

RESEARCH ARTICLE

Predatory behavior changes with satiety or increased insulin levels in the praying mantis (*Tenodera sinensis*)

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ABSTRACT

At any given moment, behavior is controlled by a combination of external stimuli and an animal's internal state. As physiological conditions change, vastly different behaviors might result from the same stimuli. For example, the motivation to hunt and hunting strategy are influenced by satiety. Here, we describe how sensory responsiveness and motor activity of a praying mantis (*Tenodera sinensis*) change as the insect feeds, leading to an altered hunting strategy. We further show that these changes can be induced by injection of insulin, which likely functions as a metabotropic indicator. Praying mantises directed their attention toward real and simulated prey less often as they fed and became sated. The range of distance and azimuth at which prey was detected decreased as did pursuit of prey, while opportunistic close-range attacks persisted. Together, these sensorimotor changes are indicative of a behavioral paradigm shift from 'pursuit' to 'ambush'. A similar effect was induced in starved praying mantises injected with 0.05 ml of 200 $\mu\text{g ml}^{-1}$ bovine insulin. These experiments showed that insulin injection into the circulating hemolymph is sufficient to decrease prey orientation as well as in prey-directed locomotor behaviors (tracking and pursuit). The effects of prey consumption and insulin injection were similarly dose dependent. These results suggest that insulin is a signal of internal, physiological conditions that can modify responses to external stimuli. A change in hunting strategy thus results from coordinated effects of a neurohormone on a set of independent sensorimotor processes and the overall activity level of the animal.

KEY WORDS: Sensory responsiveness, Motor activity, Neurohormone, Prey identification, Selective attention, State dependence

INTRODUCTION

In their natural habitat, predatory animals must extract crucial sensory information to locate and capture prey. Many obligate predators rely heavily on vision to scan for prey-specific external factors such as distance, size and direction before integrating the information downstream in the central nervous system (CNS) (Prete, 1999; Ewert, 1987; Yamawaki and Toh, 2003). Furthermore, it has been shown in mantises (as in dragonflies, spiders and amphibians) that certain spatiotemporal features implicitly represent 'prey' and are summated to elicit appetitive behavior (Olberg, 1981; Nelson and Jackson, 2012; Ewert, 1987). For mantises, known visual

stimulus parameters that fall within this schema and evoke predatory responses include: (1) size, (2) contrast to the background, (3) leading edge length, (4) speed, (5) location in the visual field, (6) relative direction of movement, (7) geometry related to movement direction, (8) retinal distance traversed, and (9) the degree to which sub-threshold stimulus elements are summed over time and (10) space (Prete et al., 2011; Kral and Prete, 2004). The resulting hunting strategy is then a species-specific combination of selective responsiveness to sensory stimuli and the predator's motor repertoire, both of which can be influenced by dynamic changes in physiological state and prior experience (Prete et al., 2013).

Although all mantises are considered to be predatory insects, there is tremendous species-level variation in their hunting and strike behaviors, which is further influenced by an individual's immediate internal and external conditions. For example, comparisons of appetitive responses reveal species-specific preferences for certain target sizes and shapes across three species with differing ecological niche specializations (Prete et al., 2011). Niche-specific characteristics may also be responsible for variation in preference for prey target speed. It was generally thought that mantises strike at rapid targets that fall within their size and shape preference range, but *Sphodromantis lineola*, was demonstrated to prefer slower moving targets (Prete et al., 1993). *Euchomenella macrops* will strike at targets that have recently ceased movement (Prete et al., 2012). Clearly, finite variation in appetitive response parameters is present in the few species tested and niche specialization is a contributing factor (Prete et al., 2011). Despite this variation, two main hunting strategies have been proposed. Cursorial mantises which occupy forest or desert floors have been shown to stalk and actively pursue prey (type 1) before capturing and consuming it (Balderson, 1991; Rossel, 1980). Alternatively, arboreal mantises which live in more heavily foliated environments predominantly display an ambush strategy (type 2), in which the predator remains motionless and allows the prey to come into range, where it is attacked and captured (Inoue and Matsura, 1983). Unfortunately, it is not known how strictly these types can be applied to mantis species. It is possible that every species is able to shift between types with varying degrees, but those that do regularly cross between type 1 and type 2 are termed generalists (Svenson and Whiting, 2004).

Matsura and Inoue hypothesized that satiety level in the generalist mantis *Tenodera augustipennis* is the most likely factor in influencing the type of hunting strategy (Inoue and Matsura, 1983; Matsura and Inoue, 1999). Subsequent experiments demonstrated that after an 8–9 day starvation period, mantises showed a substantial increase in the distance to which they would track and approach prey when compared with that after a 2–3 day starvation period (Prete et al., 1993). Additionally, it has been noted that male mantises in the high hunger group (one cricket per week) increased their strike rate but their stimulus size preference remained the same (Prete et al., 2002). Internal state can even impact a mantis's food preference as demonstrated by *S. lineola*, which will investigate and consume fruit using their antennae for detection when prey is absent (Prete

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et al., 1992). This significant shift in feeding strategy suggests chemoreceptive input contributes to state-dependent hunting strategy rather than visual cues alone. Taken together, evidence supports that the level of satiety plays a key role in tuning CNS sensitivity to food-related stimuli – a concept known as ‘central excitability’ (for review, see Simpson and Bernays, 1983; Dethier et al., 1965).

In the case of state-dependent predation, sensory systems such as vision may become less sensitive to distant cues, thereby limiting the predator’s attention to nearby targets. These changes have important consequences for the predator’s survival. As many insect predators are also prey for other animals, the movements involved in stalking should only be chanced when the predator is hungry. With satiety, the immediate need for feeding diminishes, tilting active predatory behavior (type 1) in favor of the sedentary ambush strategy (type 2). Therefore, the hunting behavior must be the calculated summation of a number of interoceptive and exteroceptive cues such as hunger state, food availability, prey attractiveness, predation risk, competition and the physical properties of the environment (for review, see Yamawaki, 2017; Copeland and Carlson, 1979).

One likely candidate for effecting satiety-based changes is the peptide hormone insulin, the main regulator of glucose metabolism from worms to humans through the highly conserved insulin signaling pathway (ISP) (for review, see Mattila and Hietakangas, 2017). Insulin-like peptides (ILPs) play a vital role in insect growth and nutrient storage (Wu and Brown, 2006). In *Drosophila*, three of the eight currently identified dILPs have been localized to the median neurosecretory cells (MNCs) of the protocerebrum but evidence of insulin’s effect on hunting strategies has not been demonstrated (Brogiolo et al., 2001).

Here, we investigated the effects of satiety on predatory behavioral responses in *Tenodera sinensis* (Saussure 1871) hunting both live cockroach nymphs and computer-generated virtual prey. Our prey consumption assays assess how satiety changes three of the components of predatory behavior: goal-oriented attention, directed locomotion and prey capture. Next, we tested the effects of abdominally injected insulin on those same behaviors. Finally, we used simulated prey to control the azimuth and distance of the stimuli, to assess how satiety and insulin alter spatial attention as part of the shifting hunting strategy. Our results show that both insulin and consumption of prey change the behavioral responses of a generalist praying mantis, ultimately switching hunting strategy from pursuit to ambush. Indeed, the changes associated with prey consumption and insulin injection follow similar dose-dependent relationships.

MATERIALS AND METHODS

Mantis maintenance and care

Adult female *T. sinensis*, 14–18 days post-eclosion, were used in all experiments. Animals were reared and housed individually in 1.8 l plastic containers, given food and water *ad libitum*, and kept on a 12 h:12 h light:dark cycle at 27°C. Laboratory-reared animals were deprived of food but not water for 5–7 days before each experiment. We selected only healthy mantises with all limbs and external sensory structures intact for experiments. All experimental animals were treated appropriately, and we operated in accordance with all ethical animal care guidelines.

Consumption assay

The experimenter presented the mantis with four cockroach nymphs (mean mass 190 mg) for 7 min trials in an acrylic area (37×29 cm) underlit with LCDs. The cockroach nymphs were selected based on overall body size relative to the virtual prey stimulus (see below). We allowed the mantis to acclimate to the arena before starting the

timer. We digitized only the instances of visual orientation to the prey items, disregarding all tactile stimulus-initiated cases. When the mantis captured a prey, the experimenter gently picked up the mantis and removed the cockroach from her grasp before placing both insects back into the arena so that repeated trials could be run at that feeding level.

