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The Judder of the Cricket: The Variance Underlying the Invariance in Behavior

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While the behavior of many animals can be identified as involving discrete and stereotyped actions, there is a persistent tension between emphasizing the fixedness of the actions ("Fixed Action Patterns") and emphasizing the variation in the components comprising those actions ("Modal Action Patterns"). One such action, the back and forward judder of crickets often exhibited in agonistic interactions, was analyzed. Judders occurring on a horizontal surface by *Gryllus bimaculatus* were compared to those occurring on an inclined platform. Although the body movements involved were variable, that variability occurred in the context of maintaining some features of judder invariant. For example, the crickets maintained their bodies so that they were horizontal relative to the substrate, not to gravity, and most features of the back and forward movement (e.g., distance moved, velocity) were maintained as fixed despite differences in posture and movement. At a theoretical level, what these findings suggest is that behavior patterns involve a combination of fixedness and variation in the service of that fixedness. It becomes an empirical issue to discern these complementary components.

A core concept of classical ethology was the *fixed action pattern* (FAP) (Lorenz, 1981). It drew attention to the fact that the repertoire of behavior available to a species is identifiable not as a continuous stream of movement, but as pieces which have a degree of stereotypy that makes them distinct from one another. From early in its history, this concept drew criticism due to the problems of defining what it is that is fixed in FAPs and the implication that fixedness is genetically based (e.g., Moltz, 1965); problems that have continued to draw fire (e.g., Dewsbury, 1978; Klopfer & Budnitz, 1990). As FAPs were studied in greater detail, the more variability was evident in their morphologies. This led George Barlow (1968, 1971) to propose a new term, the *modal action pattern* (MAP), which recognized that certain movement patterns have distinctive morphologies, and those morphologies are fixed in a statistical sense only, thus reconciling the fixed and the variable aspects of such patterns. But the nature of this reconciliation bears closer inspection.

From the first example used to describe and define the FAP, the egg retrieval behavior of geese (Tinbergen & Lorenz, 1938), it was recognized that while some aspects of the action are invariant, others are variable. The invariant components include the goose's use of the bill, rather than the feet or the wings, to retrieve the egg. Once its head engages the egg it draws its head back towards its body, and even if bill contact with the egg is lost, the goose will continue to retract its head all the way back. This is the fixed action component of the FAP. In conjunction with this fixed movement, there are variant movements of the head as the goose moves it from side to side so as to maintain the rolling of the egg towards its body, rather than it rolling off to one side. This taxis is variable, involving different combinations of movements depending on the movements of

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the egg (Tinbergen, 1951). Therefore, a FAP was conceived of as being composed of two motor mechanisms: one that does not require sensory feedback for its execution, and one that does (McFarland, 1971). For the MAP concept to be a useful replacement for the FAP it has to be the motor output, which is supposedly insensitive to sensory feedback, that has unexpected variability. Indeed, many studies of FAPs have shown that all aspects of their execution, not just the taxes involved, appear to be variable (Papini, 2008).

For example, a typical anti-predator behavior of cuttlefish is for it to bury itself in the substrate, and to do so by performing a recognizable sequence of actions. It was found that, by experimentally manipulating the coarseness of their substrate (e.g., by increasing the size of sand grains used or by using beads), that the sequence and organization of aspects of the movements performed were modified. This modification appears to arise from the changes in sensory and functional demands that are placed on the cuttlefish as they dig and move sand grains of different size and weight (Mather, 1986). Because it focuses on the variable movements performed, the statistically sensitive notion of the MAP is a better descriptive label for such an action sequence. However, it is this focus on the variable movements that fails to draw attention to the functional significance of that variation.

Consider again the goose retrieving the egg. If the egg to be retrieved is far from the nest, the goose has to stretch its neck to its fullest in order to contact the egg, whereas if the egg is only a short distance from the nest, the neck has to be partially curved (in a concave manner). Similarly, if the nest is on a slight incline, in order for the goose to pull the egg up the incline, it would be necessary for it to shift its body weight backwards to avoid falling forwards when stretching its neck forwards. In all these cases, a different combination of head, neck, body and leg positions and the associated movements would be needed to bring the bill (and egg) toward the nest. By viewing the goose's behavior in this manner, it can be seen that not only are all the components of the FAP variable, but also, that that variability is associated with differences in the sensory and functional demands of the context (Cziko, 2000). Therefore, for the goose to keep a constant, dynamic relationship between its bill, the egg and the nest, it has to modify the movements involved. Neither the original conception of the FAP, or its variation-sensitive alternative - the MAP - captures this cybernetic quality of species-typical action patterns.

Thus, when characterizing an action pattern, one should first determine what features of the behavior are kept constant and what actions the animal can vary so as to maintain that constancy (Golani, 1976; Pellis, 1985; Schleidt, 1982; Schleidt & Crawley, 1980). For example, during courtship, male mallard ducks perform a variety of displays while on the surface of ponds or other bodies of water. The descriptive problem is that of identifying what makes these FAPs distinctive from one another. Precise movements of head, neck and body indicate considerable variation within in FAPs, but by recording the height that their different body parts were maintained above the water, it was shown that the bill-to-water surface height was consistently different for different FAPs (Finley, Ireton, Schleidt, & Thompson, 1983). Therefore, despite the starting point of the ducks in

relation to the surface of the water, or whether there were disturbances due to wave action, the birds make compensatory adjustments so as to maintain constancy in the bill-to-water relationship for the particular FAP being performed.

