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Report

Visual Perception in the Brain of a Jumping Spider

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Summary

Jumping spiders (Salticidae) are renowned for a behavioral repertoire that can seem more vertebrate, or even mammalian, than spider-like in character [1–3]. This is made possible by a unique visual system that supports their stalking hunting style and elaborate mating rituals in which the bizarrely marked and colored appendages of males highlight their song-and-dance displays [2, 4, 5]. Salticids perform these tasks with information from four pairs of functionally specialized eyes, providing a near 360° field of view and forward-looking spatial resolution surpassing that of all insects and even some mammals [1], processed by a brain roughly the size of a poppy seed. Salticid behavior, evolution, and ecology are well documented [6–8], but attempts to study the neurophysiological basis of their behavior had been thwarted by the pressurized nature of their internal body fluids, making typical physiological techniques infeasible and restricting all previous neural work in salticids to a few recordings from the eyes [9, 10]. We report the first survey of neurophysiological recordings from the brain of a jumping spider, *Phidippus audax* (Salticidae). The data include single-unit recordings in response to artificial and naturalistic visual stimuli. The salticid visual system is unique in that high-acuity and motion vision are processed by different pairs of eyes [1]. We found nonlinear interactions between the principal and secondary eyes, which can be inferred from the emergence of spatiotemporal receptive fields. Ecologically relevant images, including prey-like objects such as flies, elicited bursts of excitation from single units.

Results and Discussion

An extracellular glass-insulated tungsten electrode was inserted through a small hole in the prosoma and then advanced into the brain in or just posterior to the arcuate body (Figure 1A)—a brain area similar to the central body of other arthropods both in morphology and its hypothesized role as an important center for higher-order visual processing [13, 15–17]. In making a small opening in the cuticle (approximately 100–200 μm in diameter) as opposed to the larger windows typical of arthropod neurophysiological preparations, we were able to prevent the catastrophic fluid loss that has limited recordings in spiders until now. The scale of this incision enabled the animal's clotting mechanisms to prevent continuous loss of hemolymph—ensuring the viability of the preparation without additional methodological or technical complexity. Since this study breaks new ground in neurophysiological technique, our methods are discussed in more detail in the Supplemental Experimental Procedures, sections I–III (available online). Recordings were remarkably stable, often lasting several hours, and were made from 53 sites across 33 animals. Preparation longevity was also strong, with a 2 hr mean time between the first and last recordings made from each animal (see the Supplemental Experimental Procedures, section VI). Tungsten electrodes yield extracellular recordings that can contain multiple spiking units (Figure 1B). However, conventional spike-sorting techniques enable the isolation of single units—here we employed an established method that sorts spikes based on an amplitude threshold and clustering of coefficients resulting from a wavelet decomposition of each candidate spike [14] (Figures 1B–1D; for details, see the Supplemental Experimental Procedures, section II). In order to meet statistically imposed benchmarks in the spike-sorting process, our data often contained thousands of spikes, which were sorted into single units and analyzed offline. Our recordings typically revealed a single identifiable unit.

Since this is the first investigation of neural processing in the salticid brain, we employed a range of stimuli to explore potential neural correlates of a range of behaviors that make these animals so unique. Each of three stimulus protocols aims to alternatively explore some neural basis of (1) predatory reactions to moving targets, (2) responses to ecologically relevant objects, and (3) relationships between different sets of eyes. Further, to conform to established methods [18], we also investigated basic cell characteristics using traditional sinusoidal grating stimuli. Cells typically showed a preference for 6° to 25° bars, moved horizontally at 29°/s and with high contrast (n = 17; for full details regarding cell characterizations, see the Supplemental Experimental Procedures, sections VII and VIII, and Figure S2).