Virtual prey stimulus

In the virtual prey trials, we showed a computer-generated black ellipse (2 cm×1 cm) to mimic the appearance of live prey on a white LCD screen beneath an acrylic arena. This ‘worm’-shaped stimulus has been shown to be preferred by *T. sinensis* (Prete et al., 2011). We wrote custom MATLAB scripts (The MathWorks Inc., Natick, MA, USA) using the PsychToolbox suite so that the disks could be presented to the mantis at reproducible angles and at one of five predetermined distances: 2.5, 5.0, 7.5, 10.0 and 12.5 cm (Brainard, 1997). Each oval stimulus was presented at one of eight randomly determined starting angle positions relative to the central body axis of the animal: 0, ±45, ±90, ±135 or 180 deg and moved back and forth starting with either clockwise or counter-clockwise movement at a speed of 2 cm s^{−1} (Fig. 1B). After traveling for 1 s in the initial direction, the stimulus changed to the opposite direction before changing back and forth once more. The stimulus was present for a total duration of 4 s before disappearing. We presented 40 stimuli in this fashion, eight per distance, or one per angle position to effectively cover the visual field. The distances, angles and direction of the stimuli were all randomized for each trial.

Scored behaviors

For each of the experiments, we quantified three behaviors: (1) indications of attention to the prey or target including head movement, rotation of the prothorax or leg turning movements, (2) steps taken towards the prey stimulus but only after 1, and (3) the first raptorial foreleg strike at the prey stimulus. We observed but did not quantify the following: continual tracking of the stimulus after strike, escape attempts away from the prey item and number of strikes (if greater than one per stimulus). We defined a step as the instance where the animal lifted a leg and repositioned it with the result of closing the overall distance between it and the prey item. We defined pursuit as three or more steps taken towards the prey item.

Video capture and digital analysis

All of the experimental trials were recorded at 30 frames s^{−1} using a Casio Exilim or Point Grey Flea3 camera; the video data were then digitized using Tyson Hedrick’s MATLAB-based software package DLTdv6 (Hedrick, 2008). We completed all further analysis using custom-written MATLAB scripts.

Injection treatments

Unless otherwise stated, we treated the praying mantises with 200 µg ml^{−1} bovine insulin dissolved in Blagburn and Satelle cockroach saline (Blagburn and Satelle, 1987). For control experiments, we used Blagburn and Satelle cockroach saline alone. For abdominal injection experiments, we injected 0.05 ml of room temperature solution using a hypodermic syringe underneath the eighth tergite on the left side of the ventral midline before placing the animal back into the experimental arena. The animal was given 15 min to recover from the puncture wound before testing.

Statistical analyses

Statistical significance was determined using one-way ANOVA, Kruskal–Wallis (K–W), Kolmogorov–Smirnov (K–S) and Harrison–Kanji (H–K) tests in custom-written MATLAB scripts.

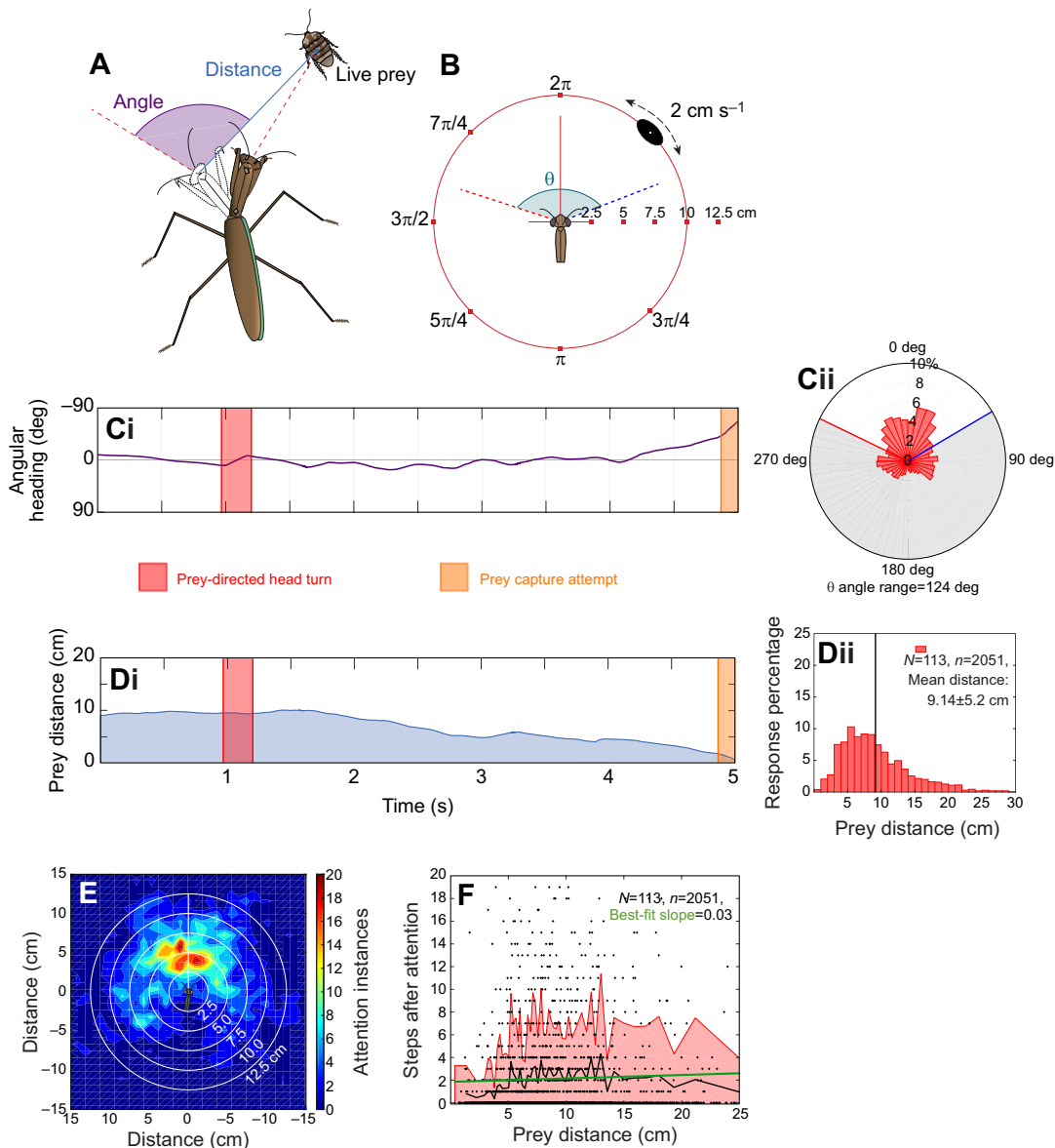


Fig. 1. Methods. (A) Schematic diagram showing the praying mantis at the point of attention, detailing the two measurements of azimuthal angle and distance. Angle was measured relative to the longitudinal axis of the mantis' head before any movement occurred. The distance was measured from the center of the praying mantis' head to the prey in the same fashion. (B) Diagram showing the distances and angles at which the virtual prey ellipse would appear before moving in a circular path around the animal. The distance, angle and start direction were randomized while the size, speed and distance traveled were held constant. The median angular range, θ , was estimated by collecting the median response angle on both hemispheres (red and blue lines) and summing the differences from 0 deg. (Ci) Example graph depicting the praying mantis' angular heading over time in degrees. The shaded areas represent the moment of the prey-directed head (red) and the moment of strike (orange). (Cii) Polar histogram showing the breakdown of head turn angles after attention. All of the response angles collected (red area in Ci) were used to find the median response angles (red and blue lines) which gave a θ angle range of 124 deg. (Di) Example graph showing the prey distance over time measured using the method described in A. (Dii) Histogram showing the response percentage of attention over prey distance. The black line represents the mean distance of attention. N , number of mantises used; n , total number of individual bouts of attention. (E) Heat map showing the cockroach position at the point of visually initiated attention in starved praying mantises. (F) Graph showing the number of steps taken in pursuit of a cockroach nymph over prey distance at the point of attention in starved praying mantises. The black line represents the mean steps per unit distance $\pm$ s.d. (red area). The line of best fit is shown in green.

Experimental data and scripts

All experimental data used for these experiments and the custom-written MATLAB scripts may be obtained upon request from the corresponding author.

RESULTS

Live prey consumption assay

We placed starved female praying mantises in an underlit arena with four cockroach nymphs for 7 min trials. The animals could attend to,

stalk and capture the prey freely but after capture, the cockroach nymph was removed from the mantis's grasp by the experimenter. We restricted consumption in this way until after the trial was completed to allow for further data collection at that satiety level. After the 7 min trial, we took the mantis out of the arena and allowed it to consume a caught nymph. Once the animal had finished its meal, we placed it back into the arena for another trial. This procedure continued until four cockroach nymphs were consumed or the praying mantis stopped attending.

