Tactile guidance of prey capture in Etruscan shrews

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Whereas visuomotor behaviors and visual object recognition have been studied in detail, we know relatively little about tactile object representations. We investigate a new model system for the tactile guidance of behavior, namely prey (cricket) capture by one of the smallest mammals, the Etruscan shrew, *Suncus etruscus*. Because of their high metabolic rate and nocturnal lifestyle, Etruscan shrews are forced to detect, overwhelm, and kill prey in large numbers in darkness. Crickets are exquisitely mechanosensitive, fast-moving prey, almost as big as the shrew itself. Shrews succeed in hunting by lateralized, precise, and fast attacks. Removal experiments demonstrate that both macrovibrissae and microvibrissae are required for prey capture, with the macrovibrissae being involved in attack targeting. Experiments with artificial prey replica show that tactile shape cues are both necessary and sufficient for evoking attacks. Prey representations are motion- and size-invariant. Shrews distinguish and memorize prey features. Corrective maneuvers and cricket shape manipulation experiments indicate that shrew behavior is guided by Gestalt-like prey descriptions. Thus, tactile object recognition in Etruscan shrews shares characteristics of human visual object recognition, but it proceeds faster and occurs in a 20,000-times-smaller brain.

active touch | barrel cortex | object recognition | *Suncus etruscus* | whisker

The sensory worlds of animals are very diverse (1). von Uexküll's early work (2) suggested that prey recognition in ticks can be explained by the detection of a few key stimuli. Whereas ticks succeed without a formal representation of a prey object, other animals rely on more elaborate schemata of their prey. The visual object representations underlying prey capture in frogs and toads have been characterized in much detail (3, 4). Accordingly, toad attacks on "worm-like" stimuli critically depend on simple features like motion (static stimuli are ignored), motion direction, stimulus orientation, and size. Visual object representations in primates appear to be very different from the toad's sensory representations. Primates readily react to static objects, and recognition can be, to a fair degree, size- and motion-invariant. More importantly, primates have segmented and structured object representations; i.e., they not only analyze simple object features (5) but are also sensitive to the figural arrangement of these features (6, 7).

Whereas visual object recognition has been studied in much detail, we are relatively ignorant about tactile object representations. Here we investigate a model system in which we could pose biologically meaningful questions about tactile object recognition. We analyze the prey (cricket) capture behavior of one of the smallest mammals, the Etruscan shrew, *Suncus etruscus*. Shrews tackle a complex task: detecting, overwhelming, and killing, in darkness, a fast-moving target that is almost as big as the predator itself. The small body size of Etruscan shrews goes along with a high metabolic rate (8, 9) and an immense pressure to obtain prey. Etruscan shrews are nocturnal animals, and work on related shrew species suggested that vision is only of limited significance in these species (10, 11). Work on crocidurean shrew species implicated vibrissae in navigation but argued against the presence of echolocation in these animals (12). Crickets are abundant in shrew natural habitats (13) and were offered as prey

in this study. Crickets are nocturnal, highly mobile animals endowed with a variety of mechanosensitive organs that mediate escape behaviors (14). Thus, the behavioral ecology of shrews and crickets predestines them to interact by means of sophisticated tactile behaviors. We combined the spatiotemporal analysis of numerous attacks with whisker removal and prey manipulation experiments to answer the following questions: (*i*) What sensory cues are used? (*ii*) What is the role of the vibrissae? (*iii*) What is the nature of shrew object representations?

We find that shrew prey capture is based on precise and fast attacks that depend on whisker information. We demonstrate that size- and motion-invariant tactile shape cues trigger shrew attacks. In particular, shrews have an acquired or innate tendency to guide their attacks based on the position of the cricket's jumping legs.

