

Current Biology

Vision Drives Accurate Approach Behavior during Prey Capture in Laboratory Mice

Highlights

- The C57BL/6J strain of mouse exhibits robust prey-capture behavior
- Vision is essential for accurate long-range approach behavior
- Vision and audition can each contribute to capture at short ranges
- A visual approach paradigm reveals the natural operating parameters of mouse vision

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In Brief

Mice are an important model system for studying vision, but relatively few ethological visually guided behaviors performed by laboratory mice have been described. Hoy et al. demonstrate that a common laboratory strain of mouse performs prey capture of live crickets and that vision is essential for accurate approaches leading to capture.



Vision Drives Accurate Approach Behavior during Prey Capture in Laboratory Mice

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SUMMARY

The ability to genetically identify and manipulate neural circuits in the mouse is rapidly advancing our understanding of visual processing in the mammalian brain [1, 2]. However, studies investigating the circuitry that underlies complex ethologically relevant visual behaviors in the mouse have been primarily restricted to fear responses [3–5]. Here, we show that a laboratory strain of mouse (*Mus musculus*, C57BL/6J) robustly pursues, captures, and consumes live insect prey and that vision is necessary for mice to perform the accurate orienting and approach behaviors leading to capture. Specifically, we differentially perturbed visual or auditory input in mice and determined that visual input is required for accurate approach, allowing maintenance of bearing to within 11° of the target on average during pursuit. While mice were able to capture prey without vision, the accuracy of their approaches and capture rate dramatically declined. To better explore the contribution of vision to this behavior, we developed a simple assay that isolated visual cues and simplified analysis of the visually guided approach. Together, our results demonstrate that laboratory mice are capable of exhibiting dynamic and accurate visually guided approach behaviors and provide a means to estimate the visual features that drive behavior within an ethological context.

RESULTS

C57BL/6J Mice Robustly Perform Prey Capture

Several species of rodents use vision to guide prey-capture behavior [6–8], but it remains unclear whether the commonly used laboratory species of mouse (*Mus musculus*) can capture prey using vision. We first tested for prey-capture behavior in *Mus musculus* by presenting live crickets (*Acheta domestica*) to cricket-naïve C57BL/6J mice in their home-cage in the presence of standard mouse chow. Within 24 hr of placing crickets in the home-cage of group-housed mice, all of the crickets

were captured and consumed. When the mice were then housed individually, 96.5% (55/57) of the mice captured and consumed crickets. This demonstrates that mice have both the inclination and ability to capture live prey.

To quantify prey-capture detection and pursuit behavior, we next recorded prey performance in an open-field arena (Figure 1A, top panel). For mice to perform reliable prey capture under our recording conditions, it was necessary to acclimate the mice to the setup (Figure 1A, training timeline). First, mice were acclimated to their handler and fed crickets once per day in their home-cage for 3 days. Then, following 24 hr of food restriction, they were exposed to the arena and to crickets within the arena. On the first day of hunting (D1) in the arena, mice approached crickets but often fled, leading to prolonged capture times or failure to capture (Figure 1B). This behavior is consistent with the natural tendencies of mice to suppress eating behaviors in novel environments [9] and to find lit open fields inherently aversive [10].

Importantly, avoidance behavior quickly receded with repeated exposure in the arena. After 3 days of capture trials, nearly all of the mice tested (96.4%, 53/55) captured prey reliably (Figures 1B and 1C). Capture performance was deemed reliable if three sequential trials each ended in capture of the cricket in under 30 s (Supplemental Experimental Procedures; Movie S1). Prey-capture performance, as measured by time to capture, reached asymptote at 13 ± 1.1 s on day 4 (D4) of hunting in the arena and was stable on day 5 (D5) (Figure 1B, bottom panel). Together, this demonstrates that the commonly used C57BL/6J mouse strain exhibits robust prey-capture behavior and that only 3 days of exposure to insects plus 3 days of contextual acclimation are required to optimize the behavior for measurement in a controlled setting.

Vision Is Necessary for Efficient Prey-Capture Performance

We next sought to establish which senses C57BL/6J mice use to detect, pursue, and capture live prey. We compared prey-capture performance under conditions where we either eliminated visual cues by allowing mice to capture prey in darkness (Movie S2) or eliminated auditory cues by implanting ear plugs [11] (Movie S3). We also tested performance when we eliminated both hearing and vision by testing ear-plugged animals in the dark (Movie S4). Testing was performed on D5, after 4 days of acclimation to capturing crickets in the arena (Figure 1A).