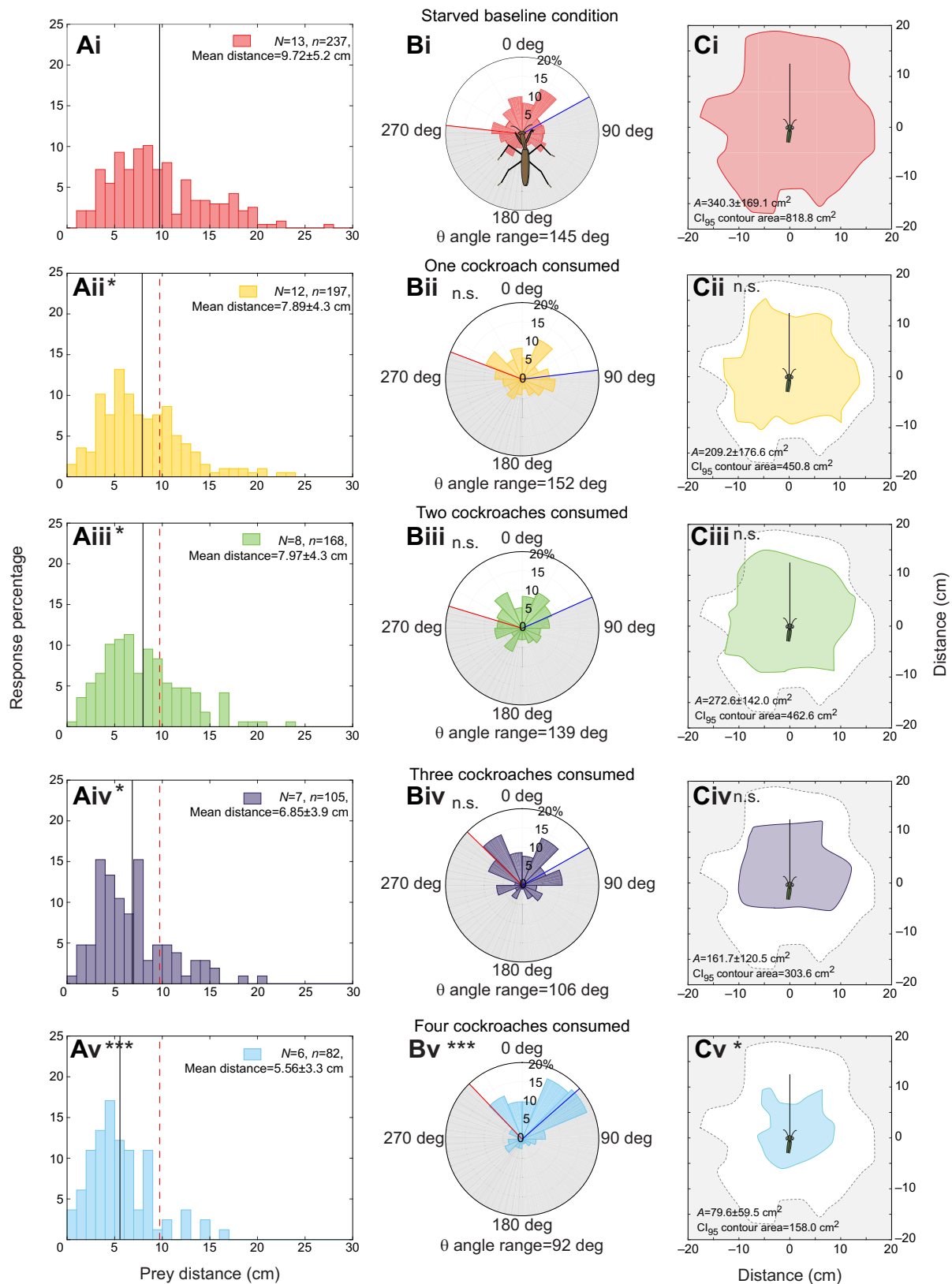


Fig. 2. See next page for legend.

The mantises showed a robust directed attention response towards the prey items, turning the head to focus on the cockroach in the center of its visual field (Movie 1). Once the mantis attended to a particular nymph, it disregarded other items even if they were closer

or in more compromised positions (i.e. on their backs, unable to escape). If the prey in question was at an obtuse angle from the midline, the mantis would enhance the head movement by turning the pronotum to center on the prey. Occasionally, the mantis

Fig. 2. The effects of consumption on prey-directed attention and search behavior towards live prey. (A) Histograms displaying the response percentage towards cockroach nymphs over distance measured from the mantis' head to the prey for five satiety conditions. The vertical black line represents the mean distance of attention and, in Aii–v, the dashed vertical red line depicts the mean distance for the baseline condition. All treatments were significantly different from baseline [two-sample Kolmogorov–Smirnov (K–S) test, $P<0.05$]. The four cockroaches consumed condition (Av) was also significantly decreased when compared with the one and two cockroaches consumed conditions ($P<0.05$). (B) Polar histograms showing the angularity of attention points relative to the midline axis divided into 16 bins of 22.5 deg. The median-bound angular area, θ , is listed below each histogram. The four cockroaches consumed condition was significantly more acute than baseline as well as when compared with the one and two cockroaches consumed conditions [Harrison–Kanji (H–K) circular ANOVA, $P<0.05$]. (C) Spatial attention clouds were created using a Gaussian-smoothed 95% confidence interval (CI₉₅) contour line to capture the maximum search area (A , cm²) for all of the satiety conditions. The dotted area in Cii–v represents the CI₉₅ contour area of the baseline condition. The four cockroaches consumed condition was significantly reduced from baseline (one-way ANOVA, $P<0.05$). *Significant difference from baseline; **significant difference from baseline and the one cockroach consumed condition; ***significant difference from baseline and the one and two cockroaches consumed conditions.

supplemented this movement by leg pivots or turns. The mantis would continue to keep the target in the center of its visual field as the nymph moved around the arena and/or the mantis pursued its prey. Once the prey item was within 1–2 cm, the mantis executed a strike by extending its raptorial forelegs outward accompanied by a forward lunge.

In our analysis, we measured the angle of the praying mantis's head at the moment of attention as well as the distance from the original head position to the prey (Fig. 1A). Similar values were also calculated for virtual prey trials (Fig. 1B). We plotted the changes in head angle associated with prey detection and the distance at which a response occurred separately (Fig. 1C,D, respectively). These data were then combined in a 2D map of angle and distance around the mantis's head where attention was evoked, later depicted as area plots bounded by the 95% confidence interval (Fig. 1E; Fig. S1A,B). Finally, the steps taken after attention were plotted against prey distance (Fig. 1F; see also Fig. S1C). With these data, we compared the head angle, distance, two-dimensional attention values, step number and strike instances as the mantis fed on increasing numbers of nymphs.

Fig. 2 details the results of the sensory changes observed in these five increasing satiety treatments. Graphs in Fig. 2A show the percentage of attention responses over the prey distance at which it occurred. We observed that after the mantis ate one cockroach nymph, the distance at which it would attend to future prey shrank significantly (Fig. 2Aii; mean distance 7.89 cm) when compared with the starved baseline condition (Fig. 2Ai; mean distance 9.72 cm). This trend continued as the number of cockroaches consumed increased. The mean distance for the four cockroaches consumed condition shown Fig. 2Av (5.56 cm) was, therefore, significantly reduced from those of the starved baseline and the one and two cockroaches consumed conditions (two-sample K–S test, $P<0.05$).

Interestingly, the angle range of interest did not decrease at the same rate, as shown in Fig. 2B. No significant reduction was observed in the one, two or three cockroaches consumed conditions when compared with the starved baseline (median angle boundary range, $\theta=145$ deg), although a non-significant trend toward restricted angles was seen with the three prey consumed condition (Fig. 2Biii). Only after eating four nymphs was a significant angular decrease observed (Fig. 2Bv; $\theta=92$ deg) (H–K circular ANOVA, $P<0.05$), suggesting different rates or mechanisms of action.

The detection range graphs in Fig. 2C visually represent the summated results from the distance and angle measurements. These plots show the maximum area that the mantis attends, constructed using scatter plot data (e.g. Fig. 1E) and a Gaussian-smoothed contour line at the 95% confidence interval. Additionally, using the individual area measurements, we collected mean areas and s.d. We determined that the four cockroaches consumed condition (Fig. 2Cv; $A=79.6$ cm²) was significantly reduced when compared with the starved baseline (Fig. 2Ci; $A=340.3$ cm²) (one-way ANOVA, $P<0.05$). Again, this completes a non-significant trend seen in the one, two and three cockroaches consumed graphs (Fig. 2Cii–Civ).

