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A novel mechanism for jumping in the Indian ant *Harpegnathos saltator* (Jerdon) (Formicidae, Ponerinae)

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Abstract. The Indian ant *Harpegnathos saltator* may be unique among insects in using its jumping capacity not only as an escape mechanism but also as a normal means of locomotion, and for catching its prey in flight. High-speed cinematography used to analyse the various phases of the jump suggests that *Harpegnathos* employs a novel jumping mechanism to mediate these behaviours: namely the synchronous activation of its middle and hindlegs. Electrophysiological recordings from muscles or nerves in pairs of middle and hindlegs show remarkably synchronous activity during fictive jumping, supporting the synchronous activation hypothesis. *Harpegnathos* is not the only ant to jump, and a cladistic analysis suggests that jumping behaviour evolved independently three times during ant evolutionary history.

Key words. Insect; behaviour; high-speed cinematography; jumping; electrophysiology; evolution.

The ability to jump has been reported for only a very few ant species, and of these, the Indian ant *Harpegnathos saltator* (Jerdon) was probably the first documented case. In fact, on observing it in Malabar, Jerdon[1] called this species 'saltator' 'from its power of making most surprising jumps which it does when alarmed or disturbed'. Since then many observations of this ant jumping have appeared in the literature[2,3], with Wroughton[4] stating that it 'made leaps of a foot or 18 inches with perfect ease, like a grasshopper'. Only a few authors[5,6], however, offer more detailed information, reporting that *Harpegnathos* use their jumping capacity (2 cm high and up to 10 cm long) not only as an escape mechanism but as a normal means of locomotion as well. One particular aspect of the jumps of *Harpegnathos* suggests that this ant may be unique among insects: workers of this ant species regularly hunt living prey by jumping into the air and catching them in flight[7]. These ants exhibit at least two important adaptations to localize and catch fast-moving prey. First, a pair of very elongate, forceps-like mandibles armed with a set of long sensory hairs and minute denticles on their masticatory border (fig. 1). Indeed, Maschwitz et al.[8] report that 'the ants snapped suddenly forwards and grasped [the prey] with their elongated forcepslike mandibles'. Secondly, these ants possess very large eyes with over 1,400 ommatidia, protruding laterally from the head capsule and frontally over the clypeus (fig. 1). The novelty of this jumping behaviour, coupled with the largely anecdotal nature of previous descriptions of the jump of *Harpegnathos*, led us to attempt a more quantitative description under controlled conditions. In this paper we use high-speed cinematography to define and analyse the pre-jump, take-off, flight and landing phases of the jump for the first time. Our results suggest that the ant *Harpegnathos saltator* (Jerdon) uses a mech-

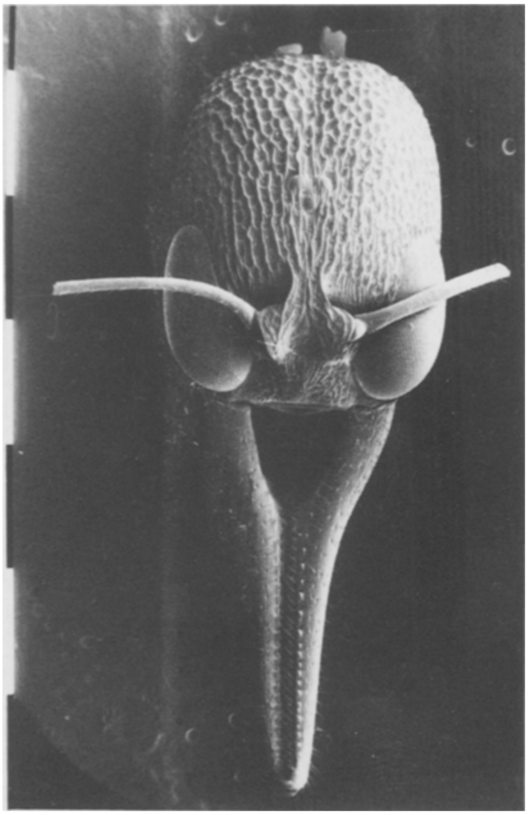

Figure 1. SEM micrograph of the head of a *Harpegnathos saltator* worker showing the large eyes, and the forceps-like mandibles bearing minute denticles and numerous sensory hairs. Scale bars: 1 mm.

anism for jumping novel among insects: namely, that the power for the jump is provided by the middle and hindlegs working in unison, rather than just the hindlegs alone as for example in the flea[9-11] or grasshopper[12-16]. Paired electrophysiological recordings from muscles or nerves in middle and hindlegs in tethered ants during fictive jumping show a remarkable degree of synchronous activity, adding weight to the four-leg hypothesis for production of the jump.