Prey-Sized Moving Targets

Jumping spiders show consistent predatory behavioral responses toward fly lures under laboratory conditions, tracking and pouncing on such targets [19]. Such lures are successful even when they are relatively simple (typically consisting of a dead housefly fixed to a thread or fishing line and moved about in a fly-like manner). While the movements of these lures are only approximations of those of actual prey, we were encouraged to deploy a video version of this stimulus in our experiments because of the behavioral reliability with which salticids respond (see the Supplemental Experimental Procedures, section IX). At the neural level, our decision to use prey-like stimuli (instead of exclusively exposing spiders to wide-field stimuli such as gratings and lines) is supported by work in other visual systems that has found single neurons that are especially responsive to small moving targets [20, 21], traits

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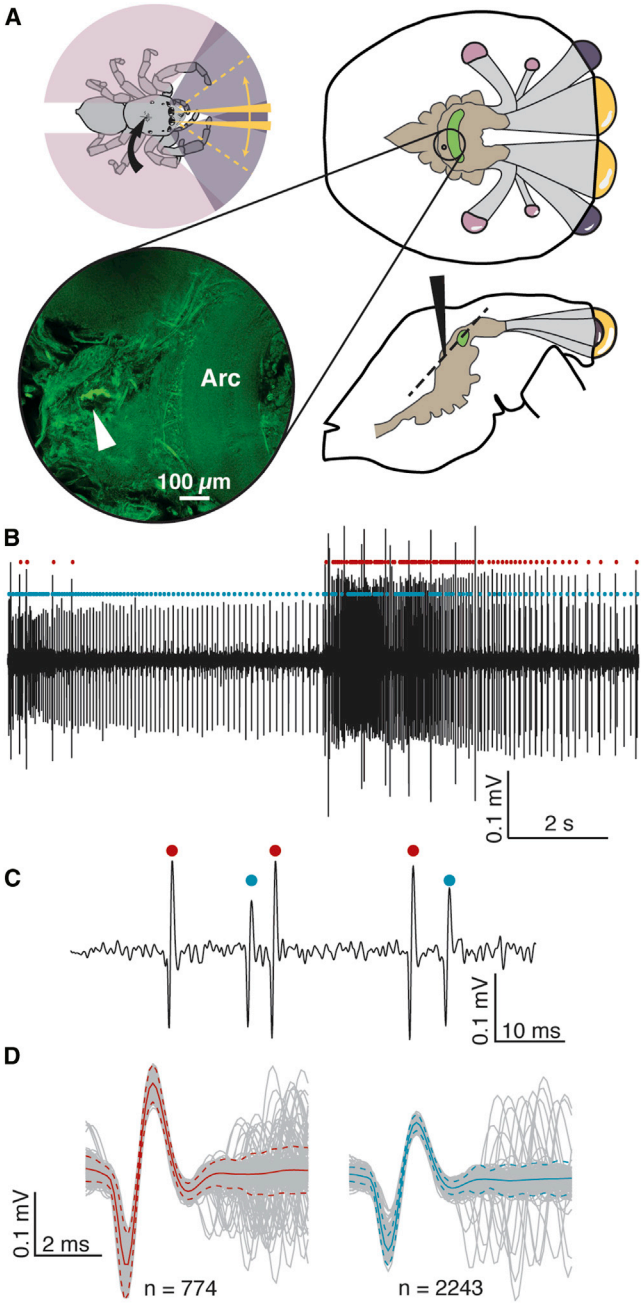

Figure 1. Recording Site and Sample Recordings

(A) Top left: approximate fields of view—principal anterior median eyes (yellow) with limits of the movable range indicated by dashed yellow lines, secondary anterior lateral eyes (dark purple), and secondary posterior lateral eyes (light purple). Visual fields for the small, secondary posterior median eyes are not shown, as these eyes are greatly reduced [11]. Overlapping fields are represented by more saturated hues. Black arrow shows electrode insertion point. Redrawn from Hill [12]. Right: dorsal (top) and lateral (bottom) views of the prosoma showing the central nervous system (CNS) and eye arrangement; eye colors are as indicated previously. The green area notes the location of the arcuate body, a region readily identifiable in histology and used as a landmark in this study [13]. The gray section is a schematic that depicts connections between eyes and the CNS (for simplicity, specific morphology of early visual centers are not shown). The black circle in the dorsal view and the black arrow in the lateral view show approximate electrode location and orientation. Based on Hill [12]. Bottom left: confocal image verifying electrode location (white arrow) just posterior to the arcuate body (Arc), evidenced by increased fluorescence surrounding damage from the electrode. The optical slice depicts area circled in the top-right image and along plane shown by dashed line in the bottom-right image.

