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Report

Selective Attention in an Insect Visual Neuron

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Summary

Animals need attention to focus on one target amid alternative distracters. Dragonflies, for example, capture flies in swarms comprising prey and conspecifics [1], a feat that requires neurons to select one moving target from competing alternatives. Diverse evidence, from functional imaging and physiology to psychophysics, highlights the importance of such "competitive selection" in attention for vertebrates [2–5]. Analogous mechanisms have been proposed in artificial intelligence [6] and even in invertebrates [7–9], yet direct neural correlates of attention are scarce from all animal groups [10]. Here, we demonstrate responses from an identified dragonfly visual neuron [11, 12] that perfectly match a model for competitive selection within limits of neuronal variability (r^2 = 0.83). Responses to individual targets moving at different locations within the receptive field differ in both magnitude and time course. However, responses to two simultaneous targets exclusively track those for one target alone rather than any combination of the pair. Irrespective of target size, contrast, or separation, this neuron selects one target from the pair and perfectly preserves the response, regardless of whether the "winner" is the stronger stimulus if presented alone. This neuron is amenable to electrophysiological recordings, providing neuroscientists with a new model system for studying selective attention.

Results

We recorded intracellularly from the "centrifugal small-target motion detector" neuron CSTMD1 [13], a recently identified binocular neuron from the dragonfly midbrain. It responds selectively to small (1°–3°) targets moving across a large receptive field in either excitatory (ipsilateral) or inhibitory (contralateral) visual hemispheres (Figure 1 and see also Figure S1 available online). CSTMD1's neuroanatomy (Figure S1A) is consistent with a possible role in attention as targets move from one visual hemisphere to the other [12, 13]. To test its possible role in the competitive selection of targets, we compared CSTMD1's response to single and paired targets (Figure 1).

Because we cannot instruct a restrained dragonfly to "attend" to one target, we instead use inhomogeneity in the receptive field to determine which of two alternative targets the neuron tracks. When we stimulate CSTMD1 by drifting a small dark target at different locations across a bright LCD screen, differences in the response time course reflect local inhomogeneity in the receptive field (i.e., variable excitatory and inhibitory synaptic inputs and local differences in spatiotemporal response tuning). Responses are strongest near a frontal "hot spot" 60° above the horizon but also depend on stimulus contrast and size (Figures 1C, 1E, and S1C). This is due in part to the optics of the eye, with a pronounced region of maximal acuity (<0.5°) in the frontal-dorsal visual field, falling 3-fold by 40° away [14]. The neuron is correspondingly more sensitive to small targets frontally and larger targets in the periphery (Figure S1C). Although CSTMD1 responds to targets of contrast below 25% (Figure 1E), the receptive field is smaller than for higher contrasts (Figure 1C), with significant responses only in the vicinity of the hot spot.

Receptive fields are similar in the same neuron in different dragonflies. They are also stable over prolonged recording periods, illustrated by the similarity in maps obtained by repeated stimulation of the ipsilateral receptive field (Figures 1B and 1D) and eight identical scans through the hot spot over 15 hr (Figure 1F). Consequently, successive scans of identical targets are very strongly correlated with one another irrespective of their size, contrast, or location (r^2 = 0.76) (Figure S2).

The reproducible and unique time-varying response to single targets thus provides a characteristic temporal "fingerprint" that allows us to test our hypothesis: if the neuron selects one target, the response to two simultaneous targets should resemble either one presented alone, not a blend, such as their sum or average. We tested this on unique trajectories T_1 and T_2 (Figure 1B), with either a single target, presented along each trajectory, or both targets presented together ("Pair"). T_1 alone yields a strong response to 2.5°, high-contrast targets (a near-optimal stimulus frontally) shortly after onset and passes through the hot spot, giving a maximal response late in the time course (Figure 1G). The more peripheral T_2 yields a response that increases more gradually before declining (at least for the neuron shown in Figure 1H). The time course depends also on the target size or contrast selected: smaller or lower-contrast targets yield weaker overall responses.

Our primary result is illustrated in Figure 2 by the Pair responses, which consistently resemble the responses for one or the other single target. In Figure 2A, T_1 (red) and T_2 (blue) were small (1.25° square) targets 20° apart. After an initial lag in which the Pair response (black) is weaker than either single target, it closely follows the temporal fingerprint for T_1 alone. Figures 2B and 2C show examples from two further neurons (N2 and N3 in Figure 2) for targets that are both small (1.25°) and low contrast. In both neurons, individual target responses are delayed, eventually responding robustly near the hot spot. Receptive field asymmetry delays the T_2 response more than T_1 (Figure 1C). Intriguingly, when we present the Pair stimulus, the response appears to "lock" onto the T_1 fingerprint, even after T_1 passes out of the receptive field on that trajectory. The response falls to baseline levels, even though T_2 is still within the receptive field. The Pair response thus appears to encode a single selected stimulus and ignore the other.

