. After all their first record goes back 400 million years (in comparison with humans' 200 thousand).

But the results also open new doors to maybe one day be able to control the swarms. And when we think that a swarm of desert locusts can reach

1200 square kilometres with 40 to 80 million individuals per square kilometre, and travel 200 kilometres a day while eating everything at its passage, it is easy to understand why it is so crucial to find new ways to stop them. Luckily, swarms only last days with those locusts not eaten by predators turning back to their solitarious form. And it is in this conversion to an innocuous life that might lay a way to stop them, and where the new research might help by pushing them back into "Mr Hyde" mode.

More information: "Phenotypic Transformation Affects Associative Learning in the Desert Locust." Patrício M.V. Simões, Jeremy E. Niven, Swidbert R. Ott. *Current Biology* - 2 December 2013 (Vol. 23, Issue 23, pp. 2407-2412)

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