(B) Example trace from an extracellular recording. Potentials were evoked in response to ecologically relevant images (see the main text and Figures 3, and S3). In this example, two units were identified using a spike-sorting algorithm [14] and are labeled accordingly by red and blue circles.

(C) Time-expanded trace from the same recording session as in (B).

(D) Overlay of spikes identified by the spike-sorting algorithm. Colors correspond to spikes shown in (B) and (C). The solid line represents the mean; dotted lines indicate 2 SDs from the mean.

that seem particularly important for predators such as salticids.

Responses of single units to the small, moving prey-like stimulus were quite robust, with firing patterns showing strong trial-to-trial consistency even across 22 repetitions encompassing 24 min of experimental recording time (Figure 2; Movies S1 and S2). However, despite this high trial-to-trial consistency, a generalized linear model based on target position, velocity, and direction could only explain a small percentage of the neural response (Supplemental Experimental Procedures, section X). Instead, the neural response might be explained by more complex models that may include additional factors.

Ecologically Relevant Images

The anatomical structure of jumping spiders' principal eyes should allow them to detect minute variations in target appearance [22], and behavioral studies have shown that they respond differentially toward objects displayed on a video screen [23, 24]. We therefore presented dorsal and lateral images of a fly (potential prey), a conspecific jumping spider (potential mate or rival), and a heterospecific jumping spider (potential prey or rival) (Figure 3; Movie S3). Each image was sized to preserve the natural angular dimensions of the object (Figure 3A) and was shown at six successive locations, approximately 2° below the spider's visual horizon (see Figures 3B and S3A). An image appeared at a given location for a total of 6 s, moving back and forth over a range of 0.8°, before disappearing and reappearing at the next location.

The response of a single unit is shown in Figure 3. This unit showed a preference for dorsal images of the fly located on the right side of the screen (locations 5 and 6; Figure S3B; for a simultaneously recorded second unit with similar response, see Figures S3C and S3D). The dynamic nature of the neural response to these images is best appreciated by viewing a video of the experiment that generated the data in Figures 3A–3C; see Movie S3.

As a control, we presented a scrambled version of the preferred fly image that retained the size and contrasting features of the fly while destroying its figural integrity, a control used in face recognition experiments in both wasps [25] and primates [26, 27]. Images of the scrambled fly were interleaved with the original stimulus set. Over a total experimental time in excess of 5 hr, there were changes in the mean firing rate due to shift in baseline firing. Responses, consisting of the mean firing rate during a stimulus presentation, were therefore normalized by the mean firing rate of each trial to facilitate statistical comparisons, giving rise to a "spike score" (Figure 3C; for details, see the Supplemental Experimental Procedures, section XII).

Responses to each stimulus were tested against the overall mean response (i.e., the shuffled response; see Figure 3C), a calculated distribution that represents the expected response

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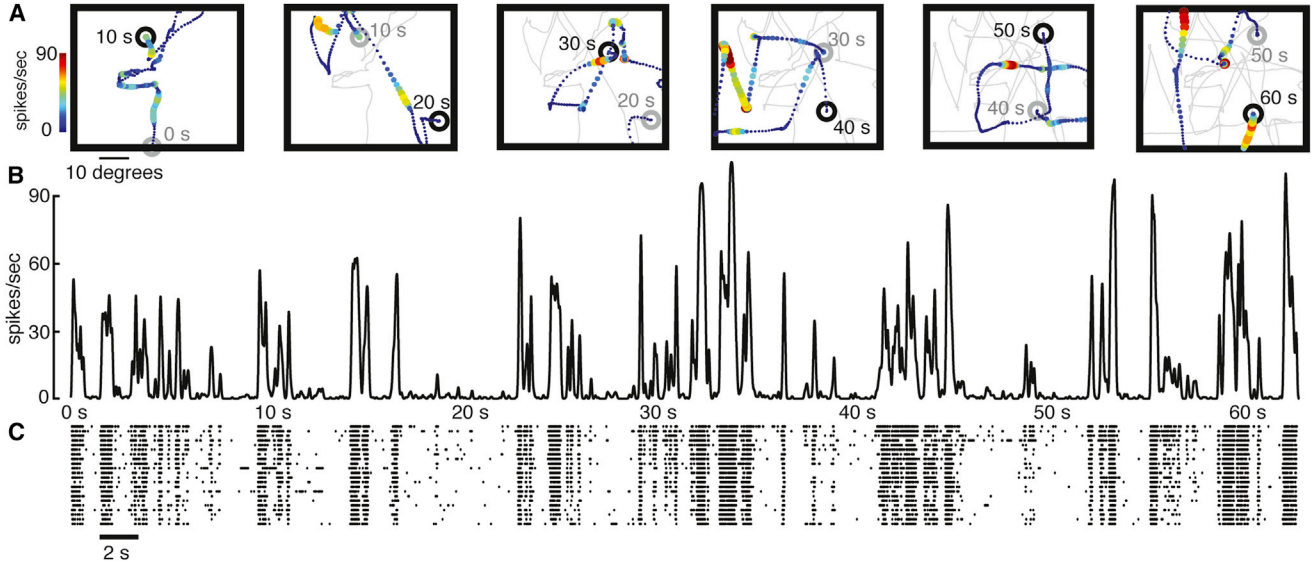