Results

Etruscan Shrews and Crickets. Etruscan shrews are small (length, 3.6–5.3 cm; weight, 1–3 g), dynamic animals (Fig. 1*A*). Whereas the shrew's eyes are small (<1 mm), a big whisker fan extends around its head (Fig. 1 *B* and *C*). We refer to the large whiskers on the side and top of the shrew's rostrum as macrovibrissae (15). The longest macrovibrissae had a length of ≈12 mm, a considerable length similar to that of mouse whiskers (15). The shrew's mouth is surrounded by a dense array of small whiskers, the so-called microvibrissae (Fig. 1*D*). Both field crickets (*Gryllus assimilis*) and house crickets (*Acheta domesticus*) were highly reactive to shrew attacks. Because we offered juvenile and adult animals, crickets covered a wide size range (length, 0.5–3.5 cm; weight, 0.1–1.2 g), with the larger ones being only slightly smaller than shrews (Fig. 1*A*). To film prey captures efficiently we offered crickets on small stages, which were easy for the shrews to enter but difficult for the crickets to leave. Almost all (>95%) of the attacks included here were filmed under infrared illumination in total darkness.

Shrew Attacks on Crickets. Etruscan shrews overwhelm and kill crickets by a series of high-speed attacks (Fig. 2 and Movie 1, which is published as supporting information on the PNAS web site). Whereas small crickets are killed or immobilized in a few (one to three) attacks, killing or immobilization of large crickets required many attacks. Such attacks occurred with incredible speed and at short interattack intervals (Fig. 2). We therefore analyzed all attacks frame by frame. Shrews placed attacks from all kinds of body positions, e.g., when lying on their sides (Fig. 2, frame 1160 ms). A large fraction (40.2%) of attacks was placed on static crickets, arguing against a role of prey motion in shrew prey recognition. Filming attacks from a variety of angles, we
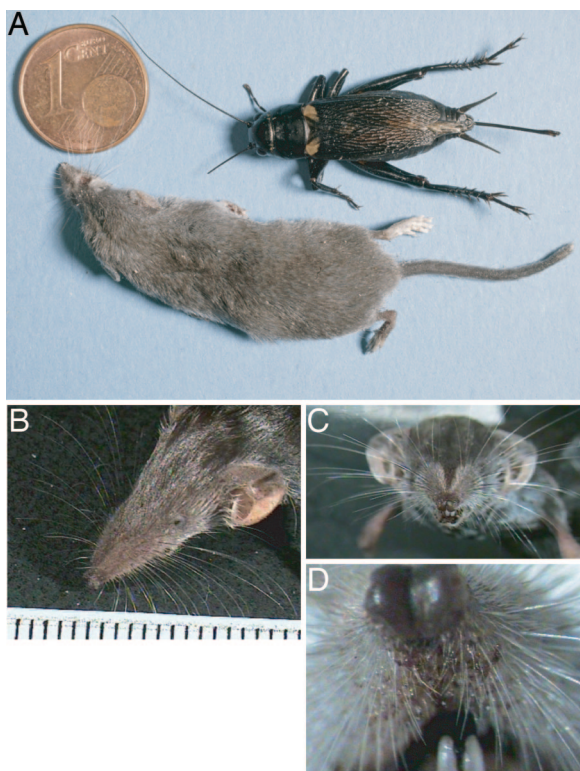
Fig. 1. Etruscan shrews and crickets. (*A*) An Etruscan shrew and a field cricket. The € cent coin is 16.25 mm in diameter. (*B*) Head of an Etruscan shrew with whisker array. The scale shows millimeters. (*C*) Frontal view of the head of an Etruscan shrew. (*D*) High-magnification view of the microvibrissae surrounding the shrew's mouth.

Fig. 2. Cricket attack sequence (see also Movie 1). Sequence of stills from an attack sequence in a 7-cm × 7-cm box. Time is shown at the bottom of each image and runs in horizontal lines from top left to bottom right. The top left image is taken immediately before the attacks. The next 10 images show the end point of attack frames of 10 consecutive attacks on the same cricket. Shortly after these attacks the shrew takes a break (bottom right). Many attacks target the thoracic region (640, 1,000, 1,160, 1,280, 1,800, and 2,000 ms).

found that attacks were always associated with a rapid protraction of the shrew rostrum toward the cricket, at the end of which the shrew bit into the cricket. At the most protracted rostrum position the shrew's movements usually briefly (for one to three frames) subsided, and we focused on these "end points of attack" frames in our analysis (Fig. 7, which is published as supporting information on the PNAS web site).