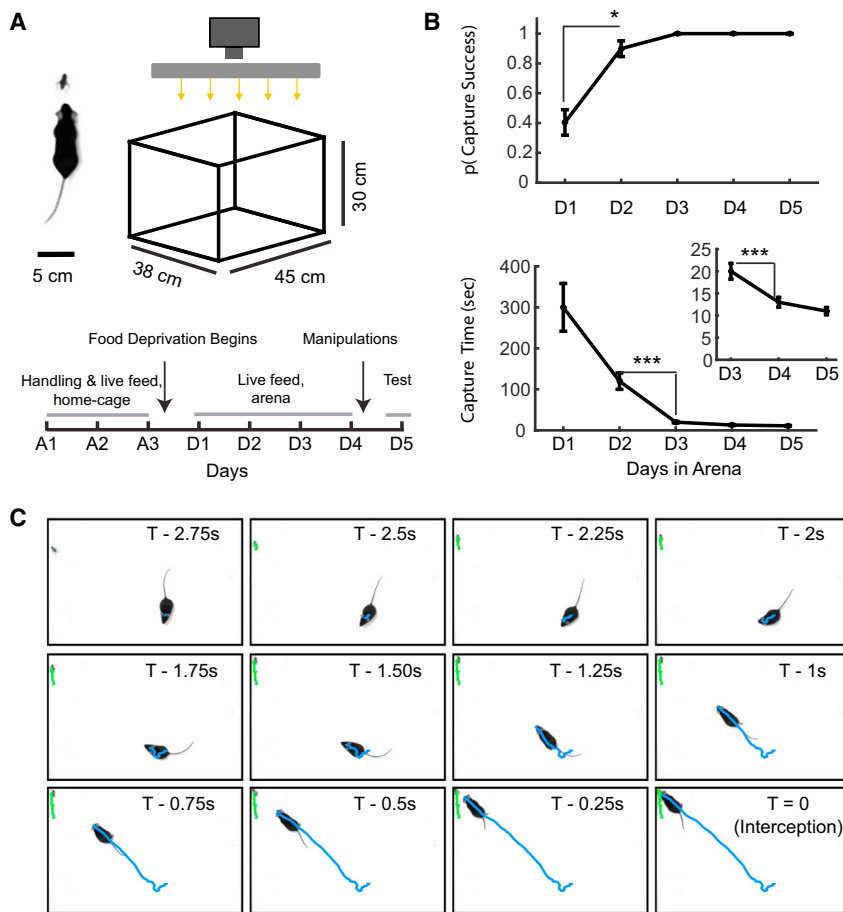


Figure 1. C57BL/6J Mice Reliably Perform Prey Capture in a Laboratory Setting

(A) Top: prey schematic diagram of the arena for prey capture. Left inset: an example video still of the mouse and cricket. Bottom: timeline of the experimental paradigm. Gray lines indicate the days that are relevant to the above label; arrows indicate that food deprivation began at the end of exposures on acclimation day 3 (A3), and sensory manipulations were performed after testing trials ended on day 4 (D4).

(B) Top: likelihood of successful capture within 10 min of exposure to cricket in the arena. By day 3 (D3), mice reached 100% capture success. Bottom: mean capture times averaged over three trials per mouse per day for successful capture trials on days 1–5 within the arena (D1–D5). Inset: the mean capture times on the final 3 days are plotted on an expanded timescale due to the 10-fold reduction in capture times from the first day of arena exposure. Data are median \pm bootstrapped SEM; $n = 47$ mice. * $p < 0.05$; *** $p < 0.001$, one-way ANOVA with Tukey-Kramer HSD post hoc and χ^2 goodness of fit applied to $p(\text{capture success})$ data.

(C) Frames from a movie of a prey-capture trial depicting a mouse orienting toward (time $[T] = -2.25$ s), approaching ($T = -1.25$ s), and intercepting ($T = 0$) a prey target. Times relative to prey interception are shown in the upper right-hand corner of each panel. The blue line shows the path of the mouse, and the green line shows the path of the cricket.

