Comparison of the Use of Active Vision for Depth Perception in Three Grasshopper Families (Orthoptera: Caelifera)

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ABSTRACT

Movement behavior immediately before a jump in an experimental arena was investigated for 17 species, representing three central European grasshopper families (Caelifera). It was found that pygmy grasshoppers (Tetrigidae) execute quick forward and backward and occasionally sideways rocking movements, whereas acridids (Acrididae) and catantopids (Catantopidae) execute slow side-to-side movements. All movements are executed without locomotion and are limited to the horizontal plane. Six movement variations were observed for each of the three families; these were the same for the acridids and catantopids. Differences in the frequency of the movement variations and in the velocity and amplitude of the movements indicate species-specific adaptations. Because the movements are translatory and are oriented toward contrast boundaries, they can be regarded as peering motions. In acridids and catantopids, it can be assumed that image displacement is used for the determination of the jump distance. Jumps executed by pygmy grasshoppers were less accurate. Possibly the more irregular rocking movements of these ground-dwelling grasshoppers do not permit such accurate distance estimation as the slower side-to-side movements of the other species, but rather they serve to aid in overall perception of obstacles in the environment, for example. Because pygmy grasshoppers are considered to be more primitive than the other two families, their peering-jump behavior may provide indications concerning the evolution of peering movements. In grasshoppers, it seems that quick rocking movements evolved earlier than slow side-to-side peering movements. It seems plausible that the movements developed from locomotory and compensatory movements preceding jump takeoff.

KEY WORDS

Orthoptera, Caelifera, pygmy grasshoppers, acridids, catantopids

Like other animals, to orient themselves in their environment, insects move so as to obtain the visual information they need from motion-related stimuli. The movement behavior can serve to eliminate or modify interfering stimuli. Many insects generate translational optic flow by means of translatory movements during locomotion. This enables them to determine their distance from surrounding objects, because the velocity of the translational optic flow is inversely proportional to the distance of the relevant object. As insects move past objects in their environment, the retinal image of closer objects moves faster than that of more distant objects. Active vision has been described, for example, for honey bees in flight (Srinivasan et al. 1990) and for fruit flies when walking (Collett 2002). Some insects are capable of using translational optic flow without the aid of locomotion (Kral and Poteser 1997). For example, mantids and locusts (Schistocerca sp.) execute translational, horizontal movements of the head and front part of the body, or of the whole body, before jumping toward an object. Behavioral analyses indicate that while executing the movements, the animals attempt to keep the direction of the line of sight as perpendicular as possible to the direction of movement. This process is aided by visual and mechanosensory information (Shepheard 1974, Collett 1978, Poteser et al. 1998). The resulting translatory retinal image motion assists in providing information concerning the distance of the landing target (Wallace 1959, Sobel 1990, Poteser and Kral 1995).

It is not known whether the ability to use active vision by means of translatory sideways motions is shared by other grasshoppers in addition to locusts. Studies have been done only for the grasshopper Phaulacridium vittatum (Sjöstedt), alpine grasshopper Miramella alpina (Kollar), and two Chorthippus species (Eriksson 1980, Kral 2008a). The few findings that are available give initial indications of the adaptability of the species movement behavior to the habitat and way of life (Kral 2008a). In addition to functional aspects, the question arises as to how movement behavior for the purpose of visual orientation has developed during the course of evolution. Like comparisons of the morphological characteristics of fossil insects with those of primitive and specialized modern descendants, behavioral comparisons also can prove informative. The aim of the present research was to...
investigate these questions. The movement behavior of representative members of primitive and specialized middle European grasshopper families was analyzed systematically with the aid of video technology, under controlled stimulus conditions.

Materials and Methods

Adult grasshoppers (suborder Caelifera) of 17 central European species were studied, representing the Tettigidae and Catantopidae families, and the Acrididae family with its two subfamilies Locustinae and Gomphocerinae (Table 1). Species identification was performed in accordance with body structure characteristics, as described in the key by Bellmann (2006). The experimental animals were collected in the Austrian provinces of Styria, Carinthia, and Burgenland, from April to September, in the years 2006–2008.