Spatial Attack Characteristics: Precise Targeting, Size Invariance, and Lateralization. *Attack location.* To assess attack targeting we determined from attack end-point video frames which one of nine cricket body parts was attacked. The resulting attack histogram (Fig. 3*A*) showed that attacks were placed selectively. In particular, the most preferred attack position (the anterior thorax) was attacked >20 times more often than the directly adjacent head. Such selectivity is remarkable, because shrews and crickets move very fast in a large fraction of attacks (Movie 1), and because the head–anterior thorax distance is <3 mm in an average-sized cricket. To corroborate these results we also determined the position of bite marks on freshly killed or immobilized crickets. There was an excellent correspondence between attack positions determined by bite marks (Fig. 3*B*) and the video analysis (Fig. 3*A*).

Size invariance. Crickets varied considerably in size. The comparison of attack histograms on small and large crickets (across a >5-fold size range) (Fig. 3*C*) suggests that the distribution of attacks is prey-size-invariant; i.e., there was no significant interaction between prey size and attack location ($P > 0.35$).

Attack directions and lateralization. Shrews attacked crickets from the side with a narrow distribution of attack angles ≈90° relative to the cricket's body axis (Fig. 3*D*). Surprisingly, there were significantly more attacks from leftward directions (239 overall)

than from rightward directions (153 overall). Because crickets tended to run away from the shrews, their bodies tended to have orientations similar to the body axes of the shrews. Further analysis then demonstrated that leftward attack biases corresponded to lateralization in the hunting behavior of individual shrews. Thus, when we plotted the attack direction of the shrew's rostrum relative to the shrew's body axis (Fig. 3*E*) we found that, although most attacks were directed straight ahead, there were significantly more rightward attacks (184 overall) than leftward attacks (133 overall). The strength of this rightward bias varied among individuals (data not shown).

Temporal Analysis: Speed, Sequence, Corrective Turns, and Recurrent Attacks. *Attack latencies and intervals.* Prey capture (Movie 1) occurred very quickly. To quantify how fast the animals place their attacks we measured the time from the encounter (defined as shrew rostrum to cricket distance, ≤1 cm) of a shrew and cricket to the end point of the first attack. As shown in Fig. 4*A* the most common time for the completion of an attack was only 200 ms, and the fastest attacks were completed in as little as 80 ms. Similarly, when we analyzed the time interval between attacks we found that the most common attack interval was only 200 ms (Fig. 4*B*).

Attack sequence. In a subset of our video data we collected the entire chain of events from the first encounter of the shrew and the cricket to the terminal attack that left the cricket dead or immobilized. In these data we analyzed the evolution of the patterning of attacks for a given encounter with a cricket (Fig. 4*C*). We found that first attacks were somewhat more broadly distributed over the cricket's body, subsequent attacks were similar to the overall distribution of attacks, and terminal attacks were almost exclusively directed to the thorax. The interaction between attack number and attack location in a sequence was highly significant ($P < 0.001$).