Figure 2. Response of a Single Neural Unit in the Brain of the Jumping Spider to Prey-like Movements of an Artificial Target

(A) A prey-sized black target (1.5°) was shown moving across a white screen at various directions and velocities (see Movie S1). Each dot indicates the position of the target for each frame of the video (displayed at 29 frames per second). The color and size of each dot indicate the average firing rate over the 34 ms of each video frame (see B and C for histogram and rasters), with large, warm-colored dots representing increased firing. Each box shows a 10 s interval beginning with the location highlighted by a gray circle and ending with the location marked by a black circle. Start and end times for the interval are also shown. Target path taken in previous 10 s intervals are shown in gray. Note that target velocity is not constant and that at times the target moves out of the frame of the screen, re-entering at a different location (e.g., in the third panel, when target moves off the bottom of the screen and reappears on the right).

(B) Line histogram (smoothed with a Gaussian filter, SD = 36 ms [18]) showing the overall responses across 22 presentations of the 64 s stimulus.

(C) Raster of spike times for each trial. Note the consistency in firing pattern from trial to trial over the entire experimental period of 24 min.

See also Figure S3.

of a given neuron (with the same mean and median firing rate as the original) if it were responding with no preference for any one stimulus [28] (see the Supplemental Experimental Procedures, section XII). The response of the unit shown in Figure 3C toward the lateral and dorsal images of the fly was significantly greater than this overall mean response (Figure 3C; median firing rates: lateral fly = 10.0 spikes/s, dorsal fly = 14.9 spikes/s, shuffled response = 7.2 spikes/s; median spike scores: lateral fly = 1.2, dorsal fly = 1.6, shuffled response = 0.9; Wilcoxon rank-sum test, $p < 0.05$ after Bonferroni correction for multiple tests; see Movie S3). The response to the intact dorsal fly image was also significantly different and greater than the response to the scrambled image (Figure 3C; median firing rates: dorsal fly = 14.9 spikes/s, scrambled fly = 5.9 spikes/s, median spike scores: dorsal fly = 1.6, scrambled fly = 1.0; Wilcoxon rank-sum test, $p < 0.05$ after Bonferroni correction for multiple tests). A different unit in this spider, as well as a unit recorded from another spider, exhibited similar response patterns (Figure S3).

The Interaction between Principal and Secondary Eyes Is Nonlinear

One of the most unusual features of salticid vision is the separation of visual tasks between anatomically distinct eyes. Of the two sets of forward-facing eyes, high-acuity vision is the domain of the large principal eyes [22], whereas motion detection is largely undertaken by the smaller secondary eyes (Figure 1A) [29–31]. We dissociated primary from secondary visual input by selectively placing eye occluders in front of each set of eyes, a simple and reversible procedure (see the Supplemental Experimental Procedures, section V). We then deployed our third stimulus protocol, a white-noise-like stimulus that allowed us to identify spatiotemporal receptive fields (STRFs), revealing preferences for specific locations within a visual field, as well as the time-dependent aspects of the neural response [32, 33]. The stimulus consisted of a 15 frame sequence of 16 × 16 pixel pseudorandomly distributed black-and-white checks, with each frame appearing for 100 ms [32] (Figure 4A; see Movie S4 for an example response and the Supplemental Experimental Procedures, section XIII, for the complete stimulus details). Sequences were separated by 500 ms of featureless gray (50%) screen, which served as an internal control (Figure 4B). After each 26 min recording session, units were identified by spike sorting, and the firing patterns of individual units were reverse correlated with the pattern of checks at every location on the screen.