The grasshoppers were placed singly on a circular raised platform with a diameter of 5 cm, in the center of a cylindrical arena. The arena had a diameter and height of 70 cm; the distance between the center of the platform and the arena wall was thus 35 cm. On the wall of the arena were four uniformly spaced vertical black bars, separated by white spaces. When viewed from the center of the arena, the black bars each had a horizontal extension of 20° and a vertical extension of 63°, and the white spaces between them each had a horizontal extension of 70°. Movement behavior immediately before a jump was studied for each experimental animal. The number of males and females investigated for each species is given in Table 1. Measured temperatures in the arena were between 24 and 27°C.

The movement behavior was recorded by using a Sony CCD-TR728E (Sony Corporation, Tokyo, Japan) videocamera, positioned on a stand perpendicular to the floor of the arena. A video card (Dazzle, Groveport, OH) was used to import the video recordings from a Hi8 video recorder (Sony Corporation). Redundant sections of the video recordings were removed by means of video processing and analysis software (Pinnacle Data Systems, Groveport, OH), and the remaining video sequences were then analyzed frame by frame. The width of the animal’s head was used as a reference for measuring the amplitude of the movements (in millimeters). The time was determined in milliseconds from the video frames (25 frames per s). A hinged transparent sheet with a calibrated grid was attached to the flat screen of the computer as an aid in measuring. GraphPad Prism, version 4 (San Diego, CA) was used to prepare the movement amplitude–time graphs.

Means ± SD were calculated from the measured data. Chi-square and t-tests were used for the statistical analysis, with the aid of GraphPad Prism, version 4 (San Diego, CA). The significance level was set to α = 5% (P = 0.05).

Results

Family Tettigidae. As soon as pygmy grasshoppers (Table 1) perceived the vertical contrast boundaries on the wall of the arena, indicated by the behavior of stopping suddenly and extending the antennae, they executed rocking movements which were oriented toward the black–white boundary between the relevant black bar and the adjacent white space (Fig. 1). Six movement variations were exhibited: movements to one side (Fig. 2A), to one side and then back to the original position (Fig. 2B), forward (Fig. 2C), forward and then back to the original position (Figs. 1, 2D),

Table 1. Overview of the grasshoppers investigated in this study (Caelifera)

| Family Tettigidae      | Species Description                                                                 | No. of Specimens | Measurements (mm) |
|------------------------|-----------------------------------------------------------------------------------|------------------|-------------------|
| Slender ground hopper, Tetrix subulata (L. 1758), n = 6 | total body length 10-15 mm                                                       | 6                | 10 x 5             |
| Long-horned ground hopper, T. tenuicornis (Sahlberg 1893), n = 2 |                                      | 2                | 12 x 2             |
| Two-spotted ground hopper, T. bipunctata (L. 1758), n = 2 |                                      | 2                | 12 x 2             |
| Family Acrididae       |                                                                                   |                  |                   |
| Subfamily Locustinae   |                                                                                   |                  |                   |
| Blue-winged grasshopper, Oedipoda caerulescens (L. 1758), n = 4 |                                      | 4                | 18 x 24            |
| Large grasshopper, Choristhia dispar (Germar 1834), n = 3 |                                      | 3                | 18 x 25            |
| Duetting grasshopper, Chorthippus biguttalus (L. 1758), n = 4 |                                      | 4                | 16 x 16            |
| Meadow grasshoppers, C. parallelus (Thunberg 1815), n = 5 |                                      | 5                | 15 x 22            |
| Common green grasshopper, Omocestus viridulus (L. 1758), n = 7 |                                      | 7                | 15 x 20            |
| Family Catantopidae    |                                                                                   |                  |                   |
| Alpine grasshopper, Podisma alpina (Kollar 1833), n = 8 |                                      | 8                | 17 x 21            |
| Odontotodidae decipiens (Ramme 1951), n = 1 |                                      | 1                | 18 x 22            |
| Micropodisma salamandra (Fischer 1853), n = 7 |                                      | 7                | 15 x 22            |
| Italian locust, Calliptamus italicus (L. 1758), n = 7 |                                      | 7                | 26 x 30            |

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sideways and forward (compare Fig. 2A and C), and sideways and forward and then back to the original position (compare Fig. 2A and D). These movement sequences were executed once or as many as several times. The six movement variations observed occurred with different frequencies; forward movements (C and D) were executed ≈11 times more frequently than sideways movements (A and B) (Table 2). Sideways rocking movements were performed by bending the front two legs on one side and stretching out the front two legs on the other side of the body. For forward and backward rocking movements, the legs on both sides of the body were bent so as to take advantage of the possible range of motion (Fig. 1).