Similarly, both Australian magpies and oriental small-clawed otters use a distinctive FAP-like tactic during play fighting, whereby the performer extricates it self from a bite/peck on the side of the head by moving its head horizontally away from the partner, then raising it vertically to face the sky and then rotating the head while in this vertical position towards the partner. Finally, with a vertical movement downward, the performer breaks the contact and faces its partner. However, depending on the starting position of the performer (e.g., raised on its hind legs or squatting) and the position of the attacker (e.g., head raised above, below or equal to the performer), the performers' actions can be highly variable, with different combinations of head, neck, body and limb movements. However, the trajectories traced, in each case, by the tip of the bill and tip of the snout are remarkably similar (Pellis, 1985).

Like for the mallard ducks, in these cases, the variability in the movements of different body parts arise from the compensatory actions taken so as to maintain some constant relationship with some aspect of the environment. Such variance in the service of maintaining some constancy is evident in other behaviors, such as the individual grooming actions and grooming sequences of rodents. This is particularly evident when grooming first emerges and some of the grooming-typical arm movements can occur independently of actual paw-to-face contact (Golani & Fentress, 1985) and in the modifications needed to compensate for body size differences among species (Berridge, 1990).

On the flip side are studies suggesting that the sequences of movements during FAPs/MAPs are themselves highly constrained. This can be seen, for example, in the head bobbing display of some lizards, where the same pumping action of the forelimbs to raise the head is present whether the lizard is on a branch facing upward or horizontal, with the shape of the bob (temporal pattern) remaining distinct across closely related species (Hunsaker, 1962). Similarly, in a range of actions, such as protecting a food item from robber by dodging laterally away, female rats use a consistently different combination of forequarter and hindquarter movements than do male rats, even when the magnitude of the resulting movement is the same between the sexes (Field & Pellis, 2008). What remains to be determined, such as the species-typical arm waving patterns of fiddler crabs (Salmon, 1967), is whether these sequences involve constrained arm and bodily movements, and so produce invariant arm displays, or whether the invariant arm-waving trajectories are produced by variable arm and body movements that arise from compensatory actions which adjust to changes in orientation to the substrate.

The range of studies discussed raises a major problem with the application of the FAP/MAP concept. That is, that the terms are applied widely across animals from widely different taxa (e.g., vertebrates, mollusks, arthropods) and to behavioral contexts that differ markedly (e.g., defensive actions directed at conspecifics or predators, actions toward some inanimate environmental target, displays that are generally insensitive to the actions of social partners). Taxonomic

and contextual factors may have different roles in shaping particular FAPs/MAPs, and this adds a considerable burden on applying a concept with a universally acceptable definition. The broader theoretical implications of this diversity will be dealt with in the discussion, but for present purposes, our theoretical stance is one with an emphasis on methodology.

We posit that a cybernetic view of behavior is applicable to the kinds of actions often labeled as FAPs or MAPs (Cziko, 2000). Based on this perspective, it is assumed that for any given action pattern, there are invariant features and these could be of various kinds. For example, the invariance could involve some fixed relationship between body parts, or of some body part to an environmental cue (animate or inanimate), or to some dynamic aspect of the pattern performed (e.g., displacement, velocity, etc.). If the cybernetic perspective is correct, then it follows that variability in individual movements by different body parts can be accounted for as compensatory actions that are enacted to preserve the invariant features. In cybernetic parlance, there is a reference signal that sets the value that the system maintains as constant, and variable behavioral output is what the system does to protect against deviation from the reference signal (Powers, 1973). This approach forces us to seek the invariant features of the behavior and then use these to ascertain whether the variable components can be explained as predicted. From this theoretical stance, it should not matter what taxonomic group the species in question belongs to or what particular action pattern is being studied. Any differences among species and types of actions should become evident as a result of empirical studies, rather than being prejudged.

In this paper, we examine a species-typical action pattern, the judder seen in crickets. A cricket judder is a rapid, back-and-forth movement of the body that commonly occurs in inter-male agonistic interactions, most often performed by the winning, dominant cricket (Alexander, 1961; Bailey & Stoddart, 1982; Souroukis & Cade, 1993). The crickets were tested in two types of enclosures so that they would have to perform these judders on either a horizontal surface or a sloping one. The difference in the postural adjustments needed would thus affect the combination and sequencing of muscular action during the judder. Under these conditions, what is held constant and what varies? If we are correct, then it should be the case that the invariant features of the judder are defended by the changes that the cricket makes to its posture and movements so as to compensate for the effects of gravity on it when it is placed on an incline.

Method

Subjects

Adult male field crickets (*Gryllus bimaculatus*) from a colony maintained in the Department of Biology, University of Lethbridge, were used. The laboratory stock originated from adults collected east of Harare, Zimbabwe, in 1994 (see Tachon, Murray, Gray, & Cade, 1999). The colony was maintained in 84 l plastic garbage bins containing water vials, cat food and pieces of cardboard for shelter. The bins were kept at a temperature between 23.5-25°C, on a 14:10 light:dark cycle.