From this analysis, we drew two inferences. First, in one recording, a significant STRF was recorded only in the unoccluded condition. This indicates a significant interaction between principal and secondary eyes. When either set of eyes was occluded, no STRF emerged (Figure 4C, top and middle). However, when both sets of eyes were unblocked, an unambiguous STRF emerged (Figure 4C, bottom). Because our analysis performs a linear reverse correlation between the stimulus and the response, the lack of a STRF in either occluded-eye condition implies that there was no linear relationship between stimuli and response when the secondary or principal sets of eyes were forced to function independently. However, when the eyes were allowed to work together, a clear linear linkage between the stimulus and the response was exposed (Figures 4C and 4D). Second, STRFs emerged only after a long delay between stimulus onset and neural response (spatiotemporal window from 80 to 160 ms; Figure 4C). The response latency was statistically significant

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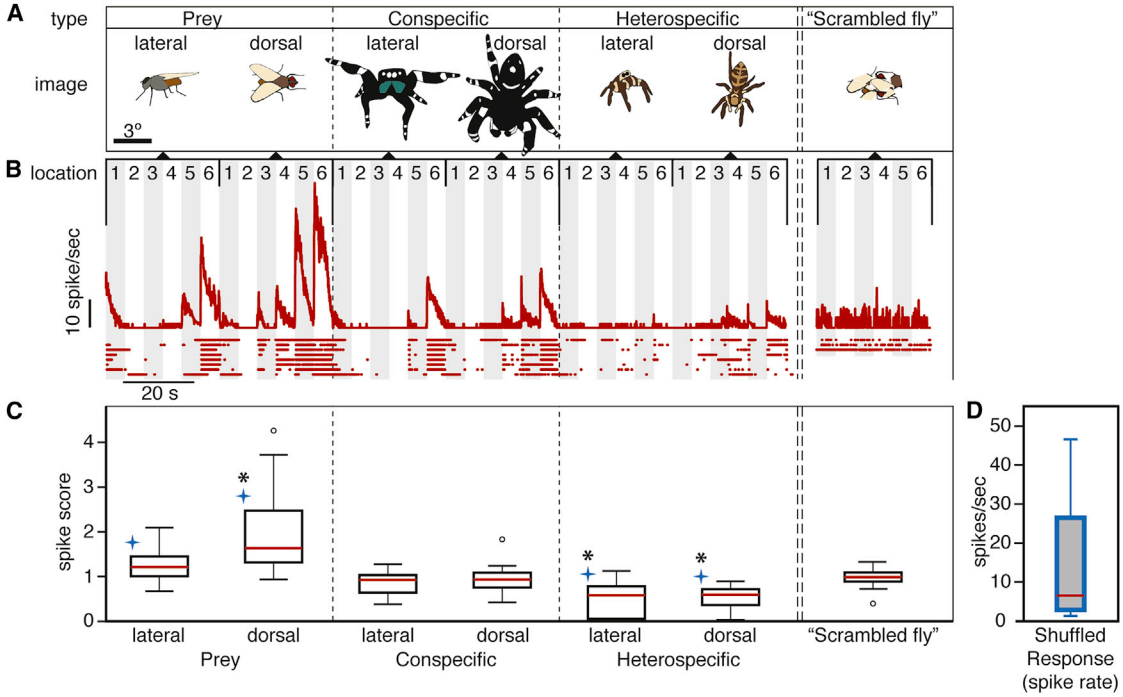

Figure 3. Response to Ecologically Relevant Images

(A) Representative drawings of images used to test responses to potentially salient objects.

(B) Responses of a single unit to images at six distinct horizontal locations (−25°, −15°, −5°, +5°, +15°, and +25° horizontally and 2° below the visual horizon; for further details, see the Supplemental Experimental Procedures, section XI) showing a subset of trials (eight8 standard trials and three scrambled trials). Rasters show spike times, and histograms were constructed as in Figure 2A. Due to the preference for the dorsal view of the fly, a scrambled fly image was constructed and tested, preserving all parts of the image but destroying its holistic identity. Presentations of the scrambled fly were interleaved with the standard stimuli and generated no differential response.