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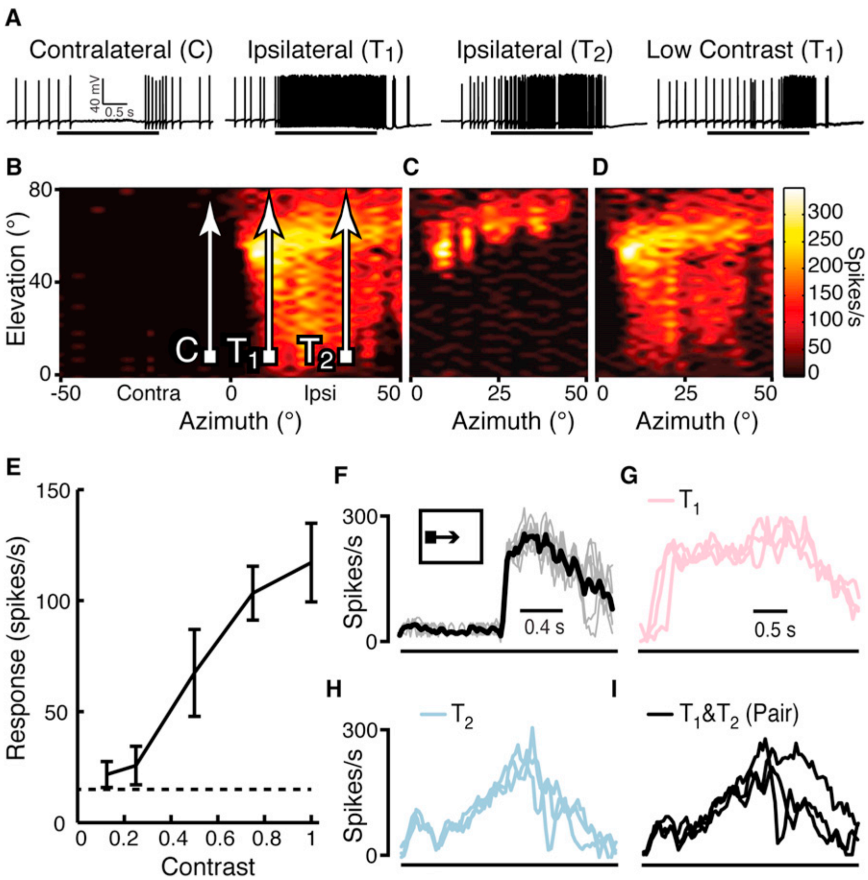

Figure 1. Receptive Fields of CSTMD1 in *Hemicordulia tau* and Response to Moving Targets

(A) Dark targets drifted vertically (42°/s) on a white background (315 cd/m^2, 120 Hz LCD display) within the contralateral field suppress intracellular responses to below spontaneous levels. Identical targets moved in the ipsilateral hemifield (T_1, T_2) evoke excitatory responses with strength dependent on stimulus contrast (high = 1, low = 0.56, $I_{difference}/I_{background}$).

(B) Target 1 (T_1) moves through the receptive field hot spot and Target 2 (T_2) is located 20° to the right.

(C) A lower-contrast target maps a smaller receptive field.

(D) Receptive field remapped as in (B), revealing consistent inhomogeneity in spatial structure.

(E) CSTMD1 ("centrifugal small-target motion detector" neuron) responses to targets of varying contrast drifted horizontally through the receptive field hot spot (mean ± SEM, n = 8 neurons, dashed line = mean spontaneous rate).

(F) Eight target scans over a 15 hr period reveal low neuronal variability (gray lines: individual responses; black line: mean).

(G) CSTMD1 response to three trials of the single T_1 stimulus (red), (H) single T_2 (blue), or (I) simultaneous presentation of both T_1 and T_2 ("Pair" black).

In two of three further trials from N2 with larger targets (2.5°), the Pair response follows T_2, despite this being weaker than T_1 (Figures 2D and 2E). In the third trial, the response is initially identical but "switches" midway to closely track the stronger T_1 (Figure 2F). In a further trial with smaller targets (1.25°) and two trials using lower contrasts, we see the opposite result: Pair now resembles the initially stronger T_1 until midway, before switching to T_2 (Figures 2G–2I). Although this switching behavior is not seen in every trial, most examples occur when responses to individual targets are equally strong, suggestive of an underlying competitive mechanism. With near-optimal stimuli (2.5° targets, high contrast) (Figures 2J–2L), both T_1 and T_2 yield very strong initial responses (>250 spikes per second), a characteristic typically shared by Pair (e.g., Figure 2J). Rarely, however, there is a pronounced delay before Pair closely tracks an individual target (e.g., Figures 2K and 2L), further suggesting initial competitive interactions.