We observed striking impairments in prey-capture behavior in the dark (dark) and ear-plug-dark (EP dark) conditions relative to the baseline light (light) and ear-plug-only (EP light) conditions (Figure 2A). Mice took over three times as long to capture a cricket in the dark condition than in the light condition (Figure 2B; light: 11 ± 2 s; dark: 36 ± 9 s, $p < 0.001$). Capture time in the EP dark condition was dramatically higher relative to that of the dark condition (230 ± 56 s versus 36 ± 9 s, $p < 0.05$). This confirms the effectiveness of the ear plug manipulation, and this difference demonstrates that hearing can contribute to prey-capture behavior in the absence of vision. However, loss of hearing alone in the EP light condition had little effect on capture performance relative to that in the light condition (Figure 2B; EP light: 15 ± 3 s; light: 11 ± 2 s, $p > 0.05$).

Importantly, we observed no significant difference across conditions in the amount of time mice spent in a stationary state (light: $1.8\% \pm 0.75\%$; dark: $1.5\% \pm 0.53\%$; EP light: $2.4\% \pm 0.82\%$; EP dark: $2.1\% \pm 0.42\%$; $p > 0.05$) or in the average locomotor speed (light: 16.4 ± 2.6 cm/s; dark: 16.0 ± 2.1 cm/s; EP light: 14.6 ± 2.2 cm/s; EP dark: 15.7 ± 2.1 cm/s) when the mouse was not contacting the cricket. In addition, all mice consumed the cricket following capture. This suggests that impaired performance is not due to differences in level of activity or motivation.

To more clearly understand how vision contributes to efficient prey capture, we quantified the orienting behaviors of the mouse. We measured the distance between the mouse's head and the

cricket, termed "range," and the angular position of the cricket relative to the bearing of the mouse's head, termed "azimuth," across the entirety of each capture trial

(Figures 2C and 2D). Consistent with the capture-time data, we found that mice spent significantly less time at close range (<4 cm) under conditions where vision was impaired (Figure 2C). In particular, mice had nearly randomly distributed range to the target when they could neither see nor hear. This suggests a limited role for olfactory and tactile cues in supporting distal orienting behaviors during prey capture under our testing conditions. In the absence of vision, hearing does allow mice to increase the likelihood of being within contact range (<4 cm), compared to the absence of both vision and hearing (χ^2 , $p < 0.01$, $n = 20$ and 16).

One of the most striking observations is that mice maintained a precise bearing centered on the target in lighted conditions. In particular, prey azimuths were sharply centered on 0° when mice could see (Figure 2D). In contrast, when mice could neither see nor hear, the relative angular position of the prey appeared random, and this distribution was significantly different from all of the other conditions tested. The distributions of range and azimuth were significantly different between dark and EP dark conditions, demonstrating that hearing facilitates prey capture orienting behaviors when vision is absent. As with the capture-time data, the range and azimuth data suggest that vision is the primary modality driving efficient prey capture behavior and that hearing may play a role when vision is absent.

To determine the cues available during prey capture, we made audio recordings of the crickets in the arena. Acoustic analysis

