16 genes by positional approaches was reported (*20*). Retrospective analysis shows that 44% (7 out of 16) of these genes had already been isolated as ESTs and mapped at the time of their cloning. This fraction increases to 69% (11 out of 16) when the data from the current map are considered.

Comparative analysis has a long and fruitful history in biology, and detailed comparative maps of mammalian genomes have shed light on chromosome evolution. The identification and cross-referencing of genes allow insights into similarities and differences of physiology and development as well as candidates for transgenesis and gene knockout experiments. Thus, it was of interest to determine the extent to which genes on the current human map could be related to orthologous genes in other mammals. Makalowski and Boguski (*21*) have assembled a set of 1880 human genes along with their rat or mouse (or both) orthologs. When these genes were analyzed for overlap with the 30,181 mapped human genes in the current study, we found that 70% of these human genes with rodent counterparts are present. This data set therefore provides an excellent index for cross-referencing the human map with emerging gene-based physical maps of the mouse and rat genomes (*22*).

Genome-scale expression monitoring or profiling (*23*), a rapidly expanding area of functional genomics, relies on the availability of large catalogs of cDNA sequences or arrays of clones (or both). The problems posed by sequence redundancy and inaccuracy are as critical for gene expression applications as they have been for transcript mapping. Furthermore, additional problems in these catalogs have become apparent, necessitating the authentication of sequences and clone reagents. Our collection of nearly 42,000 successfully mapped, gene-based STSs, representing ~30,000 unique human transcripts, provides a large, validated set of human sequences that can be used to design gene-specific oligonucleotides or select cDNA-derived polymerase chain reaction products for populating gene expression arrays (or both). Use of this set could lead to a very useful confluence of mapping and expression information for human genes.

We have produced a map containing perhaps half of all human genes. In the future, this map and subsequent versions will ultimately be replaced by the complete sequence of the human genome. Until then, this reference resource should contribute substantially to the advancement of structural and functional genomics, to comparative biology, and to the isolation of human disease genes, particularly those underlying complex traits.

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26 May 1998; accepted 21 August 1998

Ordering of the Numerosities 1 to 9 by Monkeys

Elizabeth M. Brannon and Herbert S. Terrace

A fundamental question in cognitive science is whether animals can represent numerosity (a property of a stimulus that is defined by the number of discriminable elements it contains) and use numerical representations computationally. Here, it was shown that rhesus monkeys represent the numerosity of visual stimuli and detect their ordinal disparity. Two monkeys were first trained to respond to exemplars of the numerosities 1 to 4 in an ascending numerical order (1 → 2 → 3 → 4). As a control for non-numerical cues, exemplars were varied with respect to size, shape, and color. The monkeys were later tested, without reward, on their ability to order stimulus pairs composed of the novel numerosities 5 to 9. Both monkeys responded in an ascending order to the novel numerosities. These results show that rhesus monkeys represent the numerosities 1 to 9 on an ordinal scale.

Many animal taxa can discriminate stimuli differing in numerosity (*1*). The importance of this capacity has evoked considerable controversy. Some have argued that animals have a natural ability to discriminate numerosity (*2, 3*); others maintain that animals attend to numerosity as a "last resort," that is, only if all other bases for discrimination are eliminated (for example, the shape, color, brightness, size, frequency, or duration of a stimulus) (*4*).

To defend either position, it is necessary to show that an animal's behavior is controlled by numerosity rather than by one or more non-numerical features of a test stimulus, such as density, surface area, or duration. This is best accomplished by analyzing the first-trial accuracy of responses to exemplars of the numerosity in question (*5*). Here, we show that monkeys can discriminate exemplars of the numerosities 1 to 4 when non-numerical cues are controlled.