Intact crickets, following their adult molt, were weighed and their pronotum width measured. Individuals were color marked with dots of paint on both hind legs and placed,

individually, in clear plastic containers (16 cm x 9 cm x 9 cm – length x width x height). Water, in cotton-plugged glass vials, and food, cat chow, were provided *ad libitum*. The isolated males were separately housed and maintained in a separate room (28-30°C, 14:10 light:dark cycle). The crickets were tested following 4-6 days of isolation. Before testing, the individually housed crickets were introduced to the testing room for 1 h to allow for adjustment to the lower ambient temperature (about 25°C). A total of 24 crickets forming 12 pairs were tested. Each pair was closely matched for mass and pronotum width. Behavioral testing was conducted during the light phase of the crickets' daily cycle.

Behavioral testing

Six pairs of crickets were tested in a flat-bottomed, clear, polyethylene terrarium (19 cm x 12 cm x 13 cm). The other six pairs were tested in a clear, polyethylene terrarium (19 cm x 12 cm x 13 cm) with the bottom angled at 30° lengthwise. In both cases, the floor of the enclosure was finished with a sheet of styrofoam (1 mm thick) to aid the crickets in gripping the substrate. Both containers were marked at 1 cm intervals to allow calibration during the analyses of the videotaped sequences (see below). In initial trials, we also tried to use a slope of 45°, but for many judders, the cricket often lost footing and slid partially down the incline. Therefore, unless otherwise indicated, for formal comparison with the horizontal condition, the 30° incline was used. Nonetheless, when the crickets did maintain their footing, judders performed on the more severe slope helped confirm the pattern of adjustment evident in the gentler incline.

In both conditions, males were placed in the terrarium for 5 min to acclimatize them prior to the onset of each trial. To prevent interactions during this acclimatization period, a glass vial, 4.5 cm in diameter and 9.5 cm in height, was placed over the top of each cricket. Once the vials were removed, the trial was videotaped using a JVC digital recorder (with a shutter speed of 1/500). The camera was angled at 90° to the side of the enclosure at a distance of 60 cm. Given that only video sequences in which the cricket was perpendicular to the camera were used for the most detailed analyses (see below), the duration of trials was variable (ranging from 5-15 min), depending on how long it took for suitable sequences to be filmed. In some cases, to ensure sufficient data, pairs were re-filmed following another 4-6 h isolation. In some of the subsequent trials, pairs were videotaped directly from above to permit observation of the limbs from both sides of the body.

Data analyses

Several analyses were conducted. The three main analytical approaches were used to answer three distinct questions about the judders performed in the two enclosures. The first involved examining every judder performed by the crickets when not in contact with a vertical surface. This was so as to ascertain the orientation of the longitudinal axis of the cricket's body in relationship to the ground. That is, when on the sloping surface, facing downward, did the crickets raise the anterior of their bodies so as to maintain a horizontal orientation to gravity or did they maintain a parallel orientation relative to the ground? For this analysis, a protractor was used to measure the angle of the longitudinal axis of the cricket's body relative to the ground. A total of 253 judders were scored in this manner. For the subsequent two analyses, only those cases where the crickets were perpendicular to the camera were used. This was necessary, or otherwise the length of the crickets' bodies could vary and so distort the measurements, especially those of displacement, velocity and the identification of the relative positions of the limbs.

The second analysis involved noting the orientation of the cricket's limbs relative to its body axis and to the ground, as we wished to know how a cricket positioned its limbs when it juddered, and how such positioning changes if it were then placed on a sloping surface. For this analysis, these limb positions were traced, with a marker, from the video screen onto a clear, acetate sheet. Variation and consistencies in the limb postures on the horizontal and sloping surfaces were compared. A subset of the total number of judders, that permitted seeing either all three limbs on one side clearly, or the angle of each limb emerging from the body on both sides, was used (details given in results).

The third analysis involved using a computerized digitizing system, Peak Motus 2 (Peak Performance, Inc., Englewood, CO). A frame grabber was used to project each frame and digitize

each chosen point on the image. The system enhances each of the half-frames (fields) comprising each video frame and presents them separately, thus converting 30 frames/s video sequences into 60 frames/s. The most anterior tip of the head and the most posterior tip of the abdomen were digitized. The Peak computer program could then calculate various parameters of the judders (Pellis & Pellis, 1994; Whishaw, Pellis, & Gorny, 1992), which, for our current purposes, included the linear velocity, linear displacement, angle and maximum height of each judder. While digitizing from the half-frames, the number of back and forth oscillations per judder was also recorded. Six examples from each one of the pair mates of each of the twelve pairs were so analyzed. This gave us an equal number of trials for the six crickets, for both juddering on the horizontal surface and when facing downward on the surface with a 30° slope. Data for each cricket were used to calculate a mean value for that individual. These individual scores were then used to calculate group means and variances. Each measure was compared between the horizontal and sloping surface condition using independent samples *t*-tests. In addition, for each measure, a coefficient of variation was calculated and compared across conditions using the C-statistic (Lehner, 1996). Significance for statistical comparisons was set at $p < 0.05$.