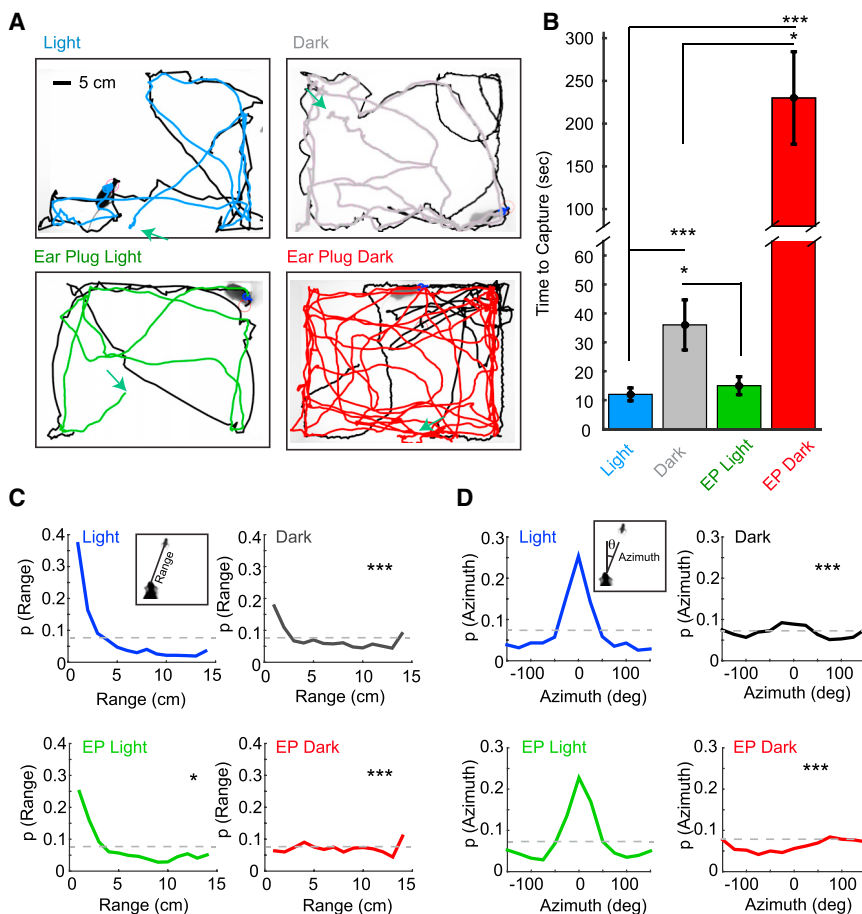


Figure 2. Selective Sensory Perturbation Demonstrates that Vision Is Necessary for Efficient Prey-Capture Performance

(A) Representative paths traveled by the mouse and cricket during a single capture trial performed under each of four sensory conditions. The paths of the mice are colored by condition, and prey trajectories are black. Green arrows depict starting locations for the mouse in each trial. Scale bar, 5 cm.

(B) Capture time for four groups of mice differentially tested in each of the four sensory conditions. * $p < 0.05$; *** $p < 0.001$, one-way ANOVA with Tukey-Kramer HSD post hoc.

(C and D) Trial-averaged probability density functions for range (C) and azimuth (D) in the four sensory conditions. Insets depict definitions of range and azimuth. Gray lines indicate chance performance. Time-to-capture group data are median \pm bootstrapped SEM; $n = 16, 10, 8$, and 8 mice and $n = 23, 20, 16$, and 16 trials for the light, dark, EP light, and EP dark conditions, respectively. * $p < 0.05$; *** $p < 0.001$, one-way ANOVA with Tukey-Kramer HSD post hoc. Two-sample, Kolmogorov-Smirnov test for differences between each sensory manipulation and the baseline condition (light, D5). The difference between dark and EP dark conditions was also tested; range: $p < 0.01$; azimuth, $p < 0.05$, two-sample, Kolmogorov-Smirnov test; $n = 20$ and 16 trials, respectively).

See also [Figures S1](#) and [S2](#) and [Movies S1](#), [S2](#), [S3](#), and [S4](#).

showed that crickets never chirped but did produce audible cues approximately 5–10 dB above the background when they moved over the substrate (see the [Supplemental Experimental Procedures](#); [Figure S2](#)). We also tested whether motion was necessary for capture in the light by measuring performance with immobile targets (fresh-frozen crickets). Under lit conditions, mice contacted immobile targets in times comparable to when they first make contact with live crickets (8.06 ± 1.08 s versus 7.6 ± 1.34 s; $n = 8$, $p > 0.05$, Mann-Whitney U). Therefore, motion was not necessary to produce optimal prey-capture behavior in the light, but auditory cues were available to the mouse when prey moved.

To verify that darkness specifically disrupts performance via visual impairment of the mouse, we also sutured the mouse's eyelids closed. We saw no significant difference between three conditions in which vision was impaired: dark, eye-sutured light, or eye-sutured dark ([Figures S1A](#) and [S1B](#)). This demonstrates that the impairment of prey-capture performance in the dark was not due to factors such as changes to cricket behavior, and it confirms the effectiveness of our visual manipulations.

Vision Guides Accurate and Precise Orienting Behaviors

Given the profound effect that vision had on overall prey-capture efficiency throughout the duration of a trial, we next sought to quantify how visual information was driving orienting behavior

during individual approach events. By examining range, azimuth, and mouse speed prior to target contact, we identified behavioral criteria that successfully detected approach epochs. The co-occurrence of a consistent decrease in range and an absolute azimuth of less than 90° , while the mouse was moving at speeds greater than 5 cm/s, predicted 100% of target interceptions under baseline conditions ([Figure 3A](#)). Therefore, we used these as criteria for defining an approach start. Importantly, many interceptions do not result in a final capture. Therefore, we also differentiate between an "interception," where the mouse successfully reaches the location of the prey, and a "capture," where the mouse successfully grabs and consumes the prey.