Materials and methods

Biomechanics of jumping. Small colonies of *H. saltator*, each comprising ca. a dozen workers, one queen, and a few larvae, were available for laboratory observations. Under laboratory conditions we seldom observed spontaneous movements of the workers which we could unequivocally define as jumps (see below). However, all workers and the queens in our insectaries regularly exhibited very flat leaps of some 10 cm in length whenever touched or disturbed by an observer.

Ten workers were used for cinematographic recordings of jumps. Escape jumps were induced by lightly touching the posterior tip of the abdomen with a fine paintbrush. A Red Lake Hycam high speed camera operating under artificial lighting was employed for 16 mm cinematography of the jump. After some preliminary trials the camera was adjusted to a speed of 1,000 frames per second (fps), allowing nearly 8 sec of filming at a time. The single frame exposure time at 1,000 fps is 0.4 msec. No worker was allowed to jump more than three times consecutively during a filming session. After three jumps (recorded or missed) an ant was transferred to a second 'resting' vial in order to recover from stress. In this way, all ants in turn were induced to jump several times without having to remove them from the original terrarium. All cinematographic recordings were performed at an air temperature around 26 °C.

The shapes of the jump trajectories, as well as the different postures of some body parts during different jump phases were analysed by conventional measurements with the ants viewed from the side on the glass screen of a Minette Sixteen viewer editor. This allowed measurements of individual photographic frames to a resolution of 1 msec. The body movements involved in jumping were reconstructed from these frames. Acceleration, speed, height, length, and other derived parameters of each jump were calculated by marking three fixed reference points on the ant's body. They were: A) the anterior border of the clypeus, B) the posterior tip of the gaster, and C) the centre of gravity. The latter had been previously determined using dead individuals and was based on the practical assumption that the loss of water due to desiccation is approximately the same over the whole body. Individual ants were mounted in the various body postures exhibited during the jump and balanced on the tip of a needle until the body axis attained the same attitude as in the frame to be analysed. Jump trajectories were calculated by applying simple vector analysis to the three reference points on each fourth photographic frame (time interval 4 msec). This allowed all the essential physical parameters for reconstruction of the jump to be evaluated.

Clearly not all the films we made were equally suitable for quantitative analysis. If, for example, the direction of the jump was not perfectly orthogonal to the axis of camera, then perspective effects made the distances covered by the animal appear shorter. The coordinates of such 'distorted jumps' were corrected by applying a cosine function which varied with the angle of deviation from the orthogonal plane (with $\cos 0° = 1$). On other occasions the ant landed off screen, or we commenced filming too early or too late. All together, three complete jumps, six starts (each including more than a half of the remaining jump), and two landings were considered sufficiently reliable for a full analysis. They constitute the basis for the reconstruction of the jump under laboratory conditions presented below.

Electrophysiological activity in leg nerves and muscles during jumping. Experiments were undertaken in an attempt to correlate nerve and muscle activity in the legs with jumping behaviour. Worker ants were first mounted by the dorsal surface onto a small wooden block using low melting point wax. Paired fine copper wires (25 μm diameter) insulated except for the tip were inserted through small holes made in the cuticle of either the femur or tibia of the second and third pairs of legs – the legs shown from the behavioural experiments to be involved in the jump. These wires recorded activity in either a leg muscle or in the main leg nerve depending on their placement within the leg. The exact identity of the muscle being recorded from within a leg segment was not determined. Wires were secured in position with low melting point wax.

Recordings were made from pairs of legs on either the same or opposite sides of the body to compare the timing of activity in the nerves or muscles of these legs during jumping. Ants mounted in the position described above and with recording wires in place were able to move all their legs freely and did so in response to visual or mechanical stimulation. Ants were induced to simulate escape jumps most readily by lightly stimulating the abdomen with soft entomological forceps. The leg movements elicited in this way comprised a mixture of struggles interspersed with coordinated actions which resembled those observed during actual jumping. It is these latter movements that are analysed in the physiological section of this paper.

Recording wires carrying muscle or nerve potentials were connected to a differential amplifier, the amplified potentials were then displayed on an oscilloscope, and recorded on magnetic tape for latter analysis. Recordings were replayed from tape onto a chart recorder for analysis (see 'Results'). All experiments were performed on a vibration-free table situated within a Faraday cage, and at normal laboratory temperature.

Results

Description of the jumping mechanics. Observations of freely moving *Harpegnathos* exploring or foraging in the arena revealed that the ants frequently jumped without apparently needing to escape from anything. In such cases, another behaviour was often temporally correlated with the actual jump, and often immediately preceding it. The ants, standing on all six legs, vibrated the gaster in a series of short, rapid, lateral oscillatory movements for about 1 sec. This behaviour, which we never observed when artificially releasing the jumps by mechanical stimulation, very often preceding spontaneous jumps. This same behaviour, however, has also been observed among solitary exploring ants and among alarmed individuals in the nest, but without necessarily being followed by the actual jump. We tentatively interpret this behaviour as a preparatory manoeuvre in which the insect assesses the load distribution across its legs in case a jump proves necessary.