Other analyses will be described as needed in the Results, but regardless of the analyses conducted, it should be noted that to ensure a non-biased selection of judders, two procedures were followed. First, for some measures (e.g., orientation of the body to the substrate), the sole criterion for inclusion was whether we could see the angle of the cricket's body axis relative to the ground. Second, for judders on which detailed measurements were made, we ensured that all judders used were when the crickets were not pressed against the enclosure walls, that they faced the appropriate direction (e.g., for the use of Peak Performance, the cage was calibrated for length and height, so the cricket had to be perpendicular to the angle of filming) and that the judder started from a preceding frame when the animal was stationary (e.g., in some cases, crickets began a judder when moving, which for some analyses was a problem if that movement involved rotation around the vertical axis). Finally, only judders where the cricket ended its back and forth movement without hurtling forward and losing footing, were used. That is, only judders involving backward and forward movement on a stable footing were used. Based on these criteria, the sequence of video for each cricket was examined and the first judder to meet the criteria set was scored, and then the next. Judders that did not fit the criteria were ignored. In this way, other than by applying the criteria, we had no way to bias which judders to use for the comparisons.

Results

Judders could occur singularly or in sequences of up to 4 or 5, but each judder began and ended before another commenced. For our analyses, we always examined the first judder in a series. During the cycle of movement occurring during the judder, the cricket moves backward and up and then forward and down. Thus, the cricket's body moves slightly off a parallel orientation to the ground, while its head traces an elliptical trajectory in space (see Figure 1 in Bailey & Stoddart, 1982). For the purposes of analysis, each judder was defined as beginning on the frame when the backward movement started and ending in the frame when the final, forward movement was complete. Each judder lasted 3-4 frames and was strikingly invariant in this regard. Using the first example of juddering for each of the six crickets from the horizontal and sloping (30° facing downward) conditions, the duration was 111.0 ms \pm 17.33 and 105.67 ms \pm 13.67, respectively (mean \pm *SD* are shown here and below). Not only did these not differ ($t = 0.59$, $df = 10$, $p > 0.05$), but they also had similar low variability (CV = 12.9% and CV = 15.6%; $C = 0.47$, $p > 0.05$). Indeed, judders where the cricket faced up the slope yielded a non-significant difference (111.0 ms \pm 17.33) to both the same crickets when facing downwards on the slope ($p > 0.05$) and to the crickets tested on the horizontal ($p > 0.05$).

When considering all judders, irrespective of the crickets' orientation relative to gravity (on the horizontal surface, facing downwards, upwards, sideways or diagonally on the sloping surface), when commencing and ending the judder, they maintained a parallel orientation to the ground. As described above, during the actual moving phase of the judder, the cricket's body moves off parallel (to around 13° , as described below). With regard to what is kept invariant in the judder, these data show that even though their orientation to gravity changed, the longitudinal axis of their bodies remained parallel to the ground. To achieve this constancy in their orientation to the ground, the crickets' limbs changed positions to compensate for the differing forces on their bodies when they were placed on the sloping surface relative to the horizontal surface. In cases where the cricket was facing the camera either with the anterior of its head or the posterior of its abdomen, the limbs facing downwards were displaced further from the body than those on the upward side of the slope. In these cases, it appeared that the downward facing limbs were used to push the body upward, bracing the body against gravity. Nevertheless, the long axis of the body was still parallel to the substrate. When juddering while facing down the sloping surface, the crickets' limbs were spread out further along the body than when they were on the horizontal surface (Figure 1). Thus, when on the sloped substrate, whether facing down, up, or across, the crickets appeared to increase the base of their support, by spreading their limbs further apart.

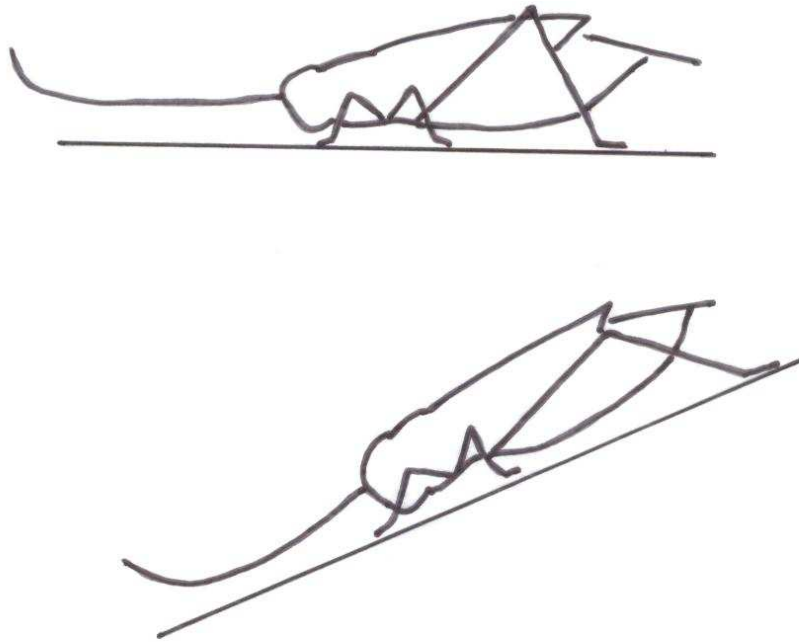


Figure 1. The posture of a cricket standing on two substrates is shown. When on the horizontal surface (upper panel), the tarsus placement is contained within the length of the longitudinal axis of the body. In contrast, when standing face down on an inclined surface (lower panel), the cricket's limbs are more spread-out as the insect braces itself against falling forward.