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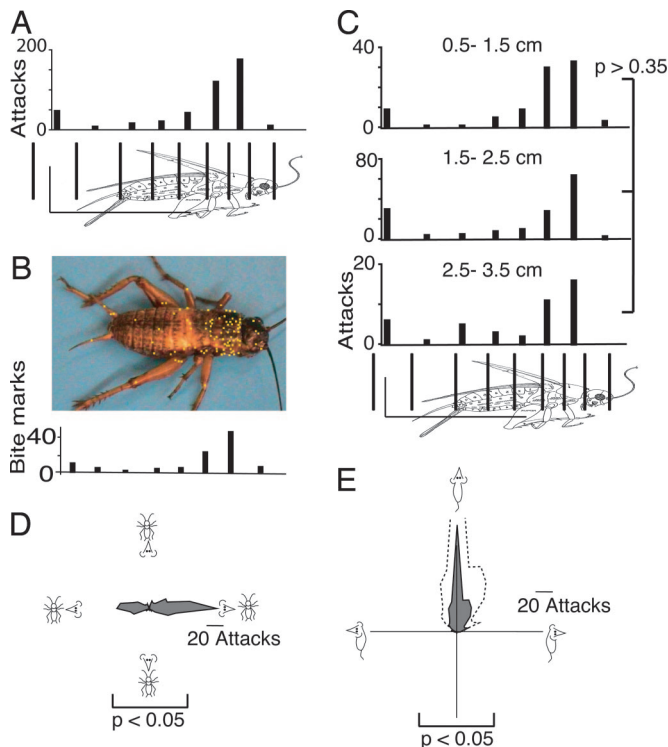
Fig. 3. Spatial analysis of shrew attacks. (*A*) Attack histogram. Histogram (*Upper*) of shrew attacks (from nine shrews) over nine cricket body parts (shown schematically in *Lower*) (*n* = 450 shrew attacks on ≈130 crickets). (*B*) Bite mark analysis. (*Upper*) Bite mark positions (yellow squares) superimposed on a cricket photograph (*n* = 94 bite marks on 25 freshly killed, immobilized, or injured crickets). (*Lower*) Bite mark histogram. (*C*) Attack histograms for different-sized prey. Data are as in *A*. The effects of prey size on attack location were evaluated by using a Poisson regression model. (*D*) Polar plot of attack directions (of the shrew's rostrum) relative to the cricket's body axis (angle β in Fig. 7*B*). Left and right side attack directions (counted in 10° bins) were compared by a two-tailed paired *t* test. (*E*) Polar plot of attack directions (of the shrew's rostrum) relative to the shrew's body axis (angle α in Fig. 7*B*). Dashed outline: Same data as shown in gray but multiplied by two without inclusion of the forward direction. Leftward and rightward attack directions (counted in 10° bins) were compared by a two-tailed paired *t* test.

Fig. 4. Attack latencies, intervals, and sequencing. (*A*) Histogram of attack latencies (time to completion of first attacks). The time from encounter to the end point of an attack on a cricket was measured; only the first attack of a shrew on a given cricket was included (*n* = 64 first attacks). (*B*) Histogram of interattack intervals (time from attack end point to attack end point). Only intervals of directly subsequent attacks were included (*n* = 180 attack intervals). (*C*) Attack sequencing. Effects of attack number on attack location were evaluated by using a Poisson regression model.

Directed corrective turns. We observed corrective head and body turns that allowed the shrew to attack the anterior thorax (the preferred attack location) directly after the shrew made contact with a nonpreferred body part. One such maneuver (an abdomen contact followed by an immediate directed turn to the thorax) is shown in slow motion at the end of Movie 1. Thus, shrews can use contact information from a distant body part to guide attacks toward the thorax.

Recurrent attacks on the same body parts. Shrews had a tendency to recurrently attack the same body part of a cricket. A striking example is shown in Movie 2, which is published as supporting information on the PNAS web site, where a shrew placed almost all of his >12 attacks on the legs of the attacked cricket. These cumulative leg attacks deviate from the expectancies according to overall statistics discussed so far, because the overall probability of a leg attack is only 10%. Shrews kept attacking the same body parts even if they briefly lost prey contact and thus may use short-term memories of prior attack positions to guide further attacks. The probability for a second attack on a previously attacked body part was 3.1 times higher than expected for this body part according to overall statistics.

Role of the Vibrissal System: Whisker Movements and Whisker Removal Experiments. *Whisker and head movements.* We documented whisker movements with a high-speed camera, sampling a large number of shrew behaviors without prey contact and a limited number (*n* = 8) of shrew attacks on crickets at 100 or 160 Hz. Whiskers were highly mobile during attacks. Whisker contacts with prey resulted (*i*) from active rhythmic back-and-forth movements of the whiskers themselves at frequencies of ≈20 Hz; (*ii*) from fast head movements, which are much more prominent in shrews than in rats or mice; and (*iii*) to a lesser extent from translational body movements. Although most whisker movements are synchronous and convergent, shrews were also capable of fractionated, divergent movements of whiskers, as have been described in rats (16).