Jump description. Tracings obtained from the analysis of the films allowed the reconstruction of a typical *Harpegnathos* jump. We have divided the time course of the jump into four phases as follows (see also fig. 2).

– Pre-jump phase. This is characterized by the ant flexing the femoro-tibial joints of mid- and hindlegs and raising the anterior part of the body, thereby increasing the angle between the longitudinal body axis and the substrate. In this way the centre of gravity of the body is moved posteriorly towards the coxae of the hindlegs, resulting in reduced torque at take-off. The average take-off angle of *Harpegnathos* workers in our films was 13.6° (n = 9). Unlike in other jumping insects, neither hind- nor mid-legs are completely flexed prior to these induced (= escape) jumps. Femora and tibiae are brought close to each other at an angle of about 90°. The assumption of the take-off body posture (phase A, fig. 2) is completed at least 4 msec before the jump forces are released and the second phase begins.

– Take-off phase. Within the space of 1 msec (the maximum resolving power of our films) the femorotibial joints on the second and third pair of legs synchronously straighten, thereby extending the tibiae. This generates an acceleration propelling the ant upwards and forwards. The trajectories observed in our films showed various angles between 21° and 42° (n = 9) with respect to the substrate. The duration of the take-off phase in our observations was always around 20 msec (table).

– Flight phase. At the end of the take-off phase the second and third pairs of legs are raised and moved forwards so that the mid- and hindlegs are level with the body's horizontal plane and at 90° to the longitudinal body axis. This change of posture essentially shifts the centre of gravity anteriorly, and this new mid- and hindleg position is maintained throughout the flight phase. The first pair of legs, by contrast, remains partly stretched and directed slightly forwards throughout phases A, B, and C as in the pre-jumping posture. In our experiments the flight phase usually lasted some 40 msec (table). The end of this phase is marked by the maximum lateral stretch of the mid- and hindlegs. Complete assumption of this body posture coincides with the end of the flight phase and with the beginning of the descending phase of the flight trajectory (landing phase).

– Landing phase. The changed position of the mid- and hindlegs during the flight phase is followed by a stretching of the forelegs on commencement of the landing phase. The body axis assumed by ants during the landing phase was very variable compared with the stereotyped position during the three earlier phases. Rotational forces that sometimes acted on the longitudinal and vertical body axes during the flight phase were not corrected for, leading an occasion to totally uncontrolled landings. Ants often landed with the body assuming very different positions, including first contacts with the ground by the tip of the sting or the thoracic or abdominal terga. It is clear that in these cases the ants had lost all manner of steering control during flight and we are inclined to attribute this to stress imposed by our experimental conditions. Such controlled jumps

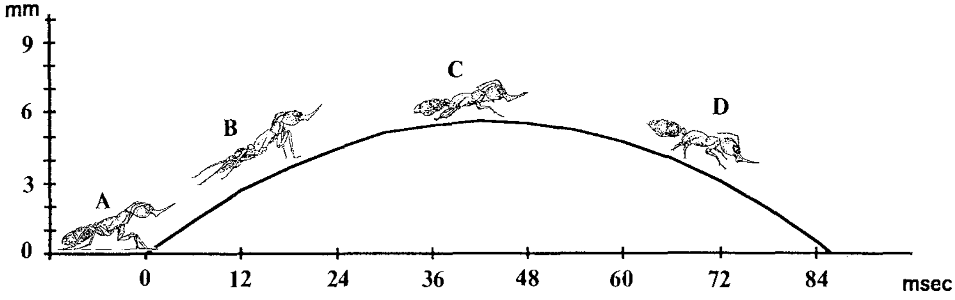

Figure 2. Schematic representation of a *Harpegnathos* jump with the body postures assumed by a jumping worker in the four phases of the jump: A, pre-jump; B, take-off; C, flight; D, landing.

Velocities recorded at different time intervals after take-off in 3 fully recorded jumps together with their mean values and mean acceleration

Time (cumulative) msec	Velocity jump 1 m/s	Velocity jump 2 m/s	Velocity jump 3 m/s	Mean velocity m/s	Mean acceleration m/s^2	Average acceleration m/s^2
0	0	0	0	0	0	0
Take-off phase						
4	0.25	0.48	0.28	0.337	84.25	30.43
8	0.4	0.34	0.38	0.373	9	
12	0.54	0.44	0.62	0.533	10	
16	0.58	0.69	0.55	0.607	18.5	
Flight phase						
20	0.62	0.65	0.58	0.617	2.5	1.56
24	0.48	0.49	0.59	0.52	−24.25	
28	0.58	0.58	0.57	0.577	14.25	
32	0.51	0.45	0.49	0.483	−23.5	
36	0.53	0.61	0.49	0.543	15	
40	0.61	0.54	0.63	0.593	12.5	
44	0.63	0.5	0.5	0.543	−12.5	
48	0.78	0.44	0.47	0.563	5	
52	0.66	0.5	0.47	0.543	−5	
56	0.69	0.51	0.55	0.583	10	
60	0.86	0.52	0.57	0.65	16.75	
64	0.46	0.7	0.59	0.583	−16.75	
68	0.63	0.97	0.47	0.69	26.75	
Landing phase						
72	0.57	1.21	0.53	0.77	20	−0.15
76	0.64	0.46	0.49	0.53	−35	
80	0.67	0.67	0.5	0.613	20.75	
84	0.34	0.51	0.26	0.37	−60.75	
88	0.3	0.62	0.64	0.587	54.25	