To formalize the measurement of these differences in limb placement, the first example of juddering for each of the six crickets from the horizontal and sloping (30° facing downward) conditions were used. Given slight differences in relative size (both due to the variation in cricket length and to the location relative to the camera), the placement of the tarsus (mid-point) of the hind limb relative to the length of the cricket's body (anterior tip of head to end of abdomen, not counting the cerci) was used for comparison. The position of the tarsus was scored in the frame preceding the beginning of the judder. In this schema, a value of greater than 100% would indicate the placement of the tarsus passed the end of the abdomen, whereas, a value smaller than 100% would indicate placement before the end of the abdomen. For the crickets on the horizontal surface, the hind tarsus is placed relative to the last tenth of the abdomen ($93.15\% \pm 6.97$), whereas on the sloped surface, the tarsus is placed just after the end of the abdomen ($104.90\% \pm 7.37$), a significant difference ($t = 2.84$, $df = 10$, $p < 0.05$). The magnitude of the limb displacement is even greater for crickets when facing up the slope ($120.34\% \pm 13.36$), a significant difference with the crickets on the horizontal condition ($t = 4.41$, $df = 10$, $p < 0.01$), and with the matched sample from crickets on the slope, but facing down ($t = 5.73$, $df = 5$, $p < 0.01$).

During the judder, even though the crickets maintain a near parallel orientation to the ground at the beginning and at the end, it is possible that the magnitude of the deviation from the parallel differs when on the horizontal versus the sloping surface. Similarly, other dynamic features of the judder (e.g., the magnitude of the forward or rear displacement, the velocity of the forward or rear displacement, etc.) could differ between the two contexts.

Trials from six crickets juddering on the horizontal surface and six from the sloping surface (with the cricket facing downward) were used to evaluate whether there were differences in the dynamic properties of the judders. The angle of maximum deviation from the body-to-ground angle at the start of the judder, the maximum angle, the maximum height above the ground, the maximum forward and maximum rear displacements, and the maximum velocity of the head moving forwards and the tip of the abdomen moving backwards, were all compared for the horizontal and sloping surface conditions. There were no significant differences between conditions for any the mean values of these measures (Table 1).

Given the likelihood that differences in body size could influence dynamic features of movement such as velocity, it is important to note that the body weight of the 12 crickets ranged from 0.67g to 1.05g and that the differences between the crickets from the two conditions (mean \pm *SD* for horizontal: 0.81 ± 0.17 , incline: 0.78 ± 0.10) did not differ significantly ($p > 0.05$). Comparing the dynamic measures (from Table 1) by correlations with body weight, revealed no significant correlations ($p > 0.05$); this suggests that the same basic pattern of forward and backward movement was preserved across crickets of differing body weights. Again, this indicates that despite individual differences in the forces experienced when performing the judders, the crickets could make appropriate compensatory movements to preserve the typical dynamic pattern. Nevertheless, there were large individual differences, with some measures showing stronger variance than others (see coefficients of variation in Table 1). Even so, the inter-individual differences

were larger than the between group differences; this suggests that changing the angle of the substrate did not systematically alter the dynamic features of the judder.

However, there was one significant effect, in that the variation in forward displacement was less when facing downwards on the slope than when horizontal (Table 1). This suggests that there is an increased risk of the cricket losing postural support when juddering. Our observation that when tested on the 45° incline, the crickets lost footing and slid forward in about 20% of cases, supports the view that the crickets' more spread-out posture on the slope as being a compensatory defensive response to the pull of gravity. Clearly, there are limits to how successful these compensatory actions for more extreme disturbances to postural stability.

Although judders meeting the criteria for inclusion while facing upwards were infrequent, those measured fit within the range of variation of those shown in Table 1. Judders occurring while the cricket was facing the slope from the side were also rare, and those that did occur in this orientation could not be analyzed using the Peak Performance system (this is because the system was calibrated for analyzing perpendicular judders). By observing such judders when filmed from above, and using clear, acetate sheets over the video screen and counting the number of frames and then measuring these distances, the results suggested, yet again, that the various dynamic measures fitted within the range of variation shown in Table 1.

Table 1

Dynamic measures of judders that are derived from computerized analyses of digitized sequences. Data are summarized as mean \pm SD, with coefficients of variation given in parentheses.