Another important question about the numerical ability of animals is whether they represent ordinal relations among numerosities or, instead, represent each numerosity as a nominal category (*6*). To evaluate knowledge of numerical ordinal relations, we tested monkeys who learned to discriminate the numerosities 1 to 4 on their ability to order pairs of the novel

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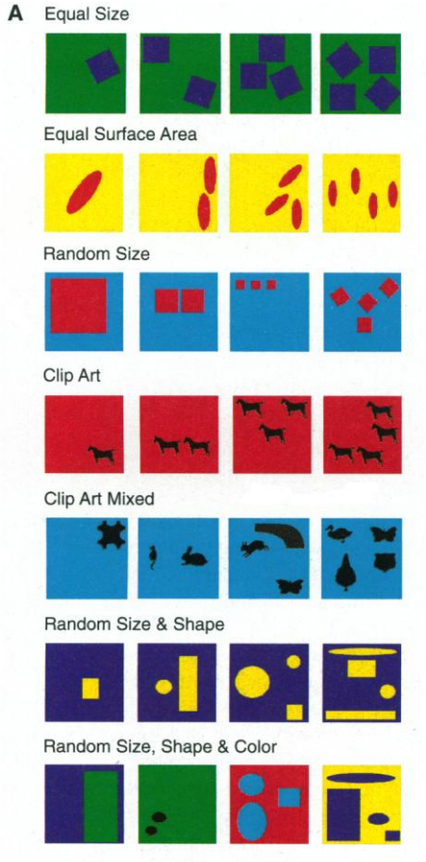

Fig. 1. (**A**) Exemplars of the seven different types of stimulus sets: equal size (elements were of the same size and shape); equal surface area (cumulative area of elements was equal); random size (element size varied randomly across stimuli); clip art (identical nongeometric elements selected from clip art software); clip art mixed (clip art elements of variable shape); random size and shape (elements within a stimulus were varied randomly in size and shape); and random size, shape, and color (same as random size and shape, but with background and foreground colors varied between stimuli). All types were used with equal frequency in both four-item training and four-item testing. (**B**) Examples of stimulus sets used in the pairwise numerosity test. The smaller numerosity had a larger cumulative surface area than the larger numerosity on 50% of all trials, and elements within each stimulus were identical in size, shape, and color.

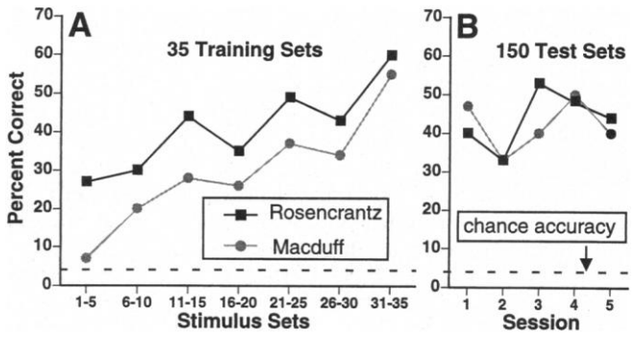

Fig. 2. (**A**) Percentage of correctly completed trials during the first session for each of 35 training stimulus sets in blocks of five sessions. Performance was above chance on the training sets [Rosencrantz, $t(34) = 11.9$, $P < 0.001$; Macduff, $t(34) = 8.8$, $P < 0.001$] and improved across blocks (Rosencrantz, $r^2 = 0.425$, $P < 0.01$; Macduff, $r^2 = 0.63$, $P < 0.01$). (**B**) Percentage of correctly completed trials on the 150 test sets. Performance exceeded chance levels [Rosencrantz, $t(4) = 12.7$, $P < 0.001$; Macduff, $t(4) = 12.8$, $P < 0.001$]. There was no decrement in performance from the last five training blocks to the five transfer sessions [Rosencrantz, $t(4) = -0.69$, $P > 0.5$; Macduff, $t(4) = -1.0$, $P > 0.36$]. The percentage of correctly completed trials varied across stimulus types (equal size, 60%; equal surface area, 57%; random size, 36%; clip art, 42%; clip art mixed, 42%; random size and shape, 32%; random size, shape, and color, 24%.).