were not used for quantitative analyses or reconstructions. Two filmed landings appeared much more natural, although only in one had we the actual impact of the ant on the ground entirely in the field. In both these landings the ants stretched the forelegs at 90° to the longitudinal body axis before impacting with the ground. In the only complete sequence we obtained, the ant performed a true 'splash down' on its mandibles, which, given their elongate shape, allowed a perfect 'skate' on the wooden substrate we used for filming. The observed trajectory of three completely analyzable jumps is described in figure 2.

Quantitative parameters of the jump. In our observations the velocity during the ballistic part of the jump following take-off varied between 0.44 and 0.54 m sec^{-1}. An average velocity of 0.49 m sec^{-1} was used in the course of the following calculations.

The acceleration can be deduced from the formula

$$v = at \qquad (1)$$

where, v is the velocity, a the acceleration, and t the time from take-off. The maximum acceleration was always reached during the first 4 msec of recording (corresponding to frames 1 and 2) with a peak of 102 m sec^{-2}, corresponding to 10.4 g (g = acceleration due to gravity). The mean observed acceleration in 9 jumps is 77.75 m sec^{-2}, corresponding to 7.93 g. The fresh weight of our ants did not vary significantly from 32 mg (n = 5). Knowing the body mass and the velocity, one can then estimate the energy released at take-off from

$$E = 0.5\ m\ v^{-2} \qquad (2)$$

where E is the energy, m the mass, and v the velocity. This, in our case, gives

$$E = 0.5 \times 32 \times 10^{-6}\ kg \times 0.49\ m\ sec^{-1} = 7.84 \times 10^{-6}\ J = 78.4\ erg.$$

The trajectory of the jumps we recorded (fig. 3) fits the curve obtained from the equation for an oblique throw in air-free space very well:

$$y = \frac{x\tan(z) - (gx^2)}{2v^2(\cos(z))^2} \qquad (3)$$

where x and y are the positions along the abscissa and the ordinate respectively, z is the starting angle, v the velocity, and g the acceleration due to gravity (fig. 4). As the jump is not performed in air-free space, then apart from the intrinsic kinetic forces of the jump, two additional forces act on the ant during flight: a) a drag force opposing the velocity vector, and b) a lift force resulting from aerodynamic lift, and opposing the drag vector. A detailed analysis of these two forces (beyond the scope of this paper) would be necessary in order to determine if their equal but opposite magnitudes cancel out and so cause the observed trajectories to fit the theoretical equation so well.

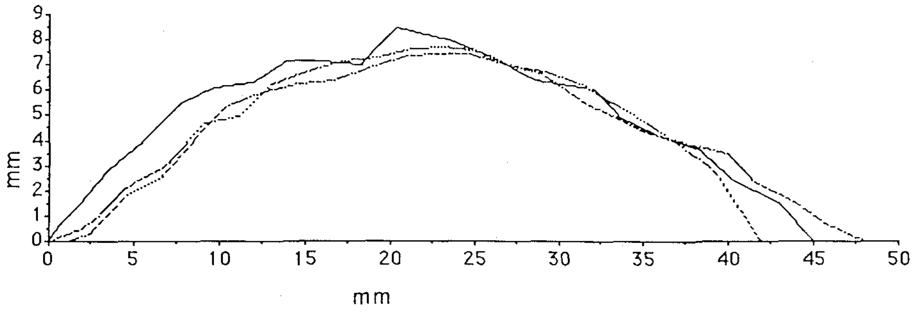

Figure 3. Schematic trajectories of three observed jumps reconstructed from high-speed cinematography. Irregularities in the trajectories represent errors in normalizing the angle between the jump trajectory and the filming plane (see 'Materials and methods'). Both axes, jump height and length, are in millimetres.

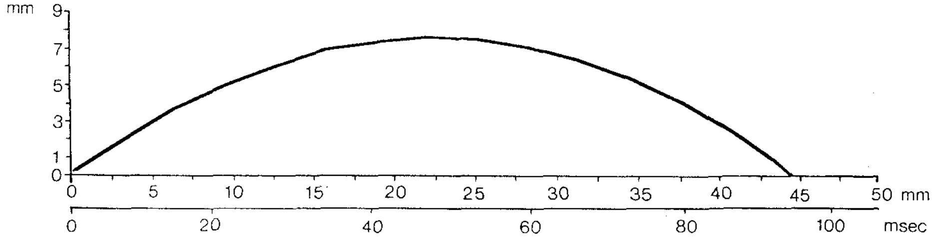

Figure 4. Theoretical trajectory of the jump of a *Harpegnathos* worker calculated from text equation 3.