A decrease in motor activity accompanied these sensory deficits. Fig. 3 displays the locomotive patterns for the same five satiety conditions shown in Fig. 2. Fig. 3A shows the number of steps taken while attending against the prey distance. We used this measurement as a proxy of overall activity and determined that the starved mantis pursues prey items reliably out to ~20 cm (Fig. 3Ai). As with the distance measurement, the overall stepping activity significantly decreased as each prey item was consumed when compared with the starved baseline condition. The four cockroaches consumed condition (Fig. 3Av; mean 0.46 steps) was significantly reduced from both the starved baseline and the one cockroach consumed condition (2.94 and 1.43 steps, respectively) (non-parametric K–W test, $P<0.05$).

Within the stalking attempts were two subsets of data: those that resulted in a strike and those that did not. We further analyzed the former group as a 'motivational pursuit' assay. These data indicated that starved mantises were willing to take more steps in pursuit of a prey item before striking than was a sated one. In these type 1 pursuit scenarios, we observed that after consuming two nymphs, the animals took significantly fewer steps before striking at the prey. Additionally, we found a significant reduction in steps in the four cockroaches consumed condition (Fig. 3Bv) from both the starved baseline and the one cockroach consumed condition (K–W test, $P<0.05$). These animals took an average of 0.28 steps before striking compared with the 3.81 steps in the starved baseline condition (Fig. 3Bi), which was a significant reduction.

As both the predator and prey were free to walk in this experiment, it is possible that most of the distance change during pursuit can be attributed to the prey's movements. We therefore analyzed the fraction of the total movement between each animal to ensure that the mantis's movement patterns were changing. The bar graphs in Fig. 3B show the percentage of the total distance attributed to the mantis compared with the prey. A reduction from 36% in the starved baseline condition to 6% in the four cockroaches consumed condition shows that the mantis, although still attending to items outside of its reach, waits for the prey to come to it instead of closing the distance itself, which is indicative of the type 2 ambush strategy. Ethologically, this relationship is supported by a significant reduction in the amount of pursuit attempts adjusted for the instances of attention (Fig. 3C) where pursuit is defined as 3+ directed steps while attending to the prey. The occurrence of pursuit behavior significantly decreased after the mantis had eaten two nymphs but the strike frequency did not decline significantly until after three nymphs had been consumed (one-way ANOVA, $P<0.05$). For reference, 49% (number of observed strikes, $n_s=116$ of 237) of the attention instances in the starved baseline condition led to an attempted prey capture.

Meal size assay

The effect seen with consumption of four cockroach nymphs could be due to the time taken to consume, digest and release substances



such as insulin or due to the total caloric value of the food consumed. In the first case, the same effect might be seen after fewer prey were consumed but with the same delay. To test this, we compared the four

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Fig. 3. The effects of consumption on prey-directed stalking and predatory behavior with live prey.

(A) Line graph showing the number of steps taken after attention against prey distance for all satiety conditions. The black line represents the mean number of steps at a given distance $\pm$ s.d. A line of best fit (purple) was fitted to the data and, in Aii–v, the dashed red line represents the best fit. All four of the post-consumption treatments were significantly decreased from baseline [two-sample Kruskal–Wallis (K–W) test, $P < 0.05$]. (B) The subset of data from A that led to strike attempts were analyzed separately. These ‘motivational pursuit’ scatter plots show the steps taken after attention but before striking at the prey over the prey’s initial distance. The dotted line represents the line of best fit. The bar highlights the mean percentage of the total movement that can be attributed to the praying mantis versus that of the prey. The two, three and four cockroaches consumed conditions were significantly different from the baseline condition (two-sample K–W test, $P < 0.05$). The four cockroaches consumed condition showed a significant difference from both the starved baseline and the one cockroach consumed conditions ($P < 0.05$). n_S , total number of strikes released. (C) Box and whisker plots showing the mean percentages of pursuit and striking behavior after attending to a cockroach nymph, normalized for attention. The level of pursuit for the two, three and four cockroaches consumed conditions was significantly reduced from baseline. Additionally, the percentage of striking was significantly reduced from baseline in the three and four cockroaches consumed conditions (one-way ANOVA, $P < 0.05$). *Significant difference from baseline; **significant difference from baseline and the one cockroach consumed condition; ***significant difference from baseline and the one and two cockroaches consumed conditions.

assay. We expected that if continued metabolism was responsible for the observed changes, we would see a significant decrease in all five behavioral measures, as shown previously in the four cockroaches consumed condition. However, in the post-consumption trial, this ‘normal-sized meal’ led to no significant reduction in the distance of attention (Fig. 4Aii; K–S test), the angularity of attention (Fig. 4Bii, H–K circular ANOVA) or the detection area (Fig. 4Cii; one-way ANOVA) from the starved baseline condition. Additionally, there was no significant decrease in the prey-directed steps of the mantis after attention (Fig. 4Dii; K–W test) or in the motivational pursuit scatter plots (Fig. 4Eii; K–W test).

In the second case, the amount of food consumed in the four prey consumed condition is the critical factor. To address this question, we tested a second group of mantises at the 75 min post-consumption time point. These mantises, however, consumed a ‘large-size meal’, equivalent to the size of the four cockroaches consumed condition. The overall mass difference in these two experimental groups was measured at +12% for the normal-sized meal cohort and +30% for the second ‘large-size meal’ group.

This large-sized meal did cause a significant decrease in the response distance compared with both the starved baseline and the normal-sized meal conditions (Fig. 4Aiii; K–S test, $P < 0.05$). The angularity (Fig. 4Biii) and detection area measurements (Fig. 4Ciii) were not significantly different from those of the other two conditions. The large-meal condition (Fig. 4Diii) showed significantly reduced stepping patterns when compared with the starved baseline (Fig. 4Di) and the normal-sized meal conditions (Fig. 4Dii; K–W test, $P < 0.05$). The motivational pursuit scatter plots further demonstrated that after consuming a large meal, the animals were significantly less likely to take steps in pursuit of a prey item. Fig. 4Eiii shows this significant reduction in the amount of steps that the animal will take to capture a prey item when compared with the starved baseline (Fig. 4Ei) as well as the normal-sized meal (Fig. 4Eii) condition (K–W test, $P < 0.05$). Instead – as previously shown in Fig. 3B – the mantis will allow the cockroach nymph to approach before striking instead of pursuing the prey itself.

The combination of these significant reductions resulted in fewer pursuit and strike attempts after attention, as shown in

Fig. 4F. The large-sized meal condition showed significantly fewer prey pursuits and strike attempts when compared with the starved baseline condition (one-way ANOVA, $P < 0.05$). From this experiment, it can be determined that although the timed release of downstream metabolic processes could have an appreciable effect on hunting behavior, the overall magnitude of the satiety change (i.e. prey size) leads to significant reductions in hunting behavior.

Insulin concentration gradient assay

With the understanding that the caloric size of the ingested meal affects the observed differences, we tested to see whether the graded release of the downstream metabolic neuromodulator insulin affected the outward behavior in a similar way to the consumption assays. Insulin is a reasonable candidate for a satiety mediator as ILP release occurs in a dose-dependent manner in response to food consumption. We tested six different concentrations of bovine insulin (6.25, 12.5, 25, 50, 100 and 200 $\mu\text{g ml}^{-1}$) in cohorts of 10 mantises each. We placed the starved mantises in the arena for 7 min trials, as described above. After completion of the trials, we injected 0.05 ml of the insulin solution into the mantis’s abdomen and then allowed the animal to rest for 15 min.

We noted that the insulin solution took effect between 5 and 10 min after injection. All insulin-injected insects showed a noticeable decrease in locomotor activity. However, they were all capable of responding, righting themselves, grasping and moving their antennae after perturbation. A select few showed brief deimatic responses in the post-injection trial but these were probably due to the abdominal injection puncture wound.

Fig. 5A shows the attention response percentages over the prey distance 15 min after injection for the six insulin concentrations. We observed a significant reduction from baseline in all six of the tested concentrations. The 100 and 200 $\mu\text{g ml}^{-1}$ concentrations showed an additional significant reduction from the 6.25, 12.5, 25 and 50 $\mu\text{g ml}^{-1}$ concentrations (Fig. 5Av,vi; K–S test, $P < 0.05$). The wide-field angularity decreased in all of the post-injection treatments (Fig. 5B) (H–K circular ANOVA, $P < 0.05$). Furthermore, the animal’s willingness to attend to oblique prey items reduced as the concentration of insulin increased. In Fig. 5Bv (100 $\mu\text{g ml}^{-1}$), we saw a further significant reduction from the 6.25 $\mu\text{g ml}^{-1}$ insulin concentration; this was narrowly missed in the 200 $\mu\text{g ml}^{-1}$ insulin condition (Fig. 5Bvi; $P = 0.0536$).