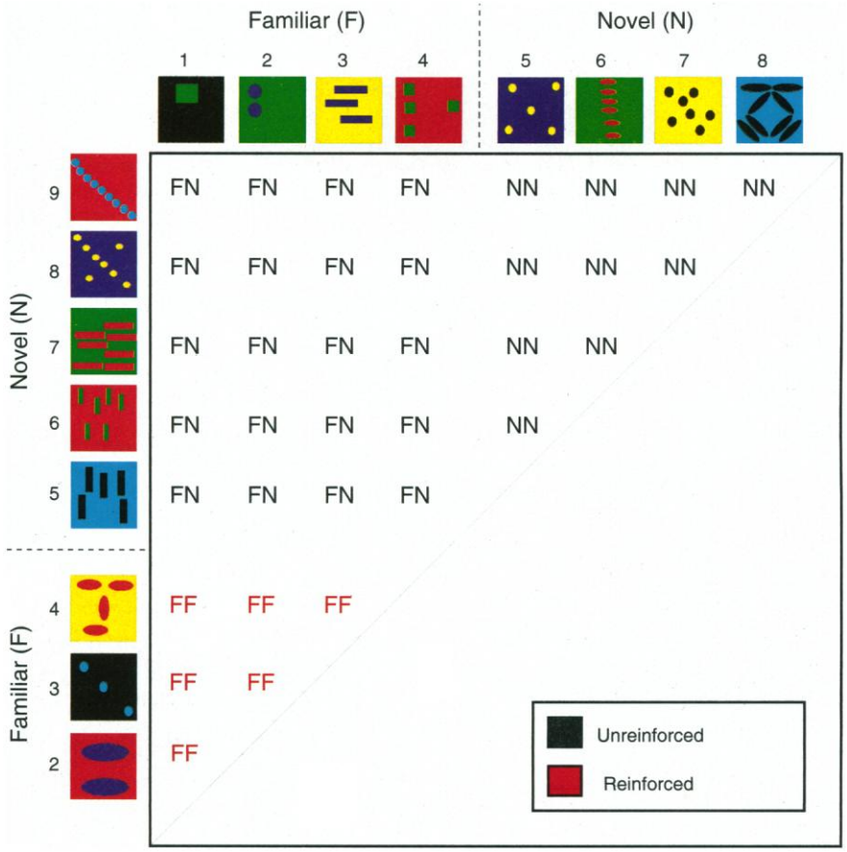

Fig. 3. The 36 pairs of the numerosities 1 to 9 used in the pairwise test. These are segregated into three types that were defined with respect to the subjects' prior experience with the constituent numerosities: familiar-familiar (FF), familiar-novel (FN), or novel-novel (NN).

numerosities 5 to 9.

The subjects were two rhesus monkeys, Rosencrantz and Macduff. They were first trained to order exemplars of the numerosities 1 to 4 (*7*). Four exemplars, one of each numerosity, were displayed simultaneously on a touch-sensitive video monitor. The configuration of the exemplars was varied randomly between trials (*8*). The subjects' task was to respond to each exemplar in an ascending numerical order. Subjects had to learn the required sequence by trial and error by remembering the consequences of their responses to each stimulus. Any error ended the trial, correct responses produced brief auditory and visual feedback, and food reinforcement was given only after a correct response to the last stimulus. The same stimulus set was presented on each trial for at least 60 consecutive trials. During the initial phase of training, subjects were trained on 35 different stimulus sets of exemplars of the numerosities 1 to 4. Examples are shown in Fig. 1A.

The percentage of trials on which subjects responded to each numerosity in the correct order was well above the chance level of accuracy for each of the 35 training sets. As shown in Fig. 2A, performance also increased with each new set. This increase could reflect either or both of the following factors: (i) Subjects learned the order in which to respond to each stimulus more rapidly, and (ii) subjects learned to use the relative numerosity of each stimulus to predict the required response order for each new stimulus set. The first explanation is plausible because subjects were trained for at least 60 trials on each stimulus set. Repeated exposure to each set provided ample opportunity to associate some non-numerical feature of each stimulus (for example, the configuration of the elements) with its ordinal position (*9*).

The opportunity to learn the correct order in which to respond to a new set of stimuli was eliminated during test sessions in which 150 new stimulus sets were presented only once (30 sets per session for five consecutive sessions) (*10*). Figure 2B shows the percentage of correctly completed trials on the 150 test sets. Numerosity was the only basis for ordering items on the test sets. Accuracy substantially exceeded the level predicted by chance and did not differ from subjects' accuracy during the last five blocks of the 35 training sets (in which subjects could have used non-numerical features of the stimuli to learn the correct order) (*11*). Rosencrantz's and Macduff's performance on the test sets shows that they learned to discriminate numerosity during training even when a non-numerical strategy would have sufficed. It should also be clear that their performance cannot be attributed to a "last resort" strategy.