Measure	Horizontal	Incline	t-test (C-statistic)
Maximum angular change from starting position (degrees)	4.92 \pm 2.42 (49.16%)	4.83 \pm 2.36 (48.81%)	ns (ns)
Maximum height of the body above ground (mm)	9.09 \pm 1.03 (11.35%)	8.73 \pm 1.83 (20.99%)	ns (ns)
Maximum angle from parallel to ground (degrees)	12.75 \pm 1.78 (13.96%)	13.25 \pm 3.47 (26.19%)	ns (ns)
Maximum forward velocity of the head (mm/s)	8.14 \pm 4.27 (52.43%)	12.82 \pm 8.97 (69.94%)	ns (ns)
Maximum rearward velocity of the abdomen (mm/s)	8.97 \pm 9.87 (110.07%)	10.47 \pm 10.07 (96.14%)	ns (ns)
Maximum forward displacement (mm)	7.04 \pm 4.52 (64.23%)	6.64 \pm 2.91 (43.85%)	ns (C = 2.37, p < 0.05)
Maximum backward displacement (mm)	5.66 \pm 1.67 (29.50%)	5.90 \pm 1.95 (33.12%)	ns (ns)

Discussion

As predicted from the cybernetic perspective, certain features of the crickets' judder were found to be invariant. The most striking and apparent invariance was that, irrespective of the slope of the floor, the crickets maintained a parallel body orientation to the surface of the floor. A plausible alternative is that the crickets could have maintained their bodies parallel to gravity, but they did not. A question arising from these data is why the animals maintained this invariant bodily orientation to the substrate. An alternative perspective to the cybernetic one, where this orientation is actively defended, is that there are bodily constraints in moving too far from the parallel orientation. For example, the angular changes between leg segments may preclude such a magnitude of deviation. The variation in bodily orientation that crickets are able to adopt in a variety of naturalistic contexts does not support this possibility (see Figure 2.7 in Alexander, 1961). Of direct relevance to this study is that in some combat situations, such as a maneuver involving a face-to-face orientation with an opponent, a cricket can raise the longitudinal axis of its body so that its anterior part is at 45° relative to the substrate. In another combat situation, a defending cricket can turn to face its opponent with its abdomen; from this position, it can then deliver kicks with its hind limbs. When it does this, the cricket can tilt its body upwards (with its abdomen moving away from the ground) to 30° . These postural orientations are well in excess of the 13° or so of movement around the axis of the vertical plane that is seen in judders.

Even if there were some morphological constraints on how far from the substrate crickets can position their bodies, the fact remains, that to remain on the inclined floor in the bodily orientation that they did, required them to place their limbs in different positions. This variation in posture, and the accompanying shifts in body weight, occurs to prevent the cricket from sliding down the slope. Again, as we predicted from the cybernetic perspective, the variability that we did find occurs in the service of maintaining bodily stability.

Once the cricket is stable on the surface, in the appropriate bodily orientation to the substrate, the dynamic features of the judder are also kept constant. Thus, the rate of the back-and-forth oscillation, the forward and backward displacement, the upward displacement and the velocity of movement, all remain the same, irrespective of the postural adjustments made. In order for these dynamic features of the judder to remain constant, irrespective of the postural adjustments made to counteract the effects of gravity, the crickets would have had to use a different combination of limb and muscle actions. The one difference between judders that occurs when a cricket is facing down an incline versus being on a horizontal substrate is that the degree of variation in moving forward is significantly smaller when on the incline (Table 1). This curtailed forward motion likely reflects restraint in this plane of movement so that the cricket can avoid losing postural stability and sliding downwards. Observation of judders occurring when the crickets are on the steeper slope, support this view, as on the steeper slope, they were more likely were they to lose their postural stability. Thus, the one significant difference in the dynamics of the judder between the sloped and

horizontal conditions seems to represent an adaptive modification for maintaining postural stability. The role of postural tactics in resisting the force of gravity in such situations has been well documented in mammals.

When facing downward on an inclined board, rats will initially push backward against gravity, but then will turn and walk up the slope or jump off onto the ground from one of the sides. Rats rendered cataleptic by haloperidol, a dopamine antagonist, will resist challenges to their bodily stability, but will not walk or run to do so (Teitelbaum, 1982). Consequently, such rats resist sliding forward by pushing backward with their limbs to such an angle that their sliding forward can no longer be prevented (Morrissey, Pellis, Pellis, & Teitelbaum, 1989). However, while haloperidol-treated male rats will push their bodies upward with their hind limbs, females will push upward with their forelimbs. This strategy allows the female to resist sliding at steeper angles (Field, Whishaw, & Pellis, 2000). Animals of differing body proportions (e.g., Gilbert, Bharadia, & Teskey, 2001), or stages of development (e.g., Kreider & Blumberg, 1999), also vary the postural tactics that they use in these situations and so in their ability to resist gravity. That is, different postural strategies exist to compensate for similar destabilizing forces. Thus, the postural variability of the crickets in confronting differing substrates is likely best explained as an adaptive adjustment to challenges to their stability. Only once their posture is stable relative to gravity are they able to execute a judder in which their body weight is shifted relative to their base of support.

Therefore, in the case of the crickets' judder, two constancies are present – there is a fixed orientation to the substrate and a fixed, dynamic pattern in the execution of the back-and-forth movement. To maintain these constancies, the cricket has to make variable limb and body movements, which must also include variable patterns of muscular activation. If only the kinematic pattern of these body segment positions and movements were measured, it could be concluded that this is a highly variable action pattern, best classified as a MAP. However, such a label would fail to note the underlying pattern of *constancy*. Similarly, to label the judder as a FAP would fail to note the underlying pattern of *variability*. Indeed, unless a suitable description was to accompany the label, it would not be known what it is that gives this action pattern its seemingly stereotyped appearance. Neither label, then, does justice to the fundamental question of what is fixed and what is variable in action patterns.