The length of the jump was measured precisely only for the three jumps for which we have complete cinematographic recordings. They measured respectively 40, 45, and 66 mm. The take-off angle alone accounts for the differences in length of these three jumps. The other jumps for which we were able to record only parts of the trajectory also lay within this range. The much longer and higher jumps occurring under natural conditions were not available for analysis but we nonetheless made an estimate of the velocity necessary to accomplish a jump of over 40 cm using the formula

$$w = \frac{v^2}{g \sin(2z)} \qquad (4)$$

Assuming air-free space (i.e. no drag), and an optimal take-off angle of 45°, a minimum velocity of 1.98 m sec^{-1} is required to cover a 0.4 m distance. This is a velocity nearly four times greater than the maximum we observed in our experiments.

In terms of energy requirements, assuming the same take-off angle of 45° and a jump distance of 0.4 m, then the minimum necessary energy for such a jump is

$$E_{min} = 1/2 \text{ m } v_{min}^2 = 1/2 \text{ } 32 \text{ mg } (1.98)^2 \text{ m/s}$$

$$= 6.28 \times 10^{-5} \text{ J} = 628 \text{ erg.}$$

Physiology of the jump. Electrophysiological recordings from leg muscles generally revealed a large amount of ongoing activity as the ant moved its legs while mounted for the experiments. This activity increased in response to mechanical stimulation of the abdomen, and on occasion we recorded bursts of large action potentials in quick succession, associated with rapid extension of the leg being recorded. The group of action potentials shown (fig. 5A) consists of short bursts (2–3 msec duration) separated from one another by a longer interval (mean duration 218 msec). Simultaneous recordings from a leg muscle in the tibia of the left middle leg, and the femur of the right hindleg (ant viewed ventrally), show that this activity is remarkably synchronous, despite being recorded from different legs (fig. 5A). The data suggest that the functionally equivalent muscle was being recorded from in each leg. Visual observation confirmed that the muscle activity was accompanied by rapid extension movements of the legs. Comparison of the time course of activity recorded in the leg muscles with the temporal sequence of an actual jump recorded by high-speed cinematography (fig. 2), suggests that each burst in the sequence of action potentials in the muscle might correspond to an individual jump.

Activity recorded in the main leg nerves of ipsilateral middle and hind legs following abdominal stimulation is shown in figure 5B. There is an initial burst of activity followed by an interval (228 msec), and finally a large maintained burst comprising the activity of a number of units. The records from the two legs, this time on the same side of the body, again exhibit a remarkable degree of synchrony.

The eyes. As an indication of the relative size of the eye of *Harpegnathos saltator* we undertook an ommatidia count of one randomly chosen worker (fig. 1). We counted a total of 1435 ommatidia in one eye alone. We