In addition to providing unequivocal first-trial evidence that monkeys can discriminate the numerosities 1 to 4 categorically, Rosencrantz's and Macduff's ability to order new exemplars of numerosity suggests that they learned an ordinal rule. An alternative explanation of their performance on the 150 test sets is that they discriminated each numerosity as a nominal category (*12*) and that they then applied an arbitrary rule to order four unrelated categories (*13*). To rule out this alternative explanation, we evaluated our subjects' ability to respond correctly to stimulus pairs of novel numerosities in an ascending numerical order (*14*).

Both monkeys were tested on each of the 36 numerosity pairs that could be generated from the numerosities 1 to 9 (Fig. 3) (*15*). The numerosities 1 to 4 were familiar by virtue of the subjects' previous training; the numerosities 5 to 9 were novel. Subjects were reinforced for responding in an ascending order on trials on which the six familiar-familiar pairs were presented (Fig. 3, red symbols), but no reinforcement was provided for the familiar-novel or novel-novel pairs (Fig. 3, black symbols). The restriction of reinforcement to familiar-familiar pairs prevented subjects from learning the ordinal relations among the novel numerosities. To control for non-numerical cues, we used new exemplars of each numerosity on each trial. The size of the elements within each stimulus was also varied to eliminate size or surface area as a non-numerical cue (Fig. 1B).

Rosencrantz's and Macduff's performance on familiar-familiar, familiar-novel, and novel-novel pairs is shown in Table 1. Both subjects responded in an ascending order on each type of numerical pair (*16*). Their use of an ascending rule on the 26 pairs that contained a familiar numerosity can, to some extent, be attributed to prior training on sequences of the numerosities 1 to 4. However, experience with familiar numerosities cannot explain Rosencrantz's and Macduff's ability to respond to novel-novel pairs in an ascending order. Nor can transitive inference explain this ability. Although nonhuman primates are capable of transitive inference (*17*), the absence of any overlap between the familiar-familiar and novel-novel pairs precludes the possibility that subjects could logically deduce the order of novel-novel pairs (for example, if A > B and B > C, then A > C). To respond to novel-novel pairs, subjects must be proficient in detecting ordinal disparities among novel numerosities and must be able to apply the ascending numerosity rule— learned previously with respect to the numerosities 1 to 4—to the numerosities 5 to 9 (*18*).

Further evidence that monkeys represent the ordinal relations among the numerosities 1 to 9 was obtained by analyzing accuracy as a function of the numerical distance between the two test stimuli (Fig. 4). The positive relation between accuracy and numerical distance is similar to that obtained from experiments with human subjects (*20*). This relation has been interpreted as evidence that numerosities are represented in an analog manner.

Our results demonstrate that rhesus monkeys can spontaneously represent the numerosity of novel visual stimuli and that they can extrapolate an ordinal rule to novel numerosities. The process or processes that a monkey uses to detect the direction of ordinal disparities remain to be determined. Our subjects could have used a counting algorithm (*19*) to judge the relative magnitude of numerosities (*20*). Alternatively, they could have used a one-to-one correspondence matching algorithm whereby the elements of each stimulus were compared (*21*). Extensions of the nonverbal numerical tasks used in our experiment should provide a basis for assessing the extent to which a monkey's performance satisfies an operational definition of counting and may also clarify the nature of basic numerical abilities in animals and preverbal human infants.

Table 1. Percent correct for the three types of numerical pairs. Both subjects' accuracy exceeded the chance-level accuracy on familiar-familiar pairs [Rosencrantz, $t(19) = 70.0$, $P < 0.0001$; Macduff, $t(19) = 40.9$, $P < 0.0001$], familiar-novel pairs [Rosencrantz, $t(19) = 25.7$, $P < 0.0001$; Macduff, $t(19) = 32.3$, $P < 0.0001$], and novel-novel pairs [Rosencrantz, $t(19) = 9.1$, $P < 0.0001$; Macduff, $t(19) = 7.3$, $P < 0.0001$].