Approximately three quarters of the jumps executed immediately after the rocking movements failed to reach the jump target, although the distance was clearly within the range of observed jump distances of >60 cm.

Families Catantopidae and Acrididae, with Subfamilies Locustinae and Gomphocerinae. Movement behavior of acridids and catantopids oriented toward a black–white boundary (Table 1) was likewise observed in the experimental arena. The movements of these grasshoppers were not jerky like those of the pygmy grasshoppers; instead, smooth sideways movements were used. During the movements, the animals seemed to move as far as they could to the side without locomotion. To a great extent, the line of sight re-

Table 2. Frequency, in percentage, of different movement variations immediately before a jump

| Family               | (A) Sideways | (B) Sideways and back to original position | (C) Forward | (D) Forward and back to original position | (A+C) Sideways and forward | (A+D) Sideways and forward and back to original position |
|----------------------|--------------|-------------------------------------------|-------------|------------------------------------------|---------------------------|--------------------------------------------------------|
| Tetrigidae (n = 28)  | 3.6          | 3.6                                       | 46.4        | 32.1                                     | 10.7                      | 3.6                                                    |
| Families and subfamilies |             |                                           |             |                                          |                           |                                                        |
| Acrididae (n = 63)   | 19.0         | 34.9                                      | 7.9         | 4.5                                      | 28.6                      | 4.8                                                    |
| Locustinae (n = 17)  | 17.6         | 47.0                                      | 11.8        | 5.9                                      | 11.8                      | 5.9                                                    |
| Gomphocerinae        | 19.6         | 30.4                                      | 6.6         | 4.3                                      | 34.8                      | 4.3                                                    |
| Catantopidae (n = 35)| 8.6          | 51.4                                      | 8.6         | 2.8                                      | 20.0                      | 8.6                                                    |

For significance level, see text.
mained directed forward; this was effected by counter-rotation of the head, as illustrated in Fig. 3.

The movement repertoire was basically the same for the two families. Six movement variations were exhibited: movements to one side (Figs. 4-6A); to one side and then back to the original position (Figs. 4-6B); to one side, then back to the original position, then back to the same side (Figs. 4-6C); to one side, then back to the original position, then to the other side (Figs. 4-6D); to one side, then back to the original position, then to the other side, then back to the original position, then to the other side, then back to the original position (Figs. 4D, five and 6E); and to one side, then back to the original position, then to the other side, then back to the original position, then to one side again (Figs. 4D, five and 6 F). These movement sequences were executed once or as many as several times. As shown in Table 2, here too the movement variations occurred with different frequencies. Movements to one side (A–C) were more frequent than movements to both sides (D–F); the ratio was 1.6:1 for acridids, 2.8:1 for catantopids, 3.2:1 for Locustinae, and 1.3:1 for Gomphocerinae. The differences in these ratios for the two families and two subfamilies were not significant (chi-square test).

As a rule, the jump immediately after the movements resulted in a safe landing on the target object. Of the acridids, only blue-winged grasshoppers jumped too far, when they raised their wings. This also occurred in the case of the catantopid Italian locusts.

