



## Pleiotropic antipredator strategies, fleeing and feigning death, correlated with dopamine levels in *Tribolium castaneum*

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A prey animal has the alternative of fleeing or feigning death to survive when it encounters predators. We found that fleeing by an artificial threat, locomotion and feigning death are pleiotropically correlated with a genetic factor related to a biogenic amine in the red flour beetle, *Tribolium castaneum*. Walking distance of adults was significantly lower in strains artificially selected for longer (L strains) than shorter duration (S strains) of death-feigning. Crosses showed that S-strain adults were dominant in the frequency and duration of death-feigning and locomotor activity compared to those of L strains, suggesting that death-feigning and activity have the same genetic basis. S-strain adults fled, but L-strain adults feigned death, when they encounter artificial threat. Not only adults that were directly selected for the duration of death-feigning, but also the larvae of L strains frequently showed tonic immobility, when they were dropped onto the ground: the larvae of S strains showed this behaviour less often. This suggests that chemical modulators of behaviour present in these insects before and after metamorphosis control both general locomotor activity and death-feigning. Brain levels of the candidate neuromodulator dopamine were, in fact, found to be significantly higher in S strains compared to L strains in the two selection replications. Thus, we suggest that two alternative behaviours related to antipredator strategies, fleeing or feigning death, are associated with the pleiotropic effects of a neuroactive substance in *T. castaneum*.

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Predation is a key selection pressure in shaping prey behaviours (Lima & Dill 1990; Sih 1992; Lima 1998). Because natural selection favours individuals that successfully avoid predators, selection has favoured antipredator behaviour. When a prey perceives danger, it often uses two alternative tactics to survive, immobilizing or running; it cannot adopt both simultaneously. Death-

feigning (sometimes called animal hypnosis, playing dead, or thanatosis), a kind of tonic immobility assumed by many animals in response to external stimuli (Ruxton et al. 2004, Ruxton 2006), has been considered a defence mechanism against predators that is shared by mammals (Franq 1969), birds (Sargeant & Eberhardt 1975), amphibians (Gargaglioni et al. 2001), fishes (Howe 1991), reptiles (McCallum 1999), crustaceans (Fedotov et al. 2006), mites (Ebermann 1991) and insects (Fabre 1900; Edmunds 1974, Miyatake et al. 2004; Ruxton et al. 2004; Hozumi & Miyatake 2005; Honma et al. 2006). On the other hand, a prey can survive by fleeing from predators. Escaping by running from predators is a common tactic for many animals (Edmunds 1974) and may be related to the level of locomotor activity of the insect.

At a physiological level, negative phenotypic relationships between death-feigning and activity have been

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observed in some insects. In the parasitoid species *Nasonia vitripennis*, the females that were least active had the greatest tendency to show thanatosis (King & Leach 2006). In the sweetpotato weevil *Cylas formicarius*, the frequency and duration of death-feigning are influenced by the behaviour before the weevil was startled: almost all resting individuals feigned death, whereas the active ones seldom did (Miyatake 2001a). Adults of *Cylas formicarius*, a nocturnal species, seldom showed death-feigning behaviour during the night, when they are active for reproduction, whereas they showed a higher frequency and longer duration of death-feigning in the daytime (Miyatake 2001a). These studies suggest the existence of two behavioural modes, active and resting, in which less and more death-feigning, respectively, occurs. If death-feigning and activity are genetically linked, then both traits may evolve together as a trade-off strategy. That is, individuals that are active at the time of threat often adopt a fleeing strategy, while inactive individuals frequently adopt a death-feigning strategy.