	Percent correct		
	FF	FN	NN
Rosencrantz	94	93	73
Macduff	92	93	75

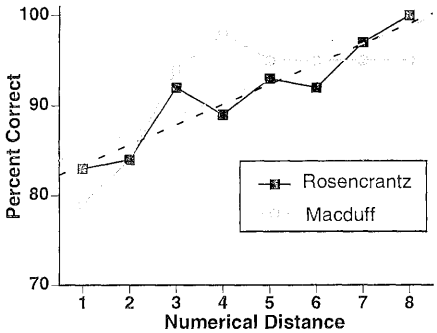

Fig. 4. Effect of numerical distance on accuracy in the pairwise test (*16*). A numerical distance of 1 includes all pairs of adjacent numerosities (1 versus 2, 2 versus 3, and so forth), whereas a numerical distance of 8 includes only the pair 1 versus 9. The dashed lines represent the best-fit linear models. The linear fits were significant for both monkeys [(Rosencrantz, $r^2 = 0.84$, $P < 0.05$; Macduff, $r^2 = 0.51$, $P < 0.05$)].

References and Notes

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Hauser, P. MacNeilage, K. E. Ware, *Proc. Natl. Acad. Sci. U.S.A.* **93**, 1514 (1996)], and chimpanzees [S. T. Boysen and G. G. Berntson, *J. Comp. Psychol.* **103**, 23 (1989); T. Matsuzawa, *Nature* **315**, 57 (1985)].
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6. Previous studies (*3*) [J. L. Emmerton and J. Niemann, *Animal Learn. Behav.* **25**, 234 (1997); J. W. C. Breukelaar and J. C. Dalrymple-Alford, *J. Exp. Psychol. Anim. Behav. Processes* **24**, 84 (1998)] assessed an animal's ability to represent ordinal relations among numerosities. Our experiment differs from those studies in that we obtained first-trial data. More important, these studies were not designed to assess an animal's ability to differentiate adjacent numerosities reliably or an animal's ability to extrapolate an ordinal relation to numerosities outside the training range.
7. Before this experiment began, both subjects were trained to order 11 four-item lists of photographs using a simultaneous chaining paradigm [H. S. Terrace, in *Quantitative Analyses of Behavior: Discrimination Processes*, M. L. Commons, R. J. Herrnstein, A. R. Wagner, Eds. (Ballinger, Cambridge, MA, 1984), pp. 115–138; K. S. Swartz, S. Chen, H. S. Terrace, *J. Exp. Psychol. Anim. Behav. Processes* **17**, 396 (1991)]. Animals were maintained in accordance with NIH guidelines.
8. There were 16 stimulus locations on the video monitor (arrayed in a 4 × 4 matrix). The configuration of the exemplars was selected randomly on each trial from a set of 43,680 spatial configurations. This ensured that subjects could not learn the correct sequence as a series of rote motor movements. Reinforcers were 190-mg banana-flavored Noyes pellets. Errors terminated the trial without reinforcement and resulted in an 8-s blackout of the video monitor. Subjects were trained to a low criterion on successive stimulus sets: correct completion of 20% of trials within a single session (under the conservative assumption of no backward errors, the expected chance level is 4% = 25% × 33% × 50% × 100%) or until three sessions on a particular stimulus set were completed. A low criterion was used to emphasize rule learning (as opposed to memorization of the correct order for a specific set of stimuli) and to establish a "learning set" for mastering new lists [H. F. Harlow, *Psychol. Rev.* **56**, 51 (1949)].
9. Rhesus monkeys learned the ordinal position of list items during training by the simultaneous chaining paradigm [S. Chen, K. B. Swartz, H. S. Terrace, *Psychol. Sci.* **8**, 80 (1997)].
10. Before the test sessions, multi-set training sessions were conducted. During multi-set training, the 35 training sets were presented randomly within each session to prepare subjects for the test sessions in which a different stimulus set was presented on each trial.
11. The decrease in the accuracy of both subjects on the second day of testing was not significant [$t(1) = 3$, $P > 0.2$].
12. Categorical discrimination of numerosity is defined as behavioral control by the number of elements contained by a particular stimulus that is independent of other discriminable dimensions such as size, color, shape, and total area.
13. Other studies of serial learning [B. McGonigle and M. Chalmers, in *Reasoning and Discourse Processes*, T. Myers, K. Brown, B. McGonigle, Eds. (Academic Press, London, 1986), pp. 141–164; N. Ohshiba, *Jpn. Psychol. Res.* **39**, 236 (1997); S. H. Hulse and N. P. Dorsky, *Learn. Motiv.* **8**, 488 (1977)] suggest that children, monkeys, and rats learn monotonic sequences more easily than nonmonotonic sequences.