We found that the average frequency of initiating approaches, measured as the number of approaches per minute, was significantly greater under both sighted conditions as compared to both dark conditions ([Figure 3B](#)). Further, the likelihood that an approach would end with target interception was significantly higher in the light conditions ([Figure 3C](#)). Taken together, these results indicate that vision is important for both prey detection and successful targeting during approaches. Surprisingly, we saw no significant differences in these measures of approach between the dark and EP dark conditions, further suggesting that hearing does not play a significant role in the long-distance approach phase of prey capture.

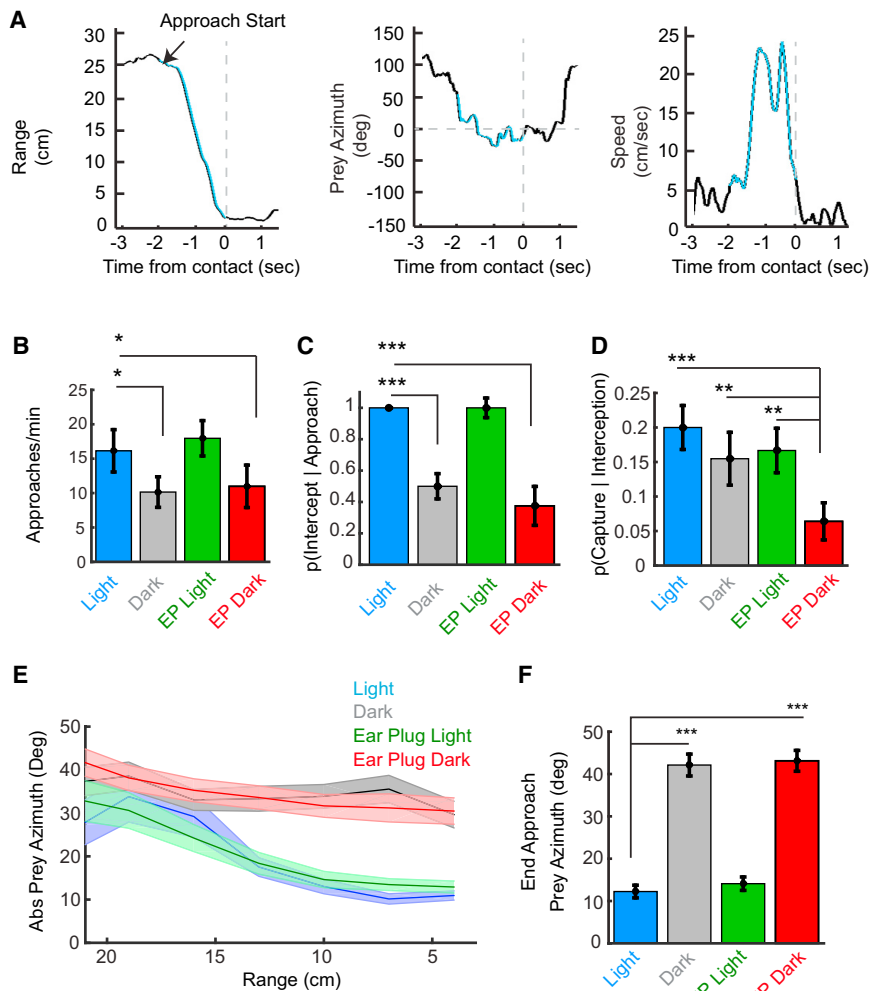


Figure 3. Accurate Approach Behavior during Prey Capture Requires Vision

(A) From left to right: range, azimuth, and mouse speed over the time preceding the prey contact event shown in Figure 1C. The “approach epoch” is shown as a blue trace overlaid on each exemplary behavioral trace.

(B) The median number of approaches per minute, averaged over trials.

(C) Probability that an approach leads to prey interception, averaged over trials.

(D) Probability that an interception will end in a final capture, averaged over trials.

(E) The mean azimuth at a given range during the mouse’s approach under the four different sensory conditions. Abs, absolute.

(F) The mean absolute azimuth at the end of each approach for each sensory condition. Azimuth data are mean \pm SEM, and all other grouped data are median \pm bootstrapped SEM; $n = 23, 20, 16$, and 16 trials, and $n = 47, 100, 46$, and 119 approaches for the light, dark, EP light, and EP dark conditions, respectively.

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$, one-way ANOVA with Tukey-Kramer HSD post hoc.

See also Figure S1.