What is in a label?

Labels are used as shorthand descriptors of phenomena, and the explicit and implicit information conveyed by them can influence how studies are interpreted and integrated into the wider research endeavor. Current textbooks on animal behavior, behavioral neurobiology and comparative psychology, adopt one of three options with regard to naming species-typical behavior patterns – they are labeled FAPs (e.g., Carew, 2000), MAPs (e.g. Papini, 2008), or they are discussed without a specific, categorical label being used (e.g., Dugatkin, 2004). In many cases, even if the term FAP is used, it is used to illustrate a particular example, but

then further species-typical behavior patterns are discussed without further reference to their status as FAPs or MAPs (e.g., Alcock, 2005). A search of the primary literature on ISI Web of Knowledge (January 21, 2009) showed that the MAP scored 26 hits (the earliest being 1971 and the latest, 2006), whereas the FAP scored 153 hits (1953-2007) with 143 of these spanning the same time period as the MAP. Perusal of many of these papers indicates that authors use one or the other term synonymously. This is an unfortunate state of affairs for two reasons. First, it becomes difficult to infer what researchers have in mind when they use such terms. Second, both variability and constancy in motor output can have multiple sources and knowing the mechanisms involved in particular cases can be useful to gain a deeper understanding of how the nervous system organizes coherent sequences of movement (e.g., Flash & Hochner, 2005; Hermer-Vazquez, Hermer-Vazquez, & Chapin, 2007; Llinas, 2001). Whatever term is used, it should be the case that a descriptive basis is provided so that the intended meaning of the term used is made explicit. Developing theoretical models that can take into account variant and invariant aspects of behavior from various species and contexts depends on such clarity.

Behavior: Constancy, compensation and noise

Attempts to classify species-typical behavior patterns by fractionating the sources of variation in motor output have shown that a measurement of motor variance can arise from multiple sources. For instance, the variation could arise from variation in the environmental context or from the intrinsic noisiness of the motor action (within and between individuals), so that even when performed in an invariant context, there is a variable motor output (Wainwright, Mehta, & Higham, 2008). Attempts to recreate the actions of living organisms using robots have clearly shown the importance of context and body morphology in shaping the actions performed and dictating the variable output from one situation to the next (e.g., Schank, May, Tran, & Joshi, 2004). We suggest that a cybernetic view of behavior is a good starting point from which to make such distinctions.

The most well developed cybernetic model for explaining behavior is that developed by William Powers called Perceptual Control Theory (PCT) (Powers, 1973). In this theory, behavior is viewed as a means to keep some perception constant. For example, when driving on a road, the car is kept in a constant orientation to the road by lining up the nearest edge of the hood to the centerline on the road. Gusts of wind, the presence of potholes and other obstacles may lead to an infinite variety of hand and arm movements, but these are in the service of moving the steering wheel in a way that minimizes the disturbance of the perception of the hood-centerline relationship. In this perspective, the first task of an analysis is to identify what, despite disturbances, remains constant, and so identify the likely controlled perceptions.

Naturally, given that PCT was developed with humans as the main target, care should be taken in using such cognitively loaded terms as perception for non-human animals. Nonetheless, the general principle underlying PCT can be widely applied, as all that needs to be present is for the organism in question to have the

capacity to stabilize some sensory input. For example, in the judder of crickets, the animals appear to be able to sense their bodies' relationship to the substrate. The level of organization of such sensory comparison needs to be empirically determined and not assumed. For example, in the optokinetic response, animals ranging from flies to mammals stabilize optic flow over their retina by compensatory movements, be they of the eyes, head or body, and this negative feedback mechanism can involve a relatively simple, physiological mechanism (von Holst & Mittelstaedt, 1950). The level of neural processing may be more complex in some organisms. For instance, in mice, it has been shown that the basic capacity to stabilize optic flow depends on subcortical mechanisms, but that increased precision arises from the additional contribution of the visual cortex (Prusky, Alam, & Douglas, 2006). Irrespective of the complexity of the mechanisms involved in stabilizing the sensory input, which in itself is an empirical issue, once the controlled 'perception' or 'variable' is identified, the variation in motor output may be traced to three sources (Cziko, 2000).

First, the reference signal for the controlled variable may have either a narrow or a wide tolerance before compensatory action is taken. For example, if a mammal defends its body temperature so that it is maintained between 36-38°, as opposed to 34-40°, there will be less variation in the measured temperature of the former compared to the latter (Satinoff, 1978). Similarly, for the crickets, if the deviation tolerated for being off parallel with the ground is 1°, rather than 10°, the overall variation in bodily orientation would differ in the two cases, as in the latter, greater deviation would be tolerated before compensatory movements are enacted. Second, how quickly a compensatory action is elicited will depend on how quickly the disturbance to the controlled variable can be detected. For example, during precopulatory encounters, both male jackals and Tasmanian devils will move backward to circle a female. For the males to shift to the next phase of the interaction, the rumps of their partners need to be in close proximity to theirs, but whereas the jackal uses visual cues, the Tasmanian devil uses tactile ones to detect the appropriate position, relative to the female. Consequently, compensatory movements made by male jackals in response to the movements of their females are produced more quickly than the responses made by male Tasmanian devils to their females. This results in more variable patterns of circling in the Tasmanian devils (Golani, 1976). Third, the motor strategies adopted to compensate for disturbances may be more or less effective in protecting the controlled variable. Recall the example discussed above, of rats, when facing downward on a sloping board, bracing against gravity. While both males and females push upward, because the females use their forepaws, rather than like the males that use their hind feet, they are able to defend against a steeper angle before losing their stability (Field et al., 2000).