Fig. 5C shows the resulting effects of concentration on the detection range. No significant differences from pre-injection were noted with 6.25 or 12.5 $\mu\text{g ml}^{-1}$ insulin (Fig. 5Ci and Cii, respectively) although a trend toward constriction was noted. Consistent with this trend, the four higher concentrations of insulin resulted in significant reduction in the overall detection area when compared with the pre-injection baseline (Fig. 5Ciii–vi; K–W test, $P < 0.05$). Fig. S3 depicts the baseline information for this experiment.

The prey-directed motor behavior after insulin injection showed similar results (Fig. 6). Fig. 6A shows a decrease in the overall stepping activity after attention, and insulin concentration correlated with the magnitude of this decrease. There was significant reduction from the pre-injection baseline in the 6.25, 100 and 200 $\mu\text{g ml}^{-1}$ insulin conditions (Fig. 6Ai,v,vi; K–W test, $P < 0.05$). When we looked at the attention trials that led to strikes (Fig. 6B), we saw that the 200 $\mu\text{g ml}^{-1}$ insulin-injected animals took significantly fewer steps than for the pre-injection baseline before striking (Fig. 6Bvi; K–W test, $P < 0.05$). There was no significant reduction for the other insulin concentrations when compared with baseline.

To gauge the rate of decrease, we plotted the individual mean distance of attention against the log-transformed concentration of

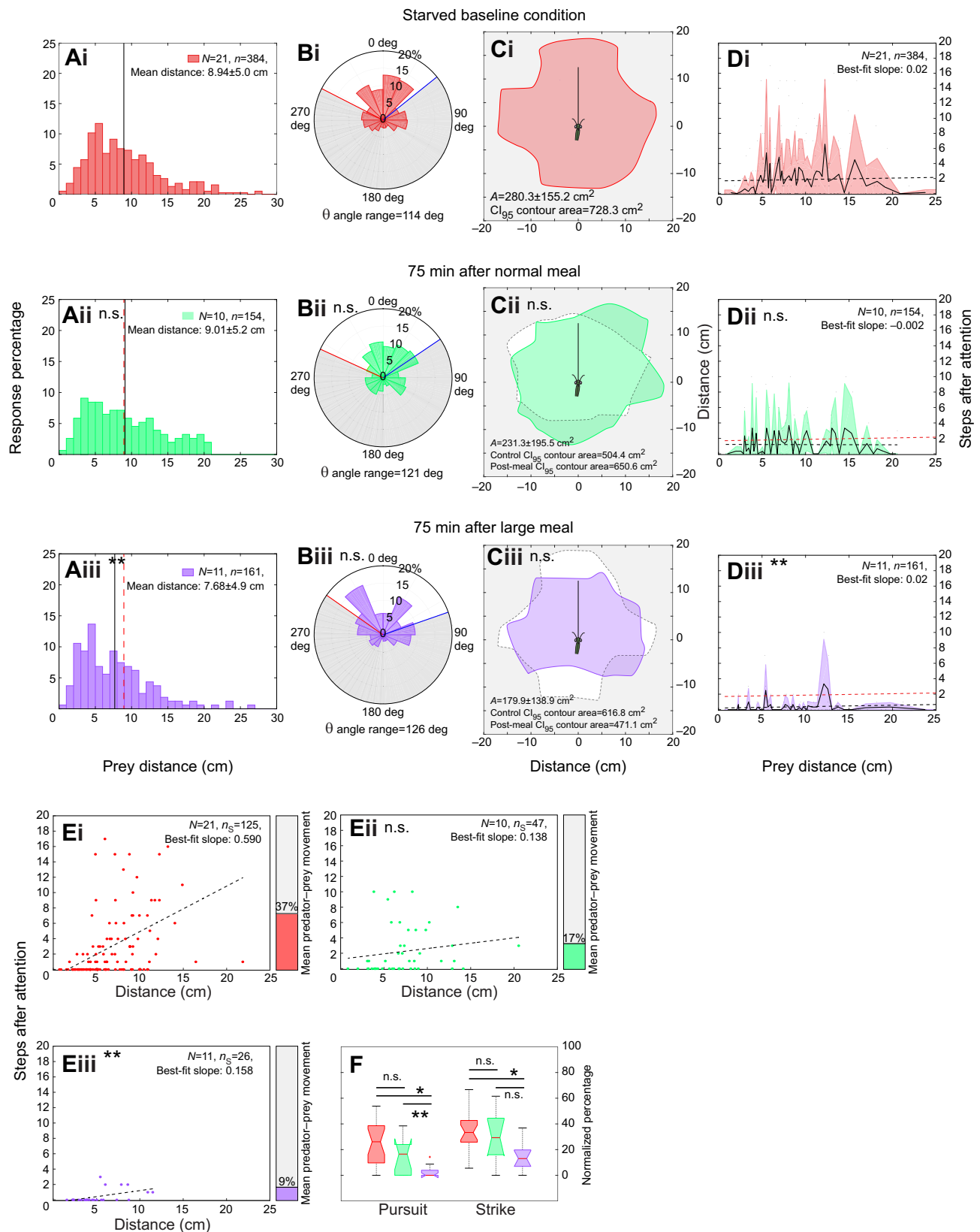


Fig. 4. See next page for legend.

insulin (Fig. 6C). The slope of the best-fit line was calculated to be -0.71 and $R^2=0.94$ where $P>0.0001$. For comparison, we plotted a similar graph with the consumption series data shown in Fig. 2

(Fig. S2Ai), from which we calculated a linear regression line from the mean distance of attention for each animal over the number of prey items consumed. This showed a significant inverse relationship

Fig. 4. The effects of different sized meals on prey-directed attention and search behavior with live prey. (A) Histograms showing the response percentage over prey distance. The response for the large meal condition (purple) was significantly reduced from that of both the starved baseline and the normal-sized meal condition (green) (two-sample K–S test, $P < 0.05$). (B) Polar histograms showing the angularity of attention relative to the animal's midline axis. No significant differences were observed between the angularities. (C) Spatial attention clouds depicting the mantis' maximum search range. No significant differences were observed between the area measurements (A, cm^2). (D) Line graphs illustrating the number of steps taken after attention over prey distance. The number of steps for the large-sized meal condition was significantly reduced from that for both the baseline (Ei) and the normal-sized meal (Eii) condition (two-sample K–S test, $P < 0.05$). (E) 'Motivational pursuit' scatter plots showing striking trials from D. The number of steps for the large-size meal condition (Eiii) was significantly reduced from that of both the baseline and the normal-sized meal condition (two-sample K–S test, $P < 0.05$). (F) Box and whisker plots showing the mean percentages of pursuit and striking after attending to a nymph, normalized for the attention instances in each condition. The level of pursuit after consuming a large-sized meal was significantly reduced from both the baseline and the normal-sized meal condition (one-way ANOVA, $P < 0.05$). The percentage of striking was also significantly reduced from baseline but not when compared with the normal-sized meal condition. *Significant difference from baseline; **significant difference from baseline and the normal meal condition.

between the two variables with a slope of -0.90 . The θ range and area measurements were similarly significant (Fig. S2Aii,iii; $P < 0.05$). We calculated similar regression lines for the median angle range and the detection area of both the consumption and concentration gradient series (Fig. S2).

As with the consumption series, a motor decrease in the percentage of pursuit attempts accompanied the sensory decrease in attention distance of the concentration gradient series (Fig. 6D). When compared with the starved baseline condition, the likelihood of prey pursuit decreased significantly with 6.25, 25, 50, 100 and 200 $\mu\text{g ml}^{-1}$ insulin. Comparatively, the effect on the number of strike attempts toward the prey was inconclusive; significant decreases were observed with 50 and 100 $\mu\text{g ml}^{-1}$ insulin but not with 6.25, 12.5, 25 and 200 $\mu\text{g ml}^{-1}$ insulin (one-way ANOVA, $P < 0.05$).

Virtual prey assay

The drawback of using live animals as prey stimuli is that they are inherently variable in their size, speed, behavior and attractiveness towards the praying mantis. Additionally, the prey items are present in the arena throughout the duration of the trial, making calculations on the level of directed attention impossible. We therefore constructed a virtual prey arena using a moving black ellipse as the prey item based on previous work by Prete and colleagues (Gonka et al., 1999; Prete and McLean, 1996; Prete et al., 2013). This method allowed us to control the size, speed, direction and distance of prey presentation while still using the same arena as in the previous experiments. We presented each starved mantis with 40 virtual prey presentations (8 angular positions at 5 distances; Fig. 1C). Then we injected the mantis with 0.05 ml of either 200 $\mu\text{g ml}^{-1}$ bovine insulin dissolved in saline or saline alone as a control for the effect of injection on behavior. We then tested the mantises again after 15 min and quantified the differences (Movie 2).