Although hearing does not affect the accuracy of individual approaches, the total capture time increased dramatically when hearing is removed in the dark. To understand this, we analyzed the probability of a successful capture given an interception event, or the $p(\text{capture}|\text{interception})$ (Figure 3D). This analysis showed that mice performed equally well in the control condition or with either visual or auditory deprivation alone. However, when both visual and auditory cues were removed, the probability of capture following an interception dropped 3-fold (Figure 3D). Moreover, when we compared the duration of each intercept that did not lead to capture, mice stayed in contact (within 4 cm) significantly longer when hearing was available (dark: 1.1 ± 0.2 s; EP dark: 0.5 ± 0.1 s; $p < 0.05$, Kruskal-Wallis, Tukey-Kramer, honestly significant difference [HSD] post hoc). These data argue that either visual or auditory cues can facilitate successful near-range pursuit and final capture after the target has been contacted. They also explain the increase in total time to capture when both sensory modalities are removed.

Next, we sought to determine the distance at which approaches are triggered and measure the accuracy of each approach. The trajectories of approaches were determined by calculating the azimuth as a function of range for each sensory

condition. At ranges of 15–20 cm or less, prey azimuth decreased significantly under the lighted conditions (Figure 3E). Furthermore, in the light, mice maintained a precise bearing as they closed in on the target ($11.4 \pm 1.4^\circ$ at end of approach; Figure 3F). The accuracy of targeting in the dark ($41.1 \pm 1.2^\circ$; Figure 3F) was near chance, since the azimuth must be less than 90° to be approaching the target. Altogether, the analysis of approaches demonstrates that vision is necessary for allowing highly accurate targeting during the approach.

Vision Is Necessary for Prey Detection and Accurate Approach in a Modified Prey-Capture Paradigm

The demonstration that C57BL/6J mice utilize vision to perform prey capture opens up the potential to study the visual neural circuitry that underlies this behavior. To facilitate these efforts, we developed a simplified approach paradigm that relies on vision. In this assay, we placed live crickets behind a clear acrylic barrier that attenuated non-visual cues (Figure 4A). Furthermore, restricting the cricket to a one-dimensional path simplified the analysis of approaches. We quantified the horizontal distance between mouse head position and cricket position during approaches, which we term “lateral error” (Figure 4B, inset). Performance in this modified paradigm was assessed on day 5 of their training protocol, identical to the timeline used in the open-field condition. Therefore, the mice were experienced in prey capture but naive to the experience of encountering prey behind an acrylic barrier.

In the light, when mice were on the side of the arena with the cricket, they nearly always directly approached and investigated