Microvibrissal removal. Shrew facial whiskers can be divided into macrovibrissae (Fig. 1 *B* and *C*) and microvibrissae (Fig. 1*D*), and we evaluated the role of vibrissae subdivisions by removal experiments. To assess whisker removal effects we distinguished between completed attacks (ending with rapid protraction of the shrew rostrum toward the cricket and a putative bite) and aborted attacks [close (<0.5 cm) approaches of the shrew toward the cricket without a rapid rostrum protraction/putative bite]. Aborted attacks occurred because of successful evasive maneuvers of crickets or because shrews failed to strike. We removed microvibrissae in three shrews that showed, before whisker removal, a large fraction of completed attacks (92%) (Fig. 5*A Upper*) and normal patterning of attacks (Fig. 5*B Upper*). After microvibrissae removal, shrews still attacked crickets, but the number of completed attacks dropped dramatically (to 52%) (Fig. 5*A Lower*). On the other hand, the patterning of attacks over the cricket's body was only slightly, but significantly, affected by microvibrissae removal (Fig. 5*B Lower*). Sham-shaving procedures had no effects (data not shown).

Macrovibrissal removal. We removed macrovibrissae in three shrews that showed, before whisker removal, a large fraction of completed attacks (91%) (Fig. 5*C Upper*) and normal patterning of attacks (Fig. 5*D Top*). After macrovibrissae removal, shrews were much more clumsy, and the number of completed attacks dropped to 52% (Fig. 5*D Bottom*). Unlike microvibrissae removal, however, macrovibrissae removal led to a much broader distribution of attacks over the cricket body (Fig. 5*D Bottom*), and the cricket head (a nonpreferred site of attack in normal shrews) became the most common point of attack. These effects

Fig. 5. Microvibrissae and macrovibrissae removal effects. (*A*) Count of aborted (open) and completed (filled) attacks on crickets in three shrews before (*Upper*) and after (*Lower*) microvibrissae removal. (*B*) Attack histogram for completed attacks in three shrews before (*Upper*) and after (*Lower*) microvibrissae removal. (*C*) Aborted (open) and completed (filled) attacks on crickets in three shrews before (*Upper*) and after (*Lower*) macrovibrissae removal. (*D*) Attack histogram for completed attacks in three shrews before (*Top*) and after (*Middle*) macrovibrissae removal. Effects of whisker removal on completed vs. aborted attacks were evaluated by using (a Yates-corrected) Pearson's χ^2 test. Effects of whisker removal on attack location were evaluated by using a Poisson regression model.

of macrovibrissal removal on the location of shrew attacks were highly significant ($P < 0.001$). Thus, both macrovibrissae and microvibrissae are required for a high rate of successful attacks, whereby the macrovibrissae are particularly relevant for attack targeting.

Evidence for Tactile Shape Recognition and Key Features. *Plastic crickets.* To evaluate the role of prey shape in triggering shrew attacks we performed a 3D scan of a cricket and generated a plastic dummy of this animal. The spatial precision of this dummy was only on the order of ≈125 μm; i.e., although the cricket shape was well captured by the dummy, the surface texture of the original cricket was not preserved. This plastic cricket and a variety of size-matched control objects (Fig. 6*A*) were presented to five shrews. A single object was presented on a single day with at least 1 day without an artificial object in between. The sequence with which different objects were introduced was varied from shrew to shrew. As shown in Fig. 6*B* and Movie 3, which is published as supporting information on the PNAS web site, shrews did not attack any of the control objects. However, four of five shrews attacked the plastic cricket, often at the same body parts where we observed attacks on normal crickets (Movie 3). Remarkably, shrews attacked the plastic cricket repetitively (Movie 3) and placed altogether 37 attacks on the dummy. The one shrew that did not attack the plastic dummy in the first place was later on presented with a dummy cricket generated with higher spatial precision (≈30 μm, i.e., with a natural surface texture), and in this case this shrew also attacked the dummy. These observations indicate that (*i*) the correct target shape is sufficient for triggering attacks; (*ii*) attacks are selective for correct target shapes, i.e., shrews do not simply attack any object; (*iii*) prey movement cues are not necessary; (*iv*) correct olfactory and gustatory cues are not required even for repetitive attacks; and (*v*) correct prey texture is not essential, although a role of texture cues cannot be ruled out.