Using this setup, the pre-injected animals responded to 50% of the virtual prey stimuli ($N=22$, $n=441/880$), where the mean distances of attention were 6.51 and 5.84 cm for the pre-saline and pre-insulin groups, respectively (Fig. 7Ai,ii). After saline injection, the insects responded to 47% of the stimuli ($N=11$, $n=207/440$) at a mean distance of attention of 5.71 cm, which was non-significant from pre-injection. Insulin injection significantly reduced the

amount of prey-directed attention to 10% ($N=11$, $n=45/440$) (Fig. 7F; one-way ANOVA, $P < 0.05$). The insulin-injected treatment reduced the mean attention distance to 4.10 cm, which was significantly different from the pre-injection treatment as well as the saline-injected control (Fig. 7Aiv; one-way ANOVA, $P < 0.05$). Likewise, we observed a significant reduction in the angularity of attention after insulin injection, encapsulated by a decrease in θ from 138 to 102 deg (Fig. 7B; H–K circular ANOVA, $P < 0.05$). The detection range plots shown in Fig. 7E mimic the changes in sensory processing whereby we measured a significant reduction in the detection area when compared with the pre-injection control animals (Fig. 7Ei,ii; one-way ANOVA, $P < 0.05$).

The number of steps taken in pursuit of the virtual prey also decreased significantly in the insulin-injected treatment when compared with the pre-injection baseline and the saline-injected control (Fig. 7C). The mean number of steps per virtual prey appearance decreased from 2.13 and 1.42 in the pre-injection baseline treatments to 1.23 and 0.16 steps in the saline-injected and insulin-injected treatments, respectively. Lastly, of those attention trials that led to strikes, none of the instances showed three or more steps taken in pursuit of the virtual prey in the insulin-injected group (Fig. 7Div). However, when we examined the strike attempts by the prey distance, the change in the percentage of strikes was only significant at distances that required the animal to pursue the prey (Table S1). That is, striking trials with virtual prey items at a distance of 2.5 cm, which simulates a type 2 ambush scenario, were unaffected by insulin. This difference in motivational pursuit characterizes a significant decrease from the pre-injected baseline treatments as well as the saline-injected control condition (Fig. 7D; K–W test, $P < 0.05$).

DISCUSSION

Here, we confirm and extend previous observations (Inoue and Matura, 1983; Matura and Inoue, 1999; Prete et al., 1992) that prey-directed behavior changes as a praying mantis (*T. sinensis*) becomes more sated. Furthermore, we demonstrate that this modulation is paralleled by injection of the peptide hormone insulin. Decreases in spatial attention levels accompanied by a reduced sensory field and lower locomotor output are characteristic of a paradigm shift in the animal's hunting strategy. This behavioral switch, in turn, is indicative of neuronal changes in the CNS. Altogether, our results lend credence to the hypothesis that ILPs through receptor activation have metabotropic effects on the central excitability patterns of the CNS.

The behavioral responses to food consumption and insulin injection were similar from both a sensory and a motor perspective: continual consumption reduced prey-initiated sensory responses and the frequency of locomotor prey pursuit significantly decreased as satiety level increased. Specifically, the distance at which the praying mantis detected and attended to either real or virtual prey decreased with either prey consumption or insulin injection as did the angular range around the mantis's head at which the prey was detected. These factors combine to shrink the field around the praying mantis where prey items evoke head movements and stalking behavior. Ultimately, these satiety changes culminate in a type 2 ambush strategy, whereby the mantis remains motionless but will readily strike prey within reach. The changes in distance detection are particularly interesting given recent studies of the unique 3D visual properties in another praying mantis species (Nityananda et al., 2018). Importantly, in previous studies, *S. lineola* tracked prey at greater distances when deprivation was increased from 2–3 days to 8–9 days (Prete et al., 1993). At

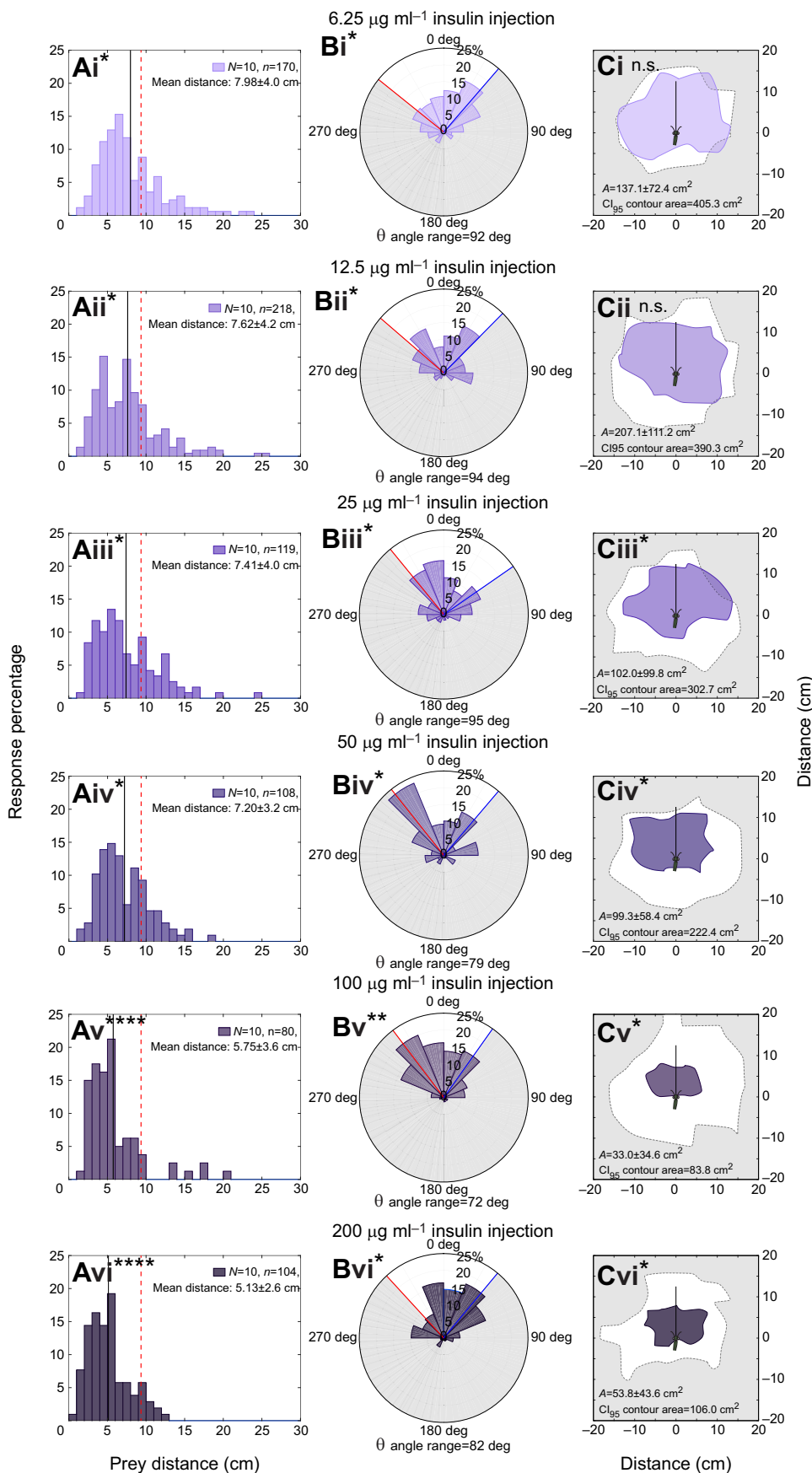


Fig. 5. The effects of six concentrations of insulin on prey-directed attention and search behavior in live prey.

(A) Histograms displaying the response percentage towards prey against distance for six concentrations of insulin. Responses to all treatments were significantly different from baseline (two-sample K-S test, $P < 0.05$). The 100 and 200 $\mu\text{g ml}^{-1}$ conditions (Av and vi) were also shown to be significantly decreased when compared with the 6.25, 12.5 and 25 $\mu\text{g ml}^{-1}$ conditions (two-sample K-S test, $P < 0.05$). For information detailing control experiments, see Fig. S3. (B) Polar histograms showing the angularity of attention. Angularity for all of the insulin-injected conditions was significantly decreased from baseline. The angularity of the 100 $\mu\text{g ml}^{-1}$ insulin concentration was significantly reduced from that of the 6.25 $\mu\text{g ml}^{-1}$ concentration in addition to the starved baseline, with a decrease in θ of 44 deg (H-K circular ANOVA, $P < 0.05$). The 200 $\mu\text{g ml}^{-1}$ insulin concentration did not show this additional significance ($P = 0.0536$). (C) Spatial attention clouds for all six insulin-injected concentrations. The area measurements (A , cm²) for the 25, 50, 100 and 200 $\mu\text{g ml}^{-1}$ conditions (Ciii–vi) were significantly reduced from the baseline condition (one-way ANOVA, $P < 0.05$). *Significant difference from baseline; **significant difference from baseline and the 6.25 $\mu\text{g ml}^{-1}$ condition; ****significant difference from baseline and the 6.25, 12.5 and 25 $\mu\text{g ml}^{-1}$ conditions.