The following general remarks can be made concerning the movement amplitude–time graphs in Figs. 2 and 5: In a cumulative presentation of the data, the movement sequences tended to be partially obscured as a result of individual variations in the measured values. Therefore, only data for individual experimental animals are shown, to illustrate typical movement sequences. The average movement velocity exhibited by pygmy grasshoppers was faster than that of the acridids or catantopids ($t$-test; $t = 23.11$; $df = 89$; $P < 0.0001$; $t = 15.21$; $df = 61$; $P < 0.0001$). Of the acridids, the Locustinae moved more slowly than the Gomphocerinae ($t = 5.68$; $df = 61$; $P < 0.0001$). The average amplitude of movements to one side executed by catantopids was larger than that of

![Fig. 3.](image-url) Left, Miramella alpina (♀) fixating the vertical contrast boundary of the target (T). The arrow shows the line of sight. Right, the grasshopper has moved the maximum distance to the left; consequently the retinal image of the target has moved to the right. The new line of sight is ≈2° to the left of the original line of sight (arrow). Counter-rotation of the head serves to keep the line of sight as perpendicular as possible to the direction of movement. Scale bar = 5 mm.

![Fig. 4.](image-url) Series of photographs documenting sideways movements directed toward a vertical contrast boundary immediately before a jump. (A) Sideways movement of Oedipoda caerulescens (♀); (B) movement sideways and back to the original position, executed by Miramella alpina (♀); (C) movement sideways, back to the original position, and then to the same side, executed by Gomphocerippus rufus (♀); and (D) movement sideways, then back to the original position, then to the other side, then back to the original position, then to the other side, then back to the original position, then to the other side, then back to the original position, then to the other side, then back to the original position, then to the other side, executed by Chorthippus brunneus (♀). The movement sequence can be seen from the relative positions of segments of the front two pairs of legs. Scale bar = 5 mm.
pygmy grasshoppers or acridids ($t = 6.08; \text{df} = 61; P < 0.0001$ and $t = 9.68; \text{df} = 96; P < 0.0001$). The data are summarized in Table 3.

**Discussion**

In the current study of the movement behavior of central European adult grasshoppers immediately before a jump, recorded under constant stimulus conditions, it was found that pygmy grasshoppers execute forward and backward, and occasionally sideways rocking movements, whereas acridids and catantopids execute only sideways movements. All of the movements were performed without locomotion and were executed in the horizontal plane. It is noteworthy that the same movement sequence variations were exhibited by both acridids and catantopids. The readily discernible differences in the morphological and biomechanical characteristics of the two families (Bellmann 2006) do not seem to play a role here. The frequency of different movement variations and the velocity and amplitude of the movements can vary, indicating adaptations to the habitat and way of life. Such adaptations have been reported in field studies...
For significance level, see text.

M. alpina

of mantids, and A. alpina and Chorthippus species (Rathet and Hurd 1983, Kral and Devetak 1999, Kral 2008a). Overall, it seems that the movement behavior plays a comparable role in each of the three grasshopper families.

As shown by the video recordings, the movement behavior in all three families is in fact purposeful and target-oriented. The behavior is clearly directed toward visual contrast boundaries in the environment and can thus be referred to as peering behavior. The peering movements bring about motion of the retinal images of the targeted vertical contrast boundaries. In the forward and backward rocking movements, it can be assumed that the pygmy grasshoppers experience contraction and expansion of the retinal image over time (looming). In the sideways movements—to one side in pygmy grasshoppers and to one or both sides in acridids and catantopids—it can be assumed that horizontal translational retinal image displacement is generated. Such image displacement can occur in one direction or in two opposing directions and can take place from once to several times. In pygmy grasshoppers, the change of direction occurs within 40 ms; in the other two families, it is significantly slower. Moreover, the direct connection between the movements and the jump decision indicates the behavioral relevance of the retinal image displacement brought about by the sequence of movements. Findings for desert locusts Schistocerca show that the retinal image displacements generated by sideways movements are a prerequisite for the robust calculation of jump distances. The relationship between image displacement and distance is used: The closer the object, the greater the velocity and amplitude of the retinal image motion (Wallace 1959, Sobel 1990, Kral and Poteser 1997; for praying mantids, see also Poteser and Kral 1995, Poteser et al. 1998). The jump behavior of the acridids and catantopids studied here suggests the operation of a similar mechanism (Kral 2008a, 2008b). Although pygmy grasshoppers have a considerably higher average movement velocity, and hence retinal image motion velocity, than is the case for the acridids and catantopids, the behavioral relevance for the pygmy grasshoppers is less clear. It was found that they miss the vertical jump target more often than they reach it reliably. The question arises as to whether the pygmy grasshoppers could not jump as accurately because their more irregular rocking movements do not permit such accurate distance estimation as the slower side-to-side movements of the other species. However, observation of the jumps also suggested that the pygmy grasshoppers deliberately jumped short of the vertical contrast boundaries that they had fixated precisely before jumping. It is possible that the rocking movements of pygmy grasshoppers are not used for the absolute distance estimation of landing targets, but rather serve to aid in overall perception, for example of obstacles in the environment. Nevertheless, it should be noted that blue-winged grasshoppers and Italian locusts also sometimes exhibited imprecise landings. Possibly, these species are better adapted for landing on horizontal rather than on vertical structures. This seemed to be indicated by the hook landings of the blue-winged grasshoppers (where they turned 90° or more about the vertical axis of the body), which is an adaptation to landing on horizontal surfaces. It should be kept in mind (as also observed in this study) that unlike acridids and catantopids, pygmy grasshoppers cannot hold onto vertical structures, because they lack the attachment pads (arolinium) that are present on the legs of the other grasshoppers (Goodwyn et al. 2006). Pygmy grasshoppers are herpetobionts. They live on the ground rather than on plants, and feed on plant debris, fungus mycelia, lichens, and the like that are found on the ground and on horizontal structures in the environment (Hennig 1969).