Cricket shape manipulations. To determine which shape characteristics are recognized by the shrews we manipulated the shapes of crickets by either gluing on an additional head or adding a pair

Fig. 6. Attacks on plastic and shape-manipulated crickets. (*A*) Control objects and plastic cricket on a centimeter scale. (*B*) Number of attacks per object for five shrews. (*C*) Attack histogram (*Upper*) from three shrews for control crickets with glue (blue dot in the cricket schematic in *Lower*) applied to their heads. See also Fig. 8*B Left*. (*D*) Attack histogram (*Upper*) from the same three shrews for shape-manipulated crickets with an extra pair of jumping legs (red in the cricket schematic in *Lower*) glued (blue in *Lower*) to their heads. Attacks on the added pair of jumping legs are given in red. See also Fig. 8*B Right*. Effects of shape manipulation on attack location were evaluated by using a Poisson regression model.

of jumping legs (Fig. 8, which is published as supporting information on the PNAS web site). To control for the effects of the added glue we compared attacks on shape-manipulated crickets with attacks on control crickets, where we also applied glue but this time without adding heads or legs. Whereas the effects of an additional head were minor (data not shown), the effects of gluing on an additional pair of jumping legs on the cricket's thorax/head (Fig. 8*B*) were dramatic. Shrew attacks on control crickets were similar to the patterning of attacks on normal crickets (Fig. 6*C*; compare to Fig. 3*A*). In contrast, the distribution of shrew attacks on shape-manipulated crickets with an additional pair of jumping legs was shifted entirely (Fig. 6*D*). The anterior thorax, a preferred attack target in normal crickets, was not attacked at all. In crickets with an additional pair of jumping legs, 54% of the shrew attacks were directed to the cricket legs (if both normal and added legs are considered), whereas this was the case in only 11% of the attacks on control crickets. Even if one excludes the attacks on the additional pair of jumping legs (shown in red in Fig. 6*C*) from the analysis, the fraction of leg attacks is greatly increased in shape-manipulated crickets to 42%. These cricket shape effects on attack location were highly significant ($P < 0.001$). Thus, jumping legs are key features in shrew prey recognition, and their manipulation leads to widespread alterations in attack patterns.

Discussion

Tactile Object Representations and the Guidance of Etruscan Shrew Prey Capture. Etruscan shrews succeed in hunting their large and fast-moving prey by precise and fast attacks. Our work charac-

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terized the underlying sensory cues and object representations: (*i*) Both macrovibrissae and microvibrissae removal severely impairs prey capture. (*ii*) Macrovibrissae removal in particular leads to deficits in attack targeting. (*iii*) Tactile shape cues are both necessary and sufficient for evoking attacks. (*iv*) In contrast, visual and olfactory cues are not necessary. (*v*) Shrew attacks are both motion- and size-invariant. (*vi*) The selective targeting and recurrence of the attacks suggest that shrews distinguish and memorize different prey features. (*vii*) Shrew behavior appears to be based on the "Gestaltwahrnehmung" of crickets; i.e., they do not recognize only local elements but instead form a global construct of the cricket: (*a*) according to dummy/control object experiments complex shape cues are recognized; (*b*) the directed corrective turns show that local contact information can be used in a global way, namely to guide attacks toward distant body parts; and (*c*) local shape manipulations (addition of a jumping leg) lead to global behavioral effects (a shift in the entire pattern of attacks).

The Shrew–Cricket Interaction. There is only a limited amount of work on Etruscan shrew prey capture (13). In line with the speed of Etruscan shrew behavior observed here, physiological work demonstrated that the skeletal musculature of Etruscan shrews is specialized for high-speed movements. Etruscan shrew leg musculature is unique in its extremely short isometric twitch contraction time and muscle fiber composition (17, 18). Haberl (11) presented common shrews (*Sorex araneus*) and European water shrews (*Neomys fodiens*) with simple prey dummies and demonstrated a tendency for front end/head region attacks. Shrews target highly selectively the cricket's thorax, the anterior parts of which are armored by the cricket's pronotum. Most likely, the effectiveness of shrew attacks results from damage to the thoracic ganglia, which are also targeted by other cricket predators like digger wasps (19). Interference with neural activity in the thoracic ganglia can lead to cricket paralysis (20) and abolishes the cricket's vigorous defensive kicking behaviors (21). Recurrent attacks on the same body parts might increase the hunting efficacy; i.e., clustered leg attacks may immobilize crickets faster than distributed attacks.