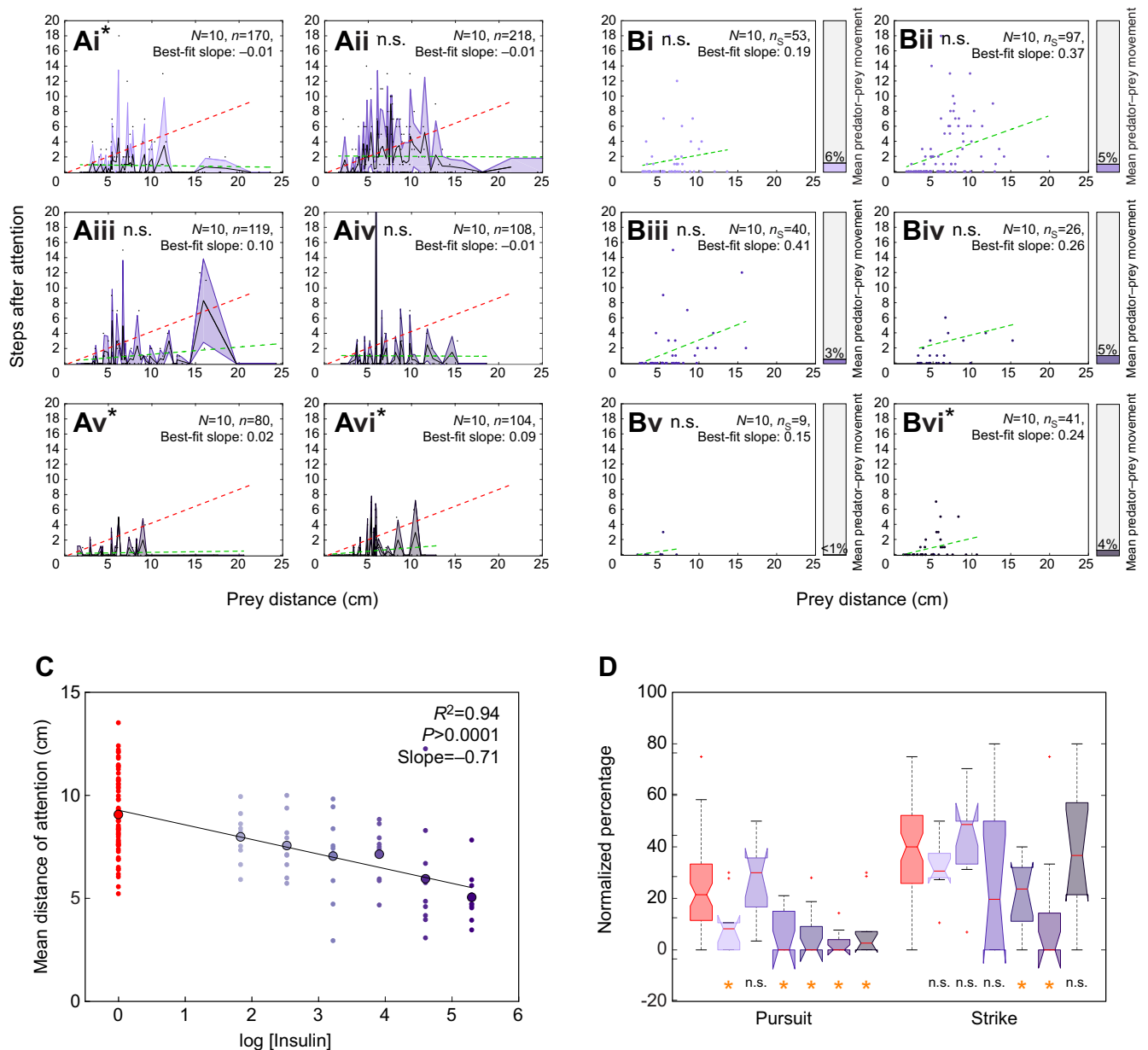


Fig. 6. The effects of six insulin concentrations on prey-directed stalking and predatory behavior using live prey. (A) Line graphs illustrating steps taken against prey distance for six insulin concentrations. The black line represents the mean number of steps at a given distance $\pm$ s.d. A line of best fit (green dashed line) was fitted to the data. The dashed red line represents the best fit for the baseline condition (Fig. S3D). The number of steps for the 6.25, 100 and 200 $\mu\text{g ml}^{-1}$ insulin concentrations (Ai,v,vi) was significantly decreased from baseline (two-sample K-W test, $P<0.05$). (B) 'Motivational pursuit' scatter plots showing the striking trials for six insulin-injected concentrations. The number of steps is plotted against prey distance. The number of steps for the 200 $\mu\text{g ml}^{-1}$ insulin concentration (Bvi) was significantly different from the starved baseline (two-sample K-W test, $P<0.05$). See Fig. S3E for relevant pre-injection baseline information. (C) Mean distance of attention over the log-normalized concentration of insulin ($\mu\text{g ml}^{-1}$) for the pre- and post-injected conditions. The line of best fit, $R^2=0.94$. (D) Box and whisker plots showing the mean percentages of pursuit and striking, normalized for the amount of attention. The level of pursuit for the 6.25, 25, 50, 100 and 200 $\mu\text{g ml}^{-1}$ concentrations was significantly reduced when compared with the baseline. The percentage of striking was also significantly reduced in the 50 and 100 $\mu\text{g ml}^{-1}$ concentrations (one-way ANOVA, $P<0.05$). *Significant difference from baseline.

6–12 days of food deprivation, *S. lineola* ate diced banana or apple, apparently utilizing chemosensory cues (Prete et al., 1992). Here, we were able to show the expected opposite result by prey consumption or insulin injection.

Insulin injection was able to mimic the sensorimotor changes evoked by prey consumption. Moreover, the effects declined along a concentration-dependent gradient as did the consumption assay. Interestingly, the actual striking behavior did not appear to be

affected by insulin. As long as the prey was close enough, the strike occurred. This observation supports the notion that the decrease in stalking stems from locomotor changes rather than a general malaise. Additionally, this result supports that the prey representation schema for *T. sinensis* does not change regardless of satiety condition. The switch to striking only when the prey is nearby is reminiscent of the ambush strategy seen in several other praying mantis species (Svenson and Whiting, 2004; Prete et al.,