Many insect behaviours are controlled by neuroactive substances or biogenic amines, including octopamine and dopamine, that are derived from the amino acid tyrosine (Evans 1980; Bicker & Menzel 1989; Stevenson et al. 2000; Libersat & Pflüger 2004). In crickets, dopamine and octopamine are required for a successful aggressive encounter (Stevenson et al. 2000), octopamine and dopamine play roles in conveying positive and negative reinforcing signals in olfactory learning (Unoki et al. 2005, 2006), and flying and fighting abilities are also regulated by biogenic amines (Hofmann & Stevenson 2000; Stevenson et al. 2005). In the cockroach, dopamine and octopamine enhances the escape response (Goldstein & Camhi 1991; Casagrand & Ritzmann 1992). In honeybees, dopamine enhances the activity level of the motor response (Božič & Woodring 1998; Menzel et al. 1999), sucrose responsiveness is increased by injection of octopamine, but decreased by dopamine (Scheiner et al. 2002), and octopamine also modulate other behaviours, such as learning, memory formation and division of labour (Scheiner et al. 2006). In *Drosophila melanogaster*, dopamine provides a role in the modulation of arousal (Kume et al. 2005) and in stress response (Chentsova et al. 2002). However, in spite of much neuro-physiological research, no study has examined the genetic relationships between insect behaviour and neuroactive substances from the view point of antipredation strategies.

We here show a negative genetic relationship between locomotor activity or fleeing and death-feigning, and a possible chemical that controls fleeing or death-feigning behaviour, using strains selected for shorter (S strains) or longer (L strains) duration of death-feigning in *Tribolium castaneum*, a model insect for the adaptive significance of death-feigning behaviour (Prohammer & Wade 1981; Miyatake et al. 2004). The death-feigning behaviour of this beetle increases its fitness for survival against a predatory spider (Miyatake et al. 2004). Heritable variation of death-feigning intensity has also been reported in this beetle (Prohammer & Wade 1981; Miyatake et al. 2004).

In the present study, first we measured adult locomotor activities, fleeing or feigning death behaviours of adults and larval tonic immobility from the S and L strains, and

examined crosses between the two strains to identify the genetic base for the locomotor activity and larval tonic immobility. We used the term 'tonic immobility', not death-feigning for larval thanatosis, because the adaptive significance for the larval immobility was not known in *T. castaneum* while for the adults the significance has been identified as avoiding attack by a model predator, the jumping spider (Miyatake et al. 2004). Second, we compared the levels of brain dopamine expression of adult beetles in selected strains, because dopamine is a biogenic amine associated with increased locomotor activity, escape behaviour and arousal in insects (Goldstein & Camhi 1991; Casagrand & Ritzmann 1992; Stevenson et al. 2000; Libersat & Pflüger 2004; Kume et al. 2005).

## METHODS

### Insects and Culture

The *Tribolium castaneum* beetle culture used in this study has been maintained in laboratories for more than 25 years. The beetles were fed wholemeal (Yoshikura Shokai, Tokyo, Japan) enriched with brewer's yeast (Asahi Beer, Toyko, Japan) as the rearing medium and kept in a chamber (Sanyo, Tokyo, Japan) maintained at 25°C and 60% RH under a photoperiod of 16:8 h light:dark cycle (lights on at 0700, light off at 2300).

### Observation of Death-feigning

One day before observation, each beetle was placed in a well of a 48-well tissue culture plate (Falcon, Becton Dickinson and Company, Lincoln Park, NJ, U.S.A.) to prevent disturbance by other beetles, which usually reduces the duration of death-feigning (Miyatake 2001a). The next day, each beetle was gently placed on its back in a white china saucer (140 mm diameter, 15 mm deep). Death-feigning behaviour was induced by touching the abdomen of the beetle with a wooden stick. A trial consisted of provoking the death-feigning behaviour and recording its duration with a stopwatch. The behaviour duration was defined as the length of time between the stick touching the beetle and detection of its first visible movement. If the beetle did not respond, the touch was repeated. When the beetle feigned death, the duration was recorded. All the trials were conducted between 1300 and 1700 hours in the chamber described above.

### Artificial Selection

One hundred males and 100 females (15 days old) were randomly selected from the stock culture and their death-feigning behaviour was observed (F0 generation). The males and females (10 each) with the shortest duration of death-feigning were selected to propagate short-duration strains (S strains); similarly, 10 males and 10 females with the longest duration were selected to propagate long-duration strains (L strains). The males and females of each strain were placed in a plastic cup (6.5 cm diameter, 2.5 cm height) with 20 g of medium and allowed to

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