Vibrissal Sensory Performance. Vibrissal functions have been studied in only a limited number of mammals. Seals have very prominent whisker arrays with which they can recognize objects (22) and track underwater turbulence caused by objects moved through water (23). Vincent (24) established early on that rat vibrissae are involved in a wide range of behaviors including navigation through mazes. It was also shown that vibrissae can mediate very fine texture/roughness discriminations (25) and distance estimation (26). In their high whisking frequency (20–25 Hz) shrew whisker movements are similar to the whisker movements of mice (27). Rat whiskers can also mediate object recognition, whereby the small frontal microvibrissae are both necessary and sufficient for object recognition (15). Our combination of whisker removal experiments and dummy experiments indicates that whisker-derived tactile shape cues play a critical role in the shrew's sensory world. The lateralization of shrew attacks compares to other sophisticated sensorimotor behaviors like speech (28), birdsong (29), or hand use (30) that are mediated through lateralized neural systems. In line with Gibson's original conclusions on tactile perception (31) shrew prey capture is based on active touch rather than on passive sensing of whisker deflection caused by prey motion.

Comparative Considerations. Prey capture requires fast and precise acquisition of information, and these needs also seem to have been a driving force in the evolution of bat echolocation (32). Shrew prey capture is based on size- and motion-invariant figural descriptions of crickets. In this respect object concepts guiding

shrew behavior have much in common with the abstract visual representations described in human and nonhuman primates. At the same time shrew representations are radically different from the nonsegmented, neither size- nor motion-invariant representations that underlie toad prey capture (3, 4). Our data show that high-level abstract sensory representations are neither restricted to the primate visual system nor tied to a large brain size. In the brains of related shrew species the relative size of cortical vibrissae representations is large (33). However, the overall brain weight of Etruscan shrews is only ≈60 mg; i.e., their brain is >20,000 times smaller than the human brain. Further work is required to determine whether the perceptual similarities between shrews and primates represent a mammalian evolutionary homology or whether they resulted from analogous ecological demands in shrews and primates. Etruscan shrews differ from primates in their short reaction times. Thus, the fastest shrew attacks were completed within 80 ms, leaving the shrew probably <40 ms to initiate the attack. A similar fast guidance of prey contacts has been recently described for the tactile prey acquisition of the star-nosed mole (34). In contrast, in the visual domain even task-experienced human observers take ≈300 ms to indicate the detection of a simple visual object (35). Part of this tactile/visual difference may be related to the faster transduction process in the vibrissal system. Additional factors like the conduction/transmission delays associated with large brain size may also contribute to the slower performance of humans.

Our work demonstrates that the accurate control of prey items combined with analysis of a very large number of attacks allows a quantitative approach even to complex animal object representations.

Methods

Etruscan Shrews. Data refer to 12 adult Etruscan shrews of both sexes. We captured 10 Etruscan shrews under a permit of the local government (permit no. N 6085/T-A31, Firenze, Italy) in the provinces Firenze and Livorno. Shrews were caught in nearly 1,200 trap nights by using 100 special live traps of type Hengstler that we sensitized for a weight of 1 g. Traps were placed along walls and trees in olive plantations and were checked three times a day. Shrews were housed in terraria containing a layer of dry soil, moss, stones, pieces of wood, and broken flowerpots. The diet consisted of crickets, mealworms, and water ad libitum. Breeding terraria contained a large block of plaster containing a system of tunnels and potential breeding chambers. Whisker removal was performed under anesthesia (by isoflurane in a 2:1 N_2O/O_2 mixture) under a microscope with a small pair of scissors.