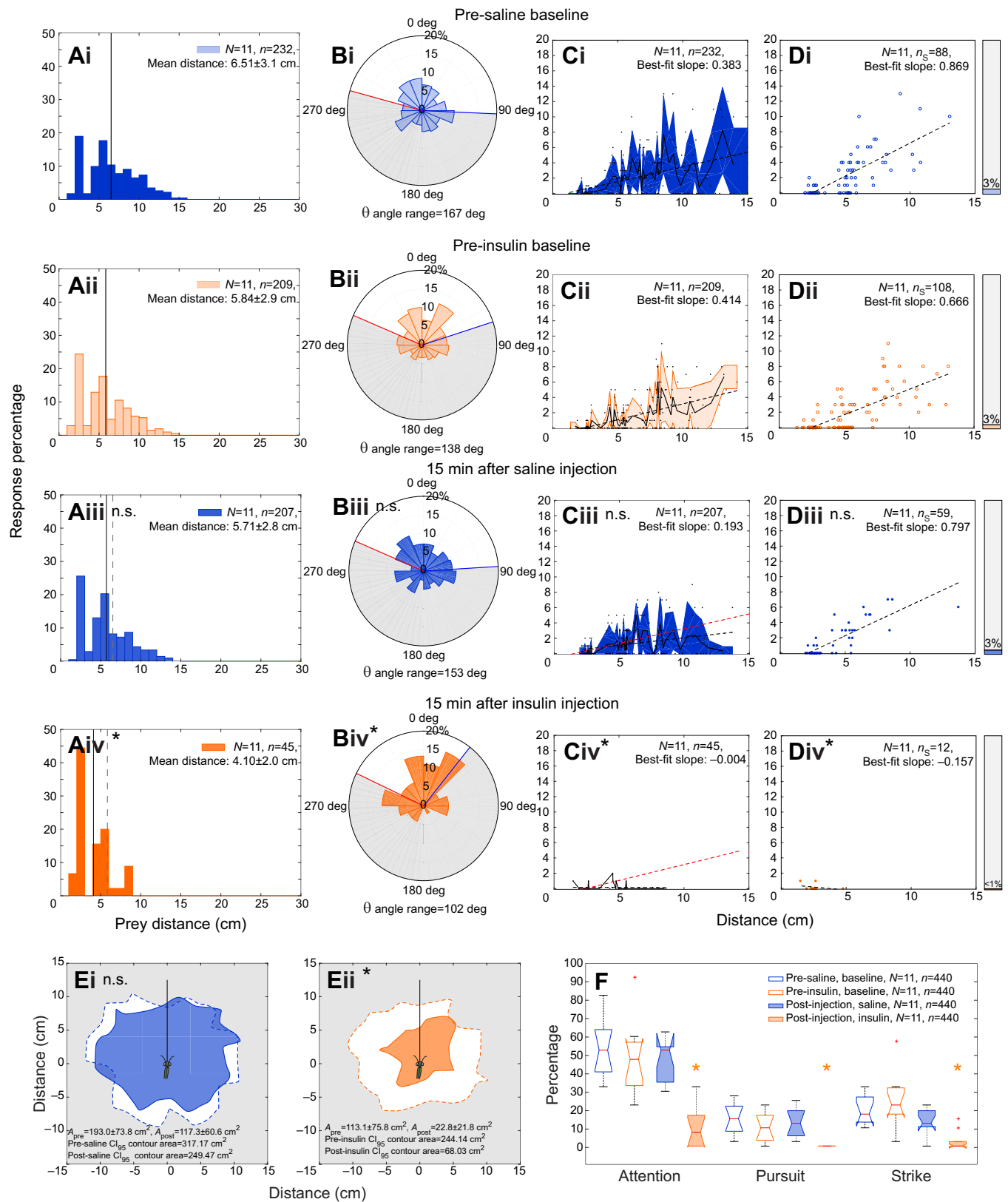


Fig. 7. See next page for legend.

2012). Lastly, we determined that the levels of visually guided selective attention significantly decrease in animals injected with insulin, leading us to propose that rising insulin levels negatively affect visually directed food search in the CNS.

Our study did not address the locus of insulin action, although ongoing experiments are aimed at that point. Insulin injected into the abdominal cavity (known to affect multiple circulating metabolites) could have its effect at several different CNS sites

Fig. 7. The effects of insulin injection on prey-directed attention and predatory behavior compared with a saline control with virtual prey.

(A) Histograms showing the response percentage of attention against prey distance. The response percentage of the insulin-injected condition was significantly reduced from the pre-injected baseline whereas that of the saline-injected condition was not significantly different (two-sample K–S test, $P < 0.05$). (B) Polar histograms showing the angularity of attention. The angularity of the insulin-injected condition was significantly reduced from the pre-injected baseline and the saline-injected control condition, showing a decrease in θ of 36 and 51 deg, respectively (H–K circular ANOVA, $P < 0.05$). The saline-injected condition was not significantly different from the pre-injection control. (C) The number of steps taken after attention against virtual prey distance. The number of steps for the insulin-injected condition (Civ) was significantly reduced from the pre-injected baseline whereas the saline-injected condition (Ciii) was not significantly different. Additional significance was measured between the saline-injected control and the insulin-injected condition (two-sample K–S test, $P < 0.05$). (D) 'Motivational pursuit' scatter plots showing steps over the prey distance. The number of steps for the insulin-injected condition (Div) was significantly reduced from that of the pre-injected control as well as when compared with the saline-injected control (two-sample K–S test, $P < 0.05$). The saline-injected condition (Diii) was not significantly different from the pre-injected control (Di). (E) The maximum detection range for virtual prey items in the pre- and post-injected conditions. There was no significant difference observed between the area measurements after saline injection (Ei, blue area) when compared to the pre-injected control condition (dotted blue line). A significant reduction in the maximum search area was seen after injection of insulin (Eii, orange area) when compared with the pre-insulin condition (dotted orange line) (one-way ANOVA, $P < 0.05$). (F) Box and whisker plots showing the mean percentages of prey-directed attention, pursuit and striking for all conditions. All three behaviors were significantly decreased after injection of insulin compared with the pre-injection conditions and with the saline-injected control (one-way ANOVA, $P < 0.05$). See Fig. S4 for relevant information. *Significant difference from baseline.

(Moreau et al., 1982). For example, it could travel through the hemolymph to the head capsule where the peptide could directly affect visual processing regions of the brain as well as association regions such as the central complex (CX) which have been shown in cockroaches to affect turning movements (Martin et al., 2015). Alternatively, it could bind to ascending neurons in the thoracic ganglia that impact the brain and motor neurons that control head movement. Of course, these possibilities are not mutually exclusive. Ascending neurons from thoracic sites could, under our experimental conditions, provide a rapid effect that bypasses the need for insulin to flow to the brain followed by a more extensive, but slower change in higher CNS centers. In *Drosophila*, the eight currently known ILPs have a number of pivotal metabolic functions, including regulation of growth, development, lifespan and reproductive processes (for review, see Nässel et al., 2013). Of these distinct peptides which target a single insulin receptor (InR), three (dILP2, 3 and 5) have been identified in the medial protocerebrum and, dILP1, 2, 3 and 5 are known to be secreted into the circulating hemolymph (Brogiolo et al., 2001). Intriguingly, a small population of neural cells in the larval fly brain has been shown to have high signaling activity tied directly to dILP2 activity (Bader et al., 2013). These results demonstrated that ILP was released in a paracrine fashion within the central brain for Imp-L2-mediated local circuit activation.

Other hormonal effects could also be triggered by the sudden increase in insulin levels. Root et al. (2011) showed that short neuropeptide F (sNPF), a pleiotropic peptide hormone implicated in the ISP, modulates the olfactory-mediated search response by facilitating synaptic transmission at the olfactory receptor neuron (ORN) level through a reduction in insulin signaling (Root et al., 2011). Where insulin levels are high, sNPF transcription decreases, thus diminishing the olfactory-driven food search response. To date,

a number of CNS neurons have been shown to express sNPF located in the central brain (including the CX and mushroom bodies), as well as along the ventral nerve cord (VNC) (Nässel et al., 2013). Kahsai et al. (2010) provided supporting evidence in that respect by showing that a population of sNPF-expressing interneurons innervating the CX are involved in the inhibition of locomotor activity levels in *Drosophila*. Recent work has shown that PAM dopaminergic neurons are active in starving flies, which promote foraging behavior (Landayan et al., 2018). Our results taken in conjunction with this growing body of literature suggest that insulin acts as a global satiety indicator and plays a critical role in coordinating sensorimotor neurons to better facilitate state-dependent hunting behavior.

Concerning the timing of this modulatory effect, the speed of the insulin response found in this study makes it unlikely that the ISP works solely through blood-borne transfer to the brain. Previous work has shown that one pair of dILP7-expressing interneurons connects the abdominal ganglion to the brain while other axons supply the hindgut or innervate the local area. Without a currently known function outside of evidence showing a role in decision making of egg-laying sites, this may argue for ascending commands from the insulin-sensitive cell bodies of the VNC to a premotor area such as the gnathal ganglion (Yang et al., 2008; Cognigni et al., 2011). Importantly, the gnathal (or subesophageal) ganglion is known to have critical roles in insect locomotion, particularly in walking, limb coordination and escape (Ritzmann and Büschges, 2007; Knebel et al., 2018; Libersat and Gal, 2013). Of course, it is probable that multiple sites of action are involved in the changes seen in our study. A rapid effect from the thoracic ganglia to ascending interneurons could be followed by a more targeted direct effect in the brain as the insulin reaches the head capsule.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: D.J.B., J.P.M., G.J.S., R.E.R.; Methodology: D.J.B., J.P.M., R.E.R.; Software: D.J.B., J.P.M.; Validation: D.J.B.; Formal analysis: D.J.B.; Investigation: D.J.B.; Resources: D.J.B., R.E.R.; Data curation: D.J.B.; Writing - original draft: D.J.B.; Writing - review & editing: D.J.B., J.P.M., G.J.S., R.E.R.; Visualization: D.J.B., R.E.R.; Supervision: G.J.S., R.E.R.; Project administration: R.E.R.; Funding acquisition: G.J.S., R.E.R.

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Supplementary information

Supplementary information available online at <http://jeb.biologists.org/lookup/doi/10.1242/jeb.197673.supplemental>

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