14. D. Washburn and D. Rumbaugh [*Psychol. Sci.* **2**, 190 (1991)] trained rhesus monkeys on a forced-choice task on which they were required to select one of two arabic numerals, each associated with a number of discrete food items. Subjects reliably chose the symbol associated with the larger number of food pellets, but hedonic value was confounded with numerosity [see also A. Olthof, C. M. Iden, W. A. Roberts, *J. Exp. Psychol. Anim. Behav. Processes* **23**, 325 (1997); L. Hiestand and H. Davis, *Math. Cognit.* **2**, 171 (1996)]. Another study [R. K. Thomas, D. Fowlkes, D. Vickery, *Am. J. Psychol.* **93**, 247 (1980)] showed that squirrel monkeys can discriminate random dot displays of adjacent numerosities; however, this study did not obtain first-trial data. Also, because the numerosity pairs were trained successively, in separate blocks, it could not be determined whether the subjects learned a series of pairwise numerical discriminations (that is, numerical categorization) or whether they used an ordinal rule.
15. We used a two-item rather than a four-item test to isolate the difficulty of particular numerosity comparisons. As in the four-item test, the two stimuli were presented in random spatial locations on each trial. Familiar-familiar pairs were presented twice as frequently (60 trials per session) as the unreinforced familiar-novel and novel-novel pairs (30 trials per session) to maintain a high level of responding throughout the 20 test sessions. On unreinforced trials, subjects were allowed to respond in any order and received neither positive nor negative feedback.
16. The binomial probability of obtaining the observed number of correct responses on each of the 10 novel-novel numerosity combinations was below 0.05 for all pairs, with the exception of 6:8, 7:8, and 8:9. There was no effect of the area of the elements on accuracy [Rosencrantz, $t(19) = -0.35$, $P > 0.7$; Macduff, $t(19) = -1.2$, $P > 0.2$]. However, performance on novel-novel pairs was lower than performance on familiar-familiar pairs [Rosencrantz, $t(19) = 7.76$, $P < 0.001$; Macduff, $t(19) = 4.26$, $P < 0.001$]. Although this pattern resembles a generalization decrement, the reduced performance could also be attributed to the observed distance effect or to Weber's law (or both). The discriminability of novel-novel pairs should be poorer than that of familiar-familiar pairs because the novel-novel pairs tend to have smaller Weber fractions and numerical distances than the pairs that contain familiar numerosities (Fig. 4).
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18. To apply an ordinal rule to novel numerosities, monkeys must be able to use a mechanism that can perform relative magnitude operations on sets of discrete items. The accumulator model (*3*) of the numerical ability of animals posits that each discrete (to be counted) event results in the closing of a neural gate, allowing a constant amount of flow into an accumulator. A similarity ratio is then computed to determine which value in reference memory is closer to the test stimulus. The resulting analog representation is well suited for judgments of relative magnitude. However, the accumulator model does not explain how an organism would create a serial input from a simultaneous display.
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20. See R. S. Moyer and T. K. Landauer [*Nature* **215**, 1519 (1967)] for a demonstration that human subjects, required to indicate the larger of two arabic numerals, show an accuracy and latency distance effect. See P. B. Buckley and C. B. Gillman [*J. Exp. Psych.* **103**, 1131 (1974)] for a similar demonstration with random dot patterns.
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1 July 1998; accepted 11 September 1998

Smart Engineering in the Mid-Carboniferous: How Well Could Palaeozoic Dragonflies Fly?

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The wings of archaic Odonatoidea from the mid-Carboniferous of Argentina show features analogous to "smart" mechanisms in modern dragonflies that are associated with the agile, versatile flight necessary to catch prey in flight. These mechanisms act automatically in flight to depress the trailing edge and to facilitate wing twisting, in response to aerodynamic loading. The presence of similar features suggests that the earliest known odonatoids were already becoming adapted for high-performance flight in association with a predatory habit.

Insect wings are the principal adult locomotory structures of the largest group of animals. They are proving to be spectacular examples of microengineering. They lack internal musculature, and their three-dimensional shape during the flapping cycle is largely determined by their elastic response to aerodynamic and inertial forces, moderated by thoracic muscles inserted at or near the base (*1*).

The dragonflies (order Odonata) are supremely versatile, maneuverable fliers, and this is reflected in their wing morphology. High-speed cinefilm, videotape, and still photographs show that the wings twist extensively along their span, allowing the insects to

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