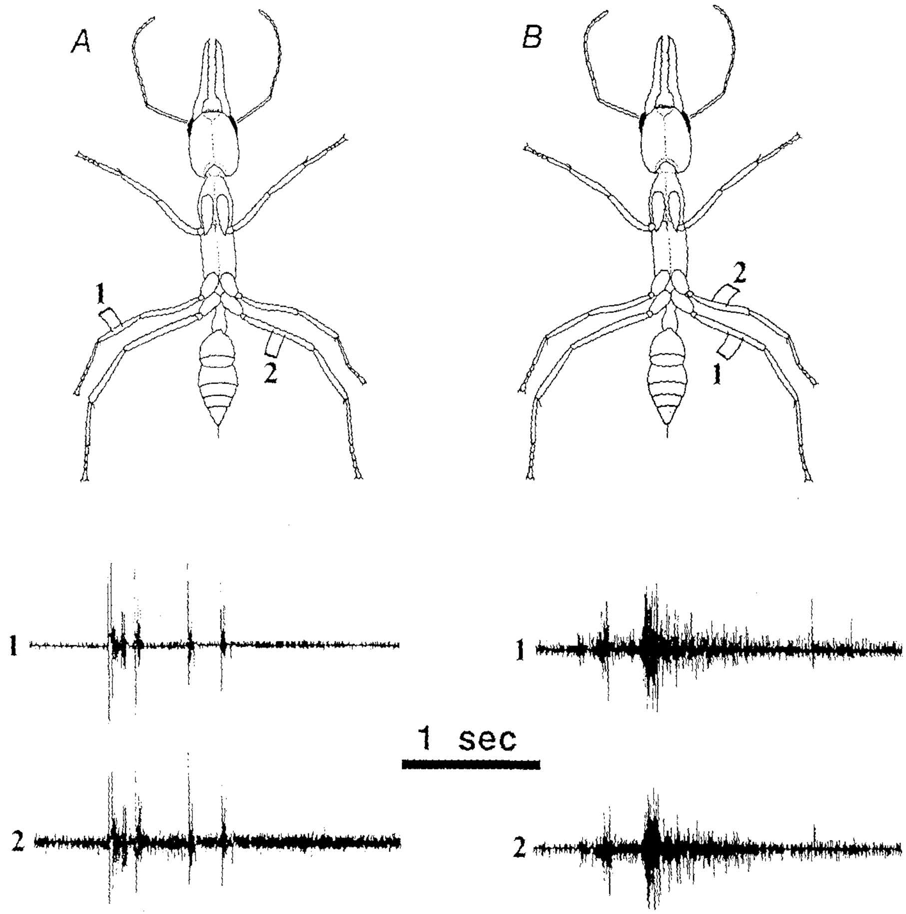

Figure 5. Recordings from nerves or muscles of pairs of legs on either the same or opposite sides of the ant body to compare the timing of activity during fictive jumping. *A* Simultaneous electrophysiological recordings from a leg muscle in the tibia of the left middle leg, and the femur of the right hindleg (ant shown schematically in ventral view). Note remarkable synchrony of activity in each trace despite being recorded from different legs. The muscle activity was accompanied by rapid extension movements of the legs. Comparison of the time course of activity recorded in the leg muscles with the temporal sequence of an actual jump recorded by high-speed cinematography (fig. 2), suggests that each burst in the sequence of action potentials in the muscle might correspond to an individual jump. *B* Activity recorded in the main leg nerves of ipsilateral mid- and hindlegs following abdominal stimulation. The initial burst of activity is followed by an interval (228 msec) and finally a large maintained burst comprising the activity of a number of units. The records from the two legs, this time on the same side of the body, again exhibit a remarkable degree of synchrony.

then performed a preliminary analysis of the visual field of the ant by tracing the horizontal projection of the visual axes of ommatidia from various regions of both eyes in space. The results (not shown) indicate that the maximum binocular overlap is centred symmetrically about the extension of the body axis through the mandibles.

Discussion

The jump of the ant *Harpegnathos saltator* (Jerdon) has been described in a more or less anecdotal way over many years[1-6,8,17-20]. Only recently, however, more accurate and quantitative descriptions of the jumping behaviour of this species have appeared in print[7]. In this paper we show that the jump of the ant *Harpegnathos saltator* (Jerdon) exhibits some characteristics that appear to be novel for insects: namely, that the ant generates the power for its parabolic jump by using its mid- and hindlegs in unison (fig. 2) rather than its hindlegs alone as is the case for the flea[9-11] or grasshopper[12-16]. The myrmecological literature reveals that a number of ant species are reported to jump. Wheeler[19] reviews them in detail and proposes a functional classification, dividing them into two groups: the 'retrosalient' and the 'prosalient', according to their capacity for jumping only backwards or forwards, respectively. The retrosalient jumpers are the best known and essentially include members of the ponerine tribe Odontomachini and of the myrmicine tribe Dacetini. All these ants share bizarre elongated mandibles often coupled with specially adapted 'trigger hairs'. When alarmed they open their mandibles to 180° or more, and contact between the trigger hairs and an obstacle then releases a sudden closing of the mandibles which is accompanied by a characteristic audible 'click'. If the obstacle is big and/or hard, then the closing action automatically propels the ant backwards. This escape mechanism is likely to be merely a consequence of the particular hunting behaviour exhibited by these ants[20].

The jump

– Energetics. Members of the genus *Harpegnathos* (two south Asian species are described in this genus) belong to the group of forward-leaping (prosalient) ants[7], even though their legs are shorter and even thinner than those of other, comparable, non-jumping ants[19]. Only the following prosalient ants are known: 1) both species described in the Asian genus *Harpegnathos* belonging to the subfamily Ponerinae which contains a few thousand species world-wide, 2) the single species of the Neotropical genus *Gigantiops* belonging to the subfamily Formicinae, equally world-distributed with some thousands of species, and 3) an imprecise (high) proportion of species of *Myrmecia*, a genus which, with 89 Australian species, constitutes the sole living representative of the subfamily Myrmeciinae. There is at least anecdotal and presumptive evidence[7,21–23] that all these ants share the behaviour of jumping at some distance towards flying or fast running prey.