Crickets. Juvenile and adult field crickets (*G. assimilis*) and house crickets (*A. domesticus*) were obtained from a local vendor (Heller Farms, Rotterdam, The Netherlands). They were kept under a warming light and fed with fruit, grass, and dry vitamin-fortified fish food. To manipulate cricket shapes we first obtained body parts from donor animals. We anesthetized crickets briefly by cooling and then attached heads/pairs of jumping legs with Versyo.com (Heraeus Kulzer, Hanau, Germany) (Fig. 8). To generate plastic crickets, 3D scans of crickets were performed at a precision of ≈30 μm on a micro CT machine (SkyScan-1076; SkyScan, Antwerpen, Belgium) at Erasmus Medical Center. Dummies were then generated by "micro rapid prototyping (microstereolithography)" at a precision of ≈125 μm or ≈30 μm (Materialise, Leuven, Belgium).

Analysis of Bite Marks on Crickets. Etruscan shrews had a tendency to first kill or immobilize most of the offered crickets. Then considerable time could elapse before they actually consumed their prey. Hence we could collect injured, immobilized, or dead crickets from the terraria. We were interested in bite marks

resulting from attacks, rather than in bite marks resulting from prey consumption, and we thus excluded crickets where the head, thorax, or abdomen was missing. Bite marks were identified under the microscope by (*i*) missing body appendages (legs, cerci); (*ii*) body fluid attachments over cuticle injuries; and (*iii*) injuries or breaks in the cuticle. Bite marks were highlighted on a photograph of the recovered cricket. Long/multiple breaks in the cuticle were counted as two bite marks. The delicate cricket antennas were excluded from the bite mark analysis.

Video and High-Speed Recordings of Attacks on Crickets and Frame-by-Frame Analysis. Crickets were offered in custom-made acrylic stages with an above-mounted infrared-sensitive video or high-speed camera. Most recordings were made in darkness but under infrared illumination. High-speed recordings were made with a Photon Focus camera (model no. MV-D640-66-CL-10; Photon Focus, Lachen, Switzerland) with a frame rate of 100 or 160 Hz. Approximately 700 attacks on crickets were recorded in ≈400 h. Video clips of attacks were imported into the Scion image analysis program (Scion, Frederick, MD) and analyzed frame by frame. A rapid protraction of shrew rostrum toward a cricket was considered to be an attack. At the most protracted rostrum position (the end point of attack) the shrew's movements usually briefly subsided, and we determined this video frame for all attacks. In this frame three spatial measurements were made (Fig. 7): (*i*) the observer assigned, by forced choice, the location of the attack (see red x in Fig. 7) on to one of nine cricket body parts; (*ii*) the relative angle (α in Fig. 7*B*) between the shrew's rostrum (b in Fig. 7*B*) and the shrew's body axis (a in Fig. 7*B*); and (*iii*) the relative angle (β in Fig. 7*B*) between the shrew's

rostrum (b in Fig. 7*B*) and the cricket's body axis (c in Fig. 7*B*). Furthermore, temporal measurements were taken at a time resolution of 25 Hz (full video frames). For the first attack on a cricket the "attack latency" was measured from the time point where the shrew's rostrum was ≤1 cm from the cricket (which corresponds roughly to the length of the shrew's whiskers) to the end point of the attack. For subsequent attacks the interattack time interval was measured.

Statistical Evaluation of Attack Distributions. To improve the numerical basis of our statistical evaluation of attacked distributions we pooled counts from the attack locations anterior abdomen, medial abdomen, posterior abdomen, and cerci to one abdomen count, we pooled counts from posterior and anterior thorax to one thorax count, and we pooled counts from head and antenna to one head count. We assumed that attack counts follow a Poisson distribution. The attack counts for the four body locations legs, abdomen, thorax, and head were evaluated by using a Poisson regression model with a log offset equal to zero and log-linear link function. The parameter of interest was defined as a condition (prey size, attack number, whiskers intact vs. removed, control vs. shape-manipulated cricket). We then tested the condition-by-location interaction by comparing the model with only the main effects of condition and location with a fully saturated model using the likelihood ratio test (deviance test).

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