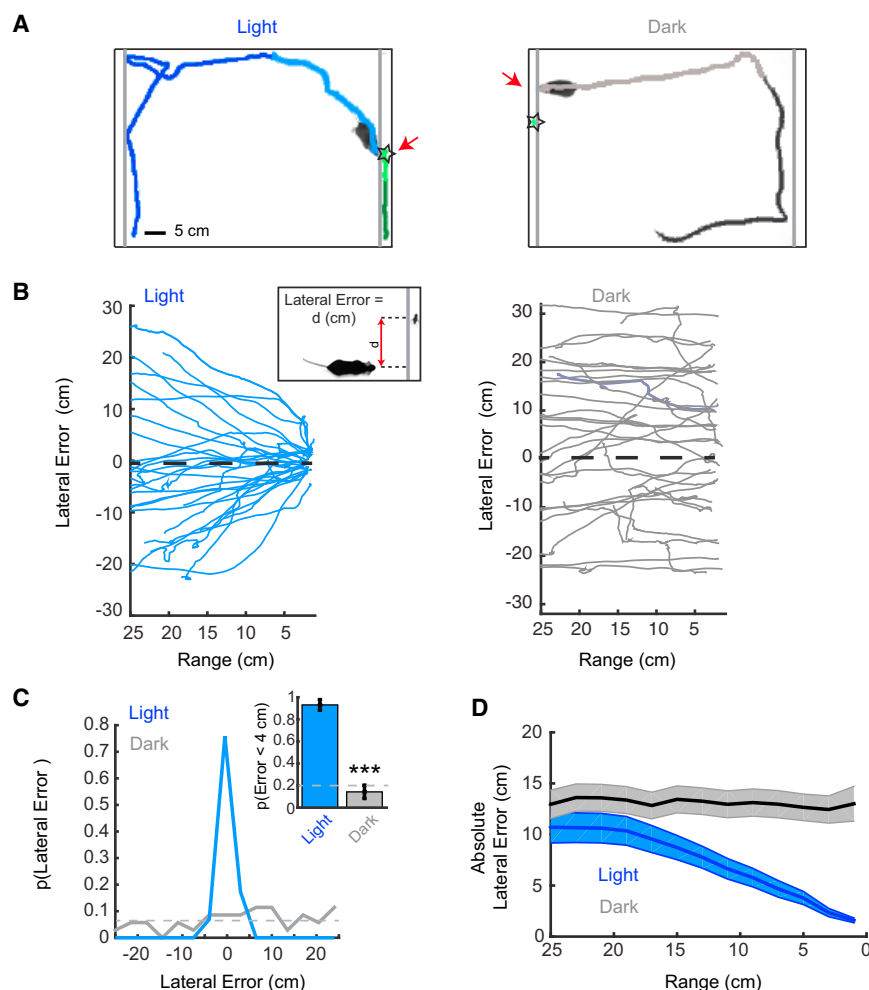


Figure 4. An Approach Paradigm Restricted to the Visual Modality

(A) Representative trials with the prey behind an acrylic barrier for the light (left) and dark (right) conditions. Gray lines indicate clear, acrylic barrier locations. The approach sequences are highlighted as lighter shading of the mouse's path. Stars indicate the prey's location when the mouse contacts the barrier. Scale bar, 5 cm.

(B) Lateral error as a function of range from the cricket for all of the mouse's approaches to the barrier in the light (left) and dark (right) conditions. Inset: lateral error was defined as the horizontal distance (d) that separated the location of the mouse's head from the location of the cricket. Positive differences denote that prey was to the left of the mouse, and negative values denote that prey was to the right of the mouse.

(C) Probability density functions of lateral errors at barrier contact in light and dark conditions. Inset: the probability that the mouse will contact the barrier at a location with a lateral error of less than 4 cm (approximately two cricket body lengths) from cricket. Gray dashed lines indicate chance performance levels.

(D) The mean absolute lateral error as a function of range during approach for light and dark conditions. Group absolute error data are mean \pm SEM; $n = 13$ and 13 mice, and $n = 29$ and 35 trials/approaches for the light and dark conditions, respectively. *** $p < 0.001$, Mann-Whitney U test. See also Movies S5 and S6.

the cricket's location (Figure 4B, left panel; Movie S5), even though they could not actually contact or capture the cricket. On average, mice contacted the barrier within a lateral error of 1.6 ± 0.2 cm of the target, or approximately the length of a cricket (Figure 4C). Further, $93\% \pm 5\%$ of mice made contact at the barrier with a lateral error of less than 4 cm from target (Figure 4C, inset).

In contrast, when mice were placed in the arena in the dark, their paths appeared directed to random locations along the acrylic barrier (Figure 4B, right panel; Movie S6). They contacted the barrier, on average, 13.5 ± 1.4 cm from the target (Figure 4C). This is almost half the length of the barrier, suggesting that barrier contact locations arose randomly. Furthermore, the mice made a "successful" contact on only $14\% \pm 6\%$ of approaches, compared to the 20% predicted by chance based on geometry (χ^2 , $p > 0.05$, $n = 35$; Figure 4C, inset). They also failed to modify their approach trajectory relative to the prey as they approached the barrier (Figure 4D). Thus, vision is necessary for successful approach behavior in this paradigm, as no other sensory modality could substitute for vision to allow performance above chance levels. Furthermore, the targeting we observed is highly accurate. This demonstrates that the paradigm produces robust, quantifiable visual orienting behaviors in the mouse.

Examining the lateral error during approaches shows that mice began deviating toward the target at a range of 15–20 cm, similar to the range at which they deviated toward the target in the open arena (Figure 3E). Given that the crickets are approximately 2 cm in length, a rough estimate of the angular size at which vision begins to guide approach at 15–20 cm is 6° – 8° . This is consistent with the receptive field diameter for many retinal ganglion cell types, although larger than the limits of visual acuity as assessed with grating stimuli [12–15]. Thus, this assay provides an estimate of the operating range of mouse vision that drives accurate approach behavior in a natural context. In future experiments, it will be possible to further explore the visual parameter space that drives prey detection and accurate orientation.

DISCUSSION

Here, we demonstrate that C57BL/6J mice pursue and capture live insect prey. Quantification of behavior under differing sensory conditions established that vision was necessary for accurate and efficient approaches. Most previous visual behavioral paradigms with laboratory mice have either relied on non-ethological operant training [1, 16–19] or navigation, including in virtual reality [20, 21]. A few recent studies of ethological mouse visual behavior have focused on visually driven fear responses to simple stimuli such as looming or light flashes [3, 4]. Therefore, our demonstration that mice use vision to detect prey stimuli and

drive precise visually guided motor output significantly advances our understanding of mouse visual neuroethology.