We recently published a set of observations on the jumping behaviour of this species under natural conditions[7]. Since the longest jump we observed under laboratory conditions occupied ca. 0.1 sec (fig. 2) then it is clear that the previous field descriptions (literature cited above), made without special equipment, rely to a considerable extent on deduction rather than on measurable observations. Indeed, the distances covered by the *Harpegnathos* jumps are relatively short (<21 cm, ref. 7) and those measured during the present laboratory study by high speed cinematography are even shorter (<7 cm). Our data suggest that energy constraints may severely limit the distance jumped. Equation 4 shows that the energy requirement for a hypothetical jump of 40 cm is considerable (628 erg), indicating that the much longer jumps reported in some earlier literature are very likely to have been overestimates. Our data for the various phases of the jump of *Harpegnathos* (table) appear to suggest that the ant may in fact be accelerating during the flight phase. This is unlikely and these figures are probably due to statistical noise resulting from the few observations contributing to our mean ($n = 3$). In fact, 5-point smoothing of the same data (not shown) reveals a slow deceleration throughout the airborne phase of the trajectory.

The ca. 78 erg of energy released at take-off (eq. 2) produces a take-off acceleration of 7.95 g in *Harpegnathos*, with instantaneous peaks of over 10.2 g. These values are in the range of the acceleration achieved by the locust (0.35 g[25], or ca. 18 g[13,27]) but are quite modest in comparison with the values recorded from other insects such as the flea (135 g[9]; 140 g[11]) or click beetle (ca. 400 g[26]). Insects with such extraordinary accelerations have been shown to possess biomechanical adaptations (click or catch mechanisms) which store energy in highly elastic elements prior to the jump[9–11,26]. Our results do not reveal the exact mechanism employed, but we tentatively interpret the relatively low acceleration achieved by *Harpegnathos* compared with the flea and the click beetle as an indication that, like the locust, the production of power for the jump involves a considerable muscular contribution (the muscles of the mid- and hindlegs), and a lesser reliance on cuticular biomechanics, than is the case in the flea or click beetle.

– Physiology. The short distance covered during a jump is consistent with the relatively low take-off acceleration we measured (see above), and may be explained, at least in part, by the ant's novel mechanism for jumping: namely, using two pairs of legs (mid- and hindlegs) in synchrony rather than relying on only the hindlegs, and/or energy-storage mechanisms, to generate the power for the jump. Our hypothesis that the synchrony of leg movements evident in our cinematographic data is the basis of this jumping mechanism is supported by electrophysiological recordings from either leg muscles (fig. 5A) or nerves (fig. 5B). Our aims for the physiological recordings were very modest. We hoped first to elicit leg movements that broadly resembled those involved in the jump. This seems to have occurred on several occasions amongst many other random and struggling movements. Secondly, we hoped that by recording simultaneously from muscles of various legs we could establish whether there was any synchronous activity during the evoked movements. The presence of such activity would support the hypothesis originating from behavioural observations that jumps are the product of synchronous activation of the mid- and hindlegs. The physiological records do display several features that suggest to us they represent at least part of the motor programme for the jump. First, the muscle potentials occur in discrete bursts. The bursts were observed to be associated with rapid, repeated, extensions of the leg. Behavioural observations shown the jumps to be rapid extensions of the tibial/femoral joint, as is the case in the grasshopper[12,14–16,28]. Secondly, simultaneous recordings from meso- and metathoracic legs known to be involved in the jump show that activity in the tibia and femur muscles is synchronous and remarkably similar (fig. 5A). Clearly our recording situation was artificial because no load was placed on the legs, and the animal could 'jump' several times in succession, something not performed in reality. This lack of load is also likely to have influenced various parts of the motor programme, for instance those elements dependent on afferent input for their timing and expression. While our physiological data do not exclude the possibility that the jump energy is stored before take-off[13], the remarkable degree of synchrony between muscle activity in mid- and hindlegs (even on opposite sides of the body) during fictive jumps (fig. 5) suggests an important role for the coordinated extension of four legs in the jump. If our hypothesis is correct, then to the best of our knowledge, the jump mechanism in *Harpegnathos saltator* appears to be unique among insects.

– Behaviour. Jumps of *Harpegnathos* may be unique among insects for another important trait: workers of this ant regularly hunt living prey by jumping up and catching them in flight[7]. We speculate that the jumping behaviour we described for *Harpegnathos* is an adaptation to accomplish this performance. Two further features could be important adaptations to localize and catch fast-moving prey. First, these ants exhibit a pair of very elongate, forceps-like mandibles armed with a long set of sensory hairs and minute denticles on their masticatory border (fig. 1). Secondly, *Harpegnathos* possess large eyes protruding laterally from the head capsule and frontally over the clypeus (fig. 1). Indeed, our ommatidia count (1435) is to the best of our knowledge the highest number of ommatidia reported for ants to date. Most ants are reported to have only around 750 or less ommatidia per eye[29,30] and the next highest ommatidia count in the literature stems from the desert ant *Cataglyphis bicolor*, with 600–1273 ommatida depending on body size[31]. This ant relies exclusively on visual acuity for its orientation, suggesting that the much larger eyes of *Harpegnathos* may provide a good optical substrate for its hunting behaviour. Our preliminary analysis of the visual field indicates that the maximum binocular overlap is centred on the mandibles. However some caution is necessary when interpreting the role of stereoscopic vision in prey-catching behaviour, since an analysis of visually mediated snapping in the bulldog ant *Myrmecia gulosa* indicates that although there is a large binocular overlap (60°), this ant cannot judge absolute distances and so does not discriminate targets of different size[24].