(C) Summary of responses from unit shown in (B) across all trials (standard images, n = 20; scrambled images, n = 14), with boxplots showing response to dorsal and lateral views of each image, pooled across all locations. Data were collected over a 5 hr time window, during which there were fluctuations in the overall firing rate. Because of changes in the baseline firing rate, a normalization process was employed to facilitate comparisons between trials, giving rise to the "spike score." Spike score reflects firing rate for a given stimulus normalized by the mean response across all stimulus-location combinations for the trial. The score is therefore multiplicative—for example, a spike score of 2 represents double the mean activity of the given trial (for details, see the Supplemental Experimental Procedures, section XII). Mean firing rate for the depicted unit across all trials was 13.7 spikes/s. The red line shows the median score, boxes extend to the 25th and 75th percentiles of the data, and whiskers extend to cover 99th percentile of a normal distribution. Data points outside of this range are shown as circles. Blue crosses denote responses that were significantly different from the shuffled response (i.e., mean response; see the main text), whereas asterisks denote responses that were significantly different from the response to the scrambled fly (Wilcoxon rank-sum test, $p < 0.05$ after Bonferroni correction for multiple tests). Median spike scores for the intact dorsal view of the fly were significantly higher than both the median of the shuffled response and the median of the responses to the scrambled fly (median spike scores: dorsal fly = 1.6, shuffled response = 0.9, scrambled fly = 1.0; median firing rates: dorsal fly = 14.9 spikes/s, shuffled response = 7.2 spikes/s, scrambled fly = 5.9 spikes/s).

(D) Median firing rate for each trial. These are the values that were used as the normalization factors (shuffled responses) to determine spike scores.

(t test, $p < 0.05$; even after correcting for multiple tests using statistical false discovery rate [34]; see the Supplemental Experimental Procedures, section XIV). This indicates that the neural response was correlated with the luminance at a specific location (in both time and space) at a level greater than chance. The long delay between stimulus onset and response suggests that there are at least several synapses between the retinae and the recording site, supporting our supposition that the recordings came from a higher-order unit in the visual system [13]. A total of nine units recorded from six animals generated statistically significant STRFs; of these, three units were tested under all eye-occlusion conditions, and all of these showed statistically significant STRFs in at least one eye condition. While only the unit presented in Figure 4 exhibited the discussed nonlinear interaction, these other units showed different nonlinear interactions (see Figure S4 for all STRFs, Movie S4, and the Supplemental Experimental Procedures, section XIV).

Conclusions

Our recordings represent possible neural correlates for well-known behaviors exhibited by jumping spiders. Salticids on the hunt detect and respond to moving, small-field visual targets, and this behavior is reflected in our recordings from interneurons toward small moving targets (Figure 2) [8, 33, 35]. Even more remarkable is the response of single units to a dynamically changing visual scene in space and time. We have uncovered nonlinear interactions between principal and secondary eyes, exemplified by a single unit that responded sensitively to a localized region of space under normal viewing conditions but that had no detectable spatio-temporal receptive field when either pairs of eyes were occluded (Figure 4). This spatial and temporal integration may be relevant to the well-known navigational abilities of salticid spiders [3], as well as to the last stages of predation, when the prey is scanned by the spider's principal eyes just before it pounces [24].

