



How is a cricket like a rat? Insights from the application of cybernetics to evasive food protective behaviour

Heather C. Bell^{a,*}, Kevin A. Judge^b, Erik A. Johnson^a, William H. Cade^b, Sergio M. Pellis^a

^a Canadian Centre for Behavioural Neuroscience, University of Lethbridge, Lethbridge, AB, Canada

^b Department of Biological Sciences, University of Lethbridge, Lethbridge, AB, Canada

ARTICLE INFO

Article history:

Received 3 April 2012

Initial acceptance 3 May 2012

Final acceptance 27 June 2012

Available online 13 August 2012

MS. number: A12-00266R

Keywords:

crickets

cybernetics

food protection

Perceptual Control Theory

robbing and dodging

Robbing and dodging is a well-documented food protective behaviour in rats. Recently, we demonstrated that a simple cybernetic rule, gaining and maintaining a preferred interanimal distance, can account for much of the variability in dodging by rats. In this paper, the field cricket, *Teleogryllus oceanicus*, was used to test whether or not the same or similar cybernetic rules are used by animals of different lineages and body plans. Pairs of female crickets were tested in a circular arena with a clear glass surface. A small food pellet was given to one of the crickets and the attempts to rob the food by the other were videotaped from beneath. The results show that, although crickets, unlike rats, use a variety of defensive strategies, all of the cases in which they use evasion to protect a portable food item conform to the same cybernetic rules used by rats.

© 2012 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Robbing and dodging, heretofore described in rats, involves one animal (the defender) possessing a portable piece of food, while another animal (the robber) attempts to steal that food. The defender evades the robbing attempts by pivoting laterally, thus dodging away from the robber (e.g. Whishaw 1988; Whishaw & Tomie 1988). Robbing and dodging in rats has been used as a model to investigate a number of issues related to the neural control of behaviour (Whishaw & Oddie 1989; Whishaw et al. 1990; Field et al. 1996, 1997a, b, 2004, 2005; Pellis et al. 2006).

We recently demonstrated that robbing and dodging in rats, rather than resulting from a stimulus–response algorithm, with which defenders calculate fixed dodging angles based on food and partner characteristics, can be succinctly accounted for by appealing to a simple cybernetic rule: gain and maintain a preferred inter-animal distance (Bell & Pellis 2011). Stimulus–response algorithms produce fixed motor responses to specific sensory stimuli; that is, when a particular sensory stimulus is experienced by an organism (e.g. an approaching robber), the behaviour that it produces as a result is the same every time (e.g. to pivot a set number of degrees away from approaching robber). In contrast, the term ‘cybernetic’ implies the use of negative feedback to continuously modify behaviour in order to compensate for changing environmental

information; that is, variable behaviour is used by the organism in the service of achieving biologically relevant goals (Wiener 1943; Powers 1973). The distinction is that, instead of using the same set of movements to evade a robbing attempt every time, which would be easy for the robber to learn and defeat, something that almost never happens (H. C. Bell, unpublished observations), the cybernetic rule involves using only the same general tactic. The cybernetic control of interanimal distance, which can be achieved by an almost infinite combination of movements, is, by virtue of its unpredictability, much more difficult for the robber to learn and defeat. In terms of behavioural output, this means that the range of angles traversed during dodging is more variable than the range of interanimal distance, as the former is varied to regulate the latter (Bell & Pellis 2011).

In light of our discovery of the existence of a cybernetic rule in rats when dodging, we determined to test whether or not other animals operate using the same principles in similar contexts. For several reasons, we chose field crickets, *Teleogryllus oceanicus*, to conduct this investigation. First, cybernetic rules have previously been used to explain some aspects of cricket behaviour (Pellis et al. 2009). Second, as crickets have also been observed to perform dodges in response to robbing attempts made by other crickets (B. Gorny & I. Q. Whishaw, unpublished observations), the same overt behaviour could be compared across the two species. Third, although they seem to perform dodges to protect food in a similar fashion, crickets have a different body plan than rats, with Arthropoda and Chordata having diverged at least 500 million years ago

* Correspondence: H. C. Bell, Canadian Centre for Behavioural Neuroscience, University of Lethbridge, 1401 University Drive, Lethbridge, AB T1K 3M4, Canada.
E-mail address: heather.bell@uleth.ca (H. C. Bell).

(Ayala & Rzhetsky 1998). For example, rats use their forepaws to hold their food, requiring them not only to shift their body weight onto their hindlegs, but also limiting their defensive movements to only two of their feet (Whishaw 1988). In contrast, crickets hold their food with their mandibles (Manton & Harding 1964), leaving all six limbs free for locomotion when evading the robber. Such differences in posture and motor strategies across the species could produce significant differences in the organization of food protection.

Four hypotheses were tested in the present paper. The first two major hypotheses were (1) that crickets use a cybernetic rule during food protective behaviour and (2) that crickets use the same 'gain and maintain a minimum interanimal distance' rule in the same way that it is used by rats; that is, despite all of the differences mentioned above between the two species, crickets and rats defend food using the same underlying principle (see Table 1). The second two minor hypotheses, dependent on the main hypotheses, were (3) that, in addition to controlling interanimal distance, defenders also control their body orientation relative to robbers, and (4) that approach orientation of the robber is related to the type of evasive action used by defenders (see Table 1).