PCT, then, provides an explicit theory for the organization of behavior patterns, and an explicit set of methodological procedures to follow. First, identify the controlled variable(s), and second, if there is variation, characterize the ways in which that variation may arise. The advantage of this approach is that the study is always anchored by what is maintained as constant, with the prediction that most variance in motor output is likely to arise from compensatory action taken to

ensure that constancy. Given the problem noted in the Introduction, that FAPs and MAPs (or, more neutrally, species-typical actions) are studied in animals from diverse taxa and in diverse contexts (e.g., social, solitary, predatory), the added advantage of the PCT approach is that it can apply equally well to all species and contexts. Application of PCT-based principles reveals how species or context differences are best explained. In this sense, it is irrelevant whether judders by crickets are more or less variable than other FAPs produced by other species, what is relevant is that the PCT approach provides a methodological framework for dissecting what is held constant and what varies.

Interestingly, studies that measure the kinematics (e.g., limb and body positions and movements) of FAPs have been the ones that have highlighted their variability (e.g., Davies, 1978; Stamps & Barlow, 1973; Wiley, 1973), whereas ones that have measured some kinetic aspect of FAP production (e.g., displacement, velocity, but, most often, duration), have highlighted their constancy (e.g., Dane, Wakott, & Drury, 1959; Dixon, Duncan, & Mason, 2008). These current findings on the cricket's judder highlight the fact that, even though variable in some aspects of the kinematics involved, an action pattern can be highly conserved in features of its kinetic performance (e.g., displacement, duration, velocity) as well as its relationship to some feature in the environment (e.g., bodily orientation to the surface). These findings suggest that the kinetic features of motor performance may be more likely candidates than its kinematics as controlled variables.

The cricket's maintenance of a parallel bodily orientation to the substrate matches the standard cybernetic view of PCT, as the animal tracks disturbances and makes appropriate compensatory adjustments to maintain a static controlled variable. That is, the variable movements maintain homeostasis of some sensory input, much like a thermostat turning a furnace on or off to maintain a particular temperature. However, the maintenance of a particular cycle of displacement or velocity by the crickets juddering on different surfaces is better thought of as homeokinetic than homeostatic, as the animal proceeds through a limit cycle of action with specific kinetic properties and does so by making compensating adjustments to its posture to defend that cycle (Golani, 1981). In this study, some evidence is provided that, under some conditions, aspects of the dynamic cycle may be curtailed so as to protect postural stability. In this case, the back and forth movement of the cricket's body axis was constrained to some extent when on the slope, as an apparent adaptive response to maintain postural stability and so reduce the cricket's likelihood of falling. Even so, all other features of the kinetics of the cricket's judder were preserved when on the slope - a constancy achieved by the compensatory limb movements it made to defend its postural stability.

Conclusion

FAPs that occur in one taxon may be more variable than those that occur in another, as may FAPs that occur in different contexts. In the present study, the low variability present may be because the subject species was an arthropod and/or because the judder was a social display. Our point is that such concerns are

premature. Rather, from a cybernetic (PCT) perspective, the first issue should be for one to identify the controlled variable, for only then can one ask whether the tolerated range of variation in that variable is greater in different species or contexts. Once the controlled perceptions are identified, it can be ascertained whether compensatory movements to defend those variables can account for all the behavioral variation present. If not, then species-level differences in sensory or motor capacities need to be taken into account. Such an approach may even be crucial when studying species from a more restricted taxonomic group that are performing FAPs in a similar context.

For example, circling of the female by the male during courtship is common to many water birds (Johnsgard, 1965). But can it be assumed that all cases of circling arise as a display by the male? In Cape Barren geese, a native Australian goose, the male, during courtship, orients to the female's rump and makes bill contact. The circular path that may arise from this does so as a consequence of the male tracking the female's retreating rump as she rotates to evade the contact (Pellis, 1982). In contrast, in the waldrapp, a type of ibis from southern Africa, the male moves in a circular path around a stationary female (Pellis, 1989). In the case of the goose, the magnitude and frequency of circling vary greatly, and indeed, if the female does not rotate, the male does not circle, but may instead zigzag, or even run in straight lines, depending on the evasive maneuvers of the female. For the waldrapp, the circling is a constant feature of courtship interactions, as it does not depend on the female's actions. In the goose, however, the circling arises as a compensatory action to defend the controlled variable (bill-to-rump opposition), and so it is best not classified as a display. In the waldrapp, if circling were a display, that is, a dynamic FAP, then from the cybernetic perspective, it would be predicted that the male would make compensatory movements to preserve its cycle of movement around the female in response to the presence of obstacles. The source of the constancy in circling and the variation in behavior when circling differs dramatically between the two species. A cybernetic perspective can help identify what to compare in such cases.

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