This study also revealed that auditory cues play a role in mouse prey-capture behavior at short target distances, although they were not sufficient for accurate long-range approaches in our paradigm. This may be due to the fact that the auditory cues generated by spontaneous cricket movement were relatively weak at distances where vision could guide approaches (Figure S2). It remains possible that mice could use audition more effectively after learning through extended experience in the dark or when pursuing targets that generate more salient sounds [22, 23]. Different environmental conditions could further affect the use of auditory cues, as the flooring substrate and acrylic walls of our arena may attenuate or reflect the sounds made by the cricket. Our results also suggest that olfactory and tactile cues are insufficient for effective orientation behavior at a distance. However, olfaction may still play a role in motivation, and mouse strains with poor visual acuity have demonstrated relatively enhanced olfactory capabilities [24, 25]. Thus, it will be interesting in future experiments to explore the conditions under which the various distance senses may modulate laboratory mouse prey-capture performance.

Although prey capture is more ethological than other recent operant visual tasks, freely moving behaviors introduce additional challenges to visual neurophysiology and imaging experiments relative to behaviors that can be performed in a head-fixed configuration. However, the development of head-mounted imaging systems [26] and eye tracking [27] may address these challenges. It may also be possible to establish head-fixed prey-capture tasks using a spherical treadmill with virtual stimuli [28].

Visual Control of Prey Capture across Species

The investigation of prey-capture behavior in many species has advanced our understanding of the neural basis of visual processing and sensory-motor integration. However, we have yet to obtain a detailed circuit-level understanding of the visual processing that underlies prey capture in the mammalian brain. Despite the advantages provided by genetic tools available in the mouse, laboratory mice have not previously been used to study prey capture. Of note, a carnivorous species of mouse, the grasshopper mouse (*Onychomys leucogaster*), has been well studied and is known to use vision for prey capture [8]. However, this wild species of mouse was subject to extreme environmental selective pressure and had acquired several physical and behavioral adaptations that are unique to the species and specifically aid prey capture. In contrast, *M. musculus* is more often considered to be a nocturnal prey species rather than a predator [29]. Nevertheless, they do consume invertebrates in the wild [30] and are active at dawn and dusk as well as night, consistent with our findings that they use vision for prey capture.

Studies of prey capture in non-mammalian species suggest a role for the superior colliculus in the behavior we observe here. Classic work investigating prey capture versus object avoidance in toads demonstrated that distinct visual pathways are required to produce the two types of visually guided behaviors: the optic tectum (non-mammalian homolog of the superior colliculus) mediates prey capture, and the pre-tectum mediates

avoidance [31–33]. In addition, recent work in the zebrafish, a genetically tractable species, has established a role for specific retinal ganglion cell types in triggering approach, as well as defined inhibitory cell types within the optic tectum that provide the size tuning that distinguishes prey versus predator stimuli [34].

In rodents, a combination of lesion and micro-stimulation experiments conducted in the superior colliculus have shown striking effects on orienting and alerting behavior [6, 35, 36]. These behaviors are thought to underlie prey-capture behavior and argue for significant conservation of visual system structure and function across vertebrate species. Moreover, recent studies of predator avoidance behavior in mice have revealed that the cortex can modulate the processing of visual stimuli that drive innate behaviors in the superior colliculus [4, 5]. Therefore, an important future goal will be to understand how defined neural circuits within both the superior colliculus and cortex contribute to prey capture, from stimulus detection to visually guided locomotor output.

SUPPLEMENTAL INFORMATION

Supplemental Information includes Supplemental Experimental Procedures, two figures, and six movies and can be found with this article online at <http://dx.doi.org/10.1016/j.cub.2016.09.009>.

AUTHOR CONTRIBUTIONS

J.L.H. conceived the project. J.L.H., M.W., and C.M.N. designed the experiments. J.L.H. and I.Y. refined experimental approaches. J.L.H. performed and supervised behavioral experiments, scoring, and tracking. J.L.H., C.M.N., and M.W. analyzed and interpreted the data. J.L.H. and C.M.N. co-wrote the manuscript. J.L.H., I.Y., M.W., and C.M.N. finalized the manuscript.

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