One issue with respect to the first hypothesis is that for crickets, and for arthropods in general, rapid defensive and offensive actions are thought to be ballistic, allowing little opportunity for modification once their behaviour is initiated (Schöne 1984; Bell 1991). If arthropods act solely in a ballistic fashion, cybernetic mechanisms, because they rely on feedback, could not be a fundamental component of the organization of cricket behaviour. However, the same algorithmic, nonupdateable type of rule was also previously thought to apply to the dodging behaviour of rats (Whishaw & Gorny 1994). Fortunately, ballistic and cybernetic rules produce distinct behavioural outcomes. If defender crickets respond only ballistically to the stimulus of the robber's approach, their behaviour should be relatively stable through time and independent of the specific movements used by the robber. Conversely, if crickets are able to use feedback to compensate for changing conditions, then defender responses should not only be variable, but should also be correlated with the specific movements used by the robber.

With respect to the second hypothesis, if the goal of the defender is to control a two-dimensional interanimal distance, then, as was discovered in the rats, interanimal distance should be less variable than any other measured variable (Bell & Pellis 2011). Furthermore, interanimal distance should not be correlated with the actions of the robber; that is, interanimal distance should remain relatively constant even though the movements of the robber do not, which is also characteristic of the rat dodging system (Bell & Pellis 2011). Finally, the same pattern of relationships between all measured variables that was present in the rats, such as a correlation between the movement of the robber and the movement of the defender, should also be present in the crickets.

With respect to hypothesis 3, our initial observations indicated that, like rats (Field et al. 1996), cricket defenders faced away from

robbers at the end of interactions. We predicted that, if defender body orientation relative to robber were controlled, specifically, if the 'facing away' orientation were preferred, then the 'facing away' orientation should be favoured over other defender orientations at the end of interactions.

With respect to hypothesis 4, unlike rats, crickets do not rely solely on dodging (i.e. pivoting away from the robber) as an evasive strategy. In many instances, crickets simply walk or run directly away from the robber. Crickets also differ from rats in the variety of approach angles that are used by robbers. A rat primarily approaches another rat holding food from a parallel orientation, with its head moving along the flank, in the direction of the defender's head. Thus, in the majority of encounters, the defender is confronted with a similar robbing orientation. In contrast, in their approach to rob, crickets do so from virtually any orientation, and this difference could account for the differing evasive strategies used by crickets. Therefore, we predicted that the point on the body of the defender targeted by the robber is related to the type of evasive strategy adopted (i.e. dodging versus running).

METHODS

Subjects

All procedures in this paper conform to the University of Lethbridge Animal Welfare Committee protocol number 0708. Ninety-two female field crickets (46 pairs), *Teleogryllus oceanicus*, that were born and reared at the University of Lethbridge were used in total; however, not all animals were used for every analysis. All animals were housed in rooms maintained at 25 °C and 70% relative humidity, on a 12:12 h light:dark cycle, with lights on at 1200 hours. Hatchlings were placed into large plastic bins (51 cm long × 37.5 cm wide × 35.5 cm high) containing layers of cardboard egg cartons for shelter, glass shell vials filled with water and stoppered with cotton for moisture, and ground and pelleted cat chow (Iams® Original with Chicken) ad libitum. Water vials were changed weekly and additional food was given as needed. Female nymphs were separated from the colony during their penultimate instar (final juvenile instar) and were then housed in groups of 10 to 20 individuals in containers (29.5 cm long × 19 cm wide × 12.5 cm high) with layers of cardboard egg cartons for shelter, and water and food provided as before. Following their final moult, the animals were placed, individually, into round plastic containers (9 cm diameter × 8 cm high). Half of the animals were randomly assigned to be subjects, defending the food, and the other half were assigned to be robbers. Half of both the defenders and the robbers were marked with a dab of typewriter correction fluid on their pronotum. Each cricket destined to be a defender was randomly assigned a partner that would act as the robber. Although isolated, the animals were housed in the colony room from which they would have been able to see, hear and smell conspecifics. Thirteen of the original 46 pairs were eventually

Table 1
Competing hypotheses and predictions tested

Hypothesis 1	Crickets use cybernetic rules to protect food from robbers	Crickets use ballistic rules to protect food from robbers
Predictions*	1. <i>Defender responses to robbing attempts are variable</i> 2. <i>Defender and robber movements correlated</i>	1. Defender responses to robbing attempts are invariant 2. Defender and robber movements not correlated
Hypothesis 2	Crickets use the same rule as rats to protect food from robbers	Crickets do not use the same rule as rats to protect food from robbers
Predictions	1. <i>Interanimal distance is invariant</i> 2. <i>Interanimal distance is not correlated with robber movement</i> 3. <i>The same pattern of relationships among all variables seen in rats is seen in crickets.</i>	1. Interanimal distance is variable 2. Interanimal distance is correlated with robber movement 3. The same pattern of relationships among all variables seen in rats is not seen in crickets.
Hypothesis 3	Defender body orientation is a controlled variable	Defender body orientation is not a controlled variable
Predictions	1. <i>Defender body orientation is the same at the end of every interaction</i>	1. Defender body orientation is variable at the end of every interaction
Hypothesis 4	Initial robber orientation predicts evasive strategy used	Initial robber orientation has no bearing on evasive strategy used
Predictions	1. <i>Initial robber orientation and evasive strategy are correlated</i>	1. Initial robber orientation and evasive strategy are not correlated

* Predictions that were supported are italicized.

Download English Version:

<https://daneshyari.com/en/article/2416521>

Download Persian Version:

<https://daneshyari.com/article/2416521>

[Daneshyari.com](https://daneshyari.com)