This may account for the marked difference in the peering behavior of pygmy grasshoppers and the other grasshoppers. Because pygmy grasshoppers are more primitive than the other two families (Sharov 1968, Hennig 1969, Dirsh 1975), their peering-jump behavior may provide indications concerning the evolution of peering movements. It can be assumed that in the transition to life on plants, initially shrubs and trees, before the appearance of herbaceous vegetation (Hennig 1969), the ancestors of modern grasshoppers were faced with the necessity of performing precise, calculated climbing and jumping. Peering motions could have evolved at this point. As a more primitive group (Sharov 1968, Hennig 1969, Dirsh 1975), pygmy grasshoppers may have retained the earlier form of peering motion, which would indicate that in grasshoppers, quick forward and backward rocking movements evolved earlier than slow side-to-side movements. The rocking movements could have developed from compensatory and locomotory movements associated with aligning the jump takeoff position, for instance, or moving forward for grasping or jumping. The fast, jerky forward and backward rocking movements seem similar to the procedure of preparing for takeoff. However, the video analyses indicate that the rocking movements of the pygmy grasshoppers are in fact distinct from the takeoff, and form an independent sequence of movements. In addition, it should be mentioned that backward and forward movements also have been observed in praying mantids; these are relatively slow rocking movements in comparison with those of pygmy grasshoppers and are executed during walking (Kral 1999). After the conclusion of

Table 3. Movement parameters measured immediately before a jump

| Families and subfamilies | Velocity (mm s⁻¹) | Amplitude (mm) |
|--------------------------|------------------|----------------|
| Tetrigidae               | 20.1 ± 3.3 (n = 28) | 1.6 ± 0.3 (n = 28) |
| Acrididae               | 7.0 ± 2.0 (n = 63)  | 1.4 ± 0.3 (n = 63)  |
| Locustidae              | 5.2 ± 0.4 (n = 17)  | 1.4 ± 0.3 (n = 17)  |
| Gomphocerinae           | 7.5 ± 1.8 (n = 46)  | 1.5 ± 0.3 (n = 46)  |
| Catantopidae            | 8.3 ± 2.8 (n = 35)  | 3.3 ± 1.4 (n = 35)  |

For each family and subfamily, the data for males and females of all species were pooled. Measurement values are given as means ± SD. For significance level, see text.
the rocking movements, the pygmy grasshopper assumes a takeoff position, either raising the front part of its body or turning to view another contrast boundary or to assume a jump position. A comparison with the movement variations exhibited by other Caelifera families is necessary to elucidate the evolution of the movements. In particular, investigations of groups that it was not possible to consider in the current study, including pygmy mole crickets (Tridactylidae), which may share a common ancestor with pygmy grasshoppers (Hennig 1969); spear-headed grasshoppers (Pyrgomorphidae); and toad grasshoppers (Pamphagidae), could prove very helpful.

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