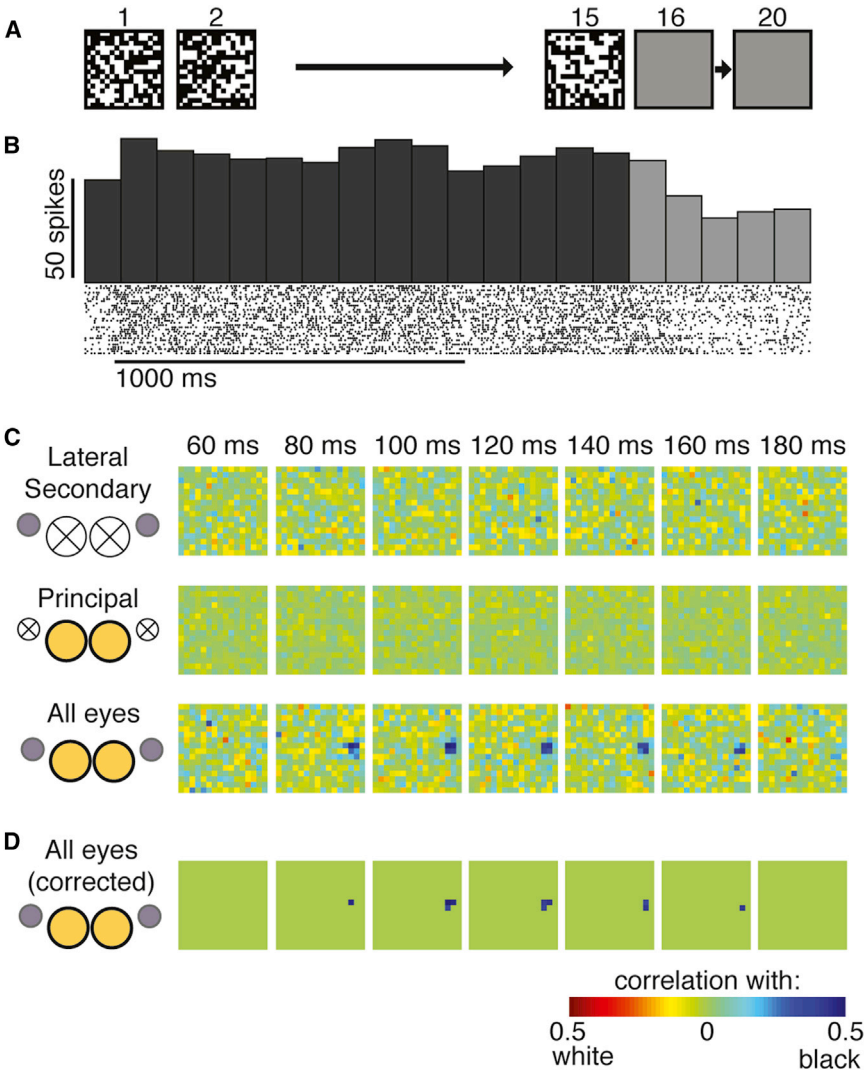

Figure 4. Spatiotemporal Receptive Fields

(A) Stimuli were sequences of 16 × 16 grids of black-and-white checks. Each sequence was made up of 15 frames, with each frame presented for 100 ms and each 15-frame sequence separated from the next by 500 ms of solid gray (50%) as an internal control (for details, see the Supplemental Experimental Procedures, section XIII).

(B) Typical summary statistics for a single unit after spike sorting, with spike rasters (bottom) and a histogram of spike times in 100 ms bins (top). Note the typical drop in firing rate when gray frames are present (light bars) relative to the response to the checkered frames (dark bars).

(C) Spike times and check contrast at each location were reverse correlated to generate STRFs for each eye treatment. As shown in the scale bar at bottom, blue denotes correlation with black checks, red denotes correlations with white, and green denotes no correlation with either. Numerical values below the scale bar reflect the strength of the correlation. Top: secondary eyes only (principal occluded). Middle: principal eyes only (secondary occluded). Bottom: all eyes intact (none occluded).

(D) STRF for the all-eyes condition showing only locations where the correlation values are significant (t test; $p < 0.05$ after correction for false discovery rate; see the Supplemental Experimental Procedures, section XIV). This was the only condition with a statistically significant response for this cell—significant STRFs were not observed for the conditions in which the principal eyes or secondary eyes were occluded.

See also Figure S4.

The behavioral repertoire of salticid spiders includes other acts that seem more mammal like than spider like [1, 36]. Our preliminary findings, not meant to be definitive, open the behavioral world of jumping spiders to investigation with the powerful techniques of neurobiology. It should now be possible to perform a neuroethological analysis of processing in the brain of jumping spiders to unravel the mechanisms that underlie the remarkable visual behavior of one of nature's truly charismatic little animals.

Supplemental Information

Supplemental Information includes Supplemental Experimental Procedures, four figures, and four movies and can be found with this article online at http://dx.doi.org/10.1016/j.cub.2014.09.029.

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