Other adaptations to preying by jumping, like specialized hind legs, as described in *Gigantiops* and *Myrmecia*[20] but absent in *Harpegnathos*, synchronous triggering of mid- and hind-legs (as described in this paper for *Harpegnathos* but unknown in other ants), and specialized, elongate mandibles (present in *Harpegnathos* and *Myrmecia*, but absent in *Gigantiops*) represent secondary 'improvements' of a primitively rewarding mechanism. To this extent, then, the presence of different mandibular morphologies and jump mechanisms among these taxa could have been predicted on the basis of their phylogenetic distance.

Evolution of jumping behaviour. Ants are currently assumed to have evolved from a vespoid ancestor with well developed eyes; reduction or loss of the eyes is assumed to be a secondary adaptation of several specialized ant

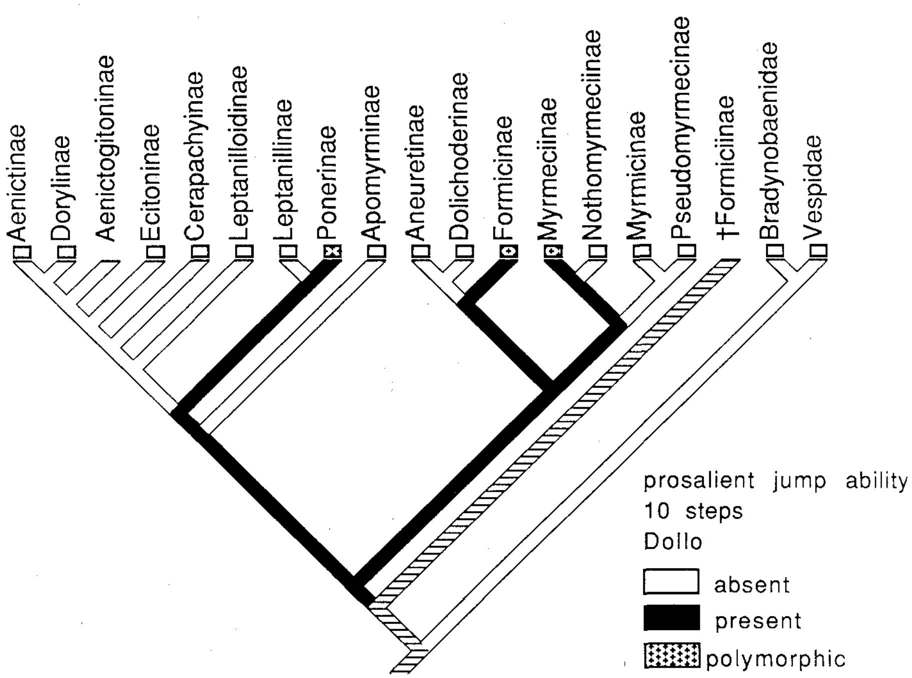

Figure 6. Cladistic representation showing the most parsimonious evolution of ants' jumping behaviour. In this figure behavioural inheritance by common ancestry is tested. Acceptance of this hypothesis implies a minimum of at least 10 independent losses of jumping to account for the presence of non-jumping ants. Convergent acquisition of jumping, on the other hand, needs only 3 evolutionary steps and hence is favoured in this paper. For further explanations see text. Character optimization, tracing, and graphic display by MacClade 3.1[34].

taxa[32]. Given that the ancestral ant is likely to have possessed large eyes[31], one possible hypothesis for the acquisition of jumping is that the first wingless worker ants jumped at their prey as a substitute for the loss of flight ability. This jumping mechanism could then have been lost secondarily in different taxa as a result of adaptation to honeydew feeding and/or to the convergent or parallel acquisition of various behavioural mechanisms for the recruitment of nestmates to large food sources[32]. To explore the hypothesis that jumping may be a primitive character present in the ant ancestor, the capacity of various ants to jump was traced using the latest ant phylogeny[33] and shown in figure 5. If we assume the 'Dollo' evolutionary model in which a character state can originate only once and parallel gains of the derived condition are not allowed[34], the model predicts that a minimum of 10 independent evolutionary steps are necessary to explain the retention of jumping via homologous evolution in the three unrelated ants species, and consequently its secondary loss in the remaining ant clades (see fig. 6). Both the 'ordered' and 'irreversible' character evolutionary models[34], by contrast, predict that only three evolutionary steps are necessary for the acquisition of jumping via a convergent or parallel mechanism. We therefore favour the latter explanation of an independent acquisition of jumping ability in the three subfamilies Ponerinae, Formicinae and Myrmeciinae.

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