We tested stimuli, as illustrated by Figure 2, across varied combinations of size, contrast, or separation of target pairs. Individually, these produce radically different response time courses for T_1 and T_2. The Pair response, however, consistently appears to select one target. Nevertheless, selection is somewhat independent of the potency of a stimulus, at least as evidenced by the receptive field of CSTMD1. The selected target can be either T_1 or T_2, regardless of which one causes stronger CSTMD1 responses (Figure S3A). This variation in target choice suggests that selection involves a process akin to selective attention in vertebrates, a "cognitive" filter to focus on one particular target even in the presence of an equally (or more) salient distracter [15–17].

Could the qualitative match between Pair and T_1 or T_2 be a chance observation resulting from neuronal variability? Figure 3 shows scatter plots (color saturation indicates the density of multiple points; 25 ms bins) for responses within the receptive field from 72 trials at 20° separation, pooled across all four combinations of target size and contrast, over nine neurons. We see a weak correlation when we plot responses for Pair against either T_1 (r^2 = 0.58) or T_2 (r^2 = 0.35) (Figures 3A and 3B). This confirms that the response to the Pair stimulus does not simply reflect the response to T_1 or T_2 alone. However, if we assume that competitive selection operates to track either target at a given time point, by plotting Pair against either T_1 or T_2, after computing whichever provides the least difference, we see a very strong correlation (r^2 = 0.83) (Figure 3C). Were T_1 and T_2 similar to one another, some improvement in this correlation might be expected from neuronal variability, because this analysis compares Pair with two possible alternatives at each time point. Our deliberate selection of different trajectories for T_1 and T_2, however, ensures that this is rarely the case, evidenced by both the raw data (Figure 2) and the much weaker correlation of T_1 with T_2 (r^2 = 0.27) (Figure 3D). Indeed, the assumption of competitive selection yields a correlation as strong as for subsequent repetitions of identical trials at T_1 or T_2 mean (r^2 = 0.76) (Figure S2). We conclude that, within limits of neuronal variability, the Pair response is usually identical to that for one of the targets presented alone.

We can further quantify whether Pair responses reflect competitive selection by considering differences between Pair and alternative combinations of T_1 and T_2. Figure 4A shows an example model for hypothetically "perfect" competitive selection based on the actual values of T_1 or T_2 responses that correspond most closely to the Pair response. The close match between this model and the observed Pair response

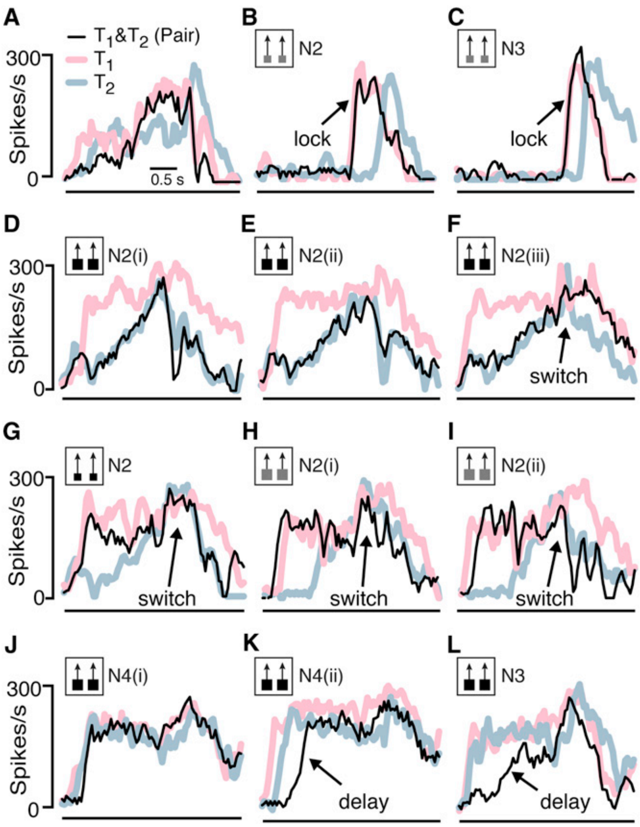

Figure 2. Instantaneous Spike Rate Plots from Single Trials in Four Different CSTMD1 Neuron Recordings, Using a Variety of Sizes and Contrasts

Targets were presented either individually along the trajectories shown in Figure 1B (T_1, red lines; T_2, blue lines) or as a Pair stimulus along both trajectories simultaneously (black lines).

(A) Pair response of neuron 1 (N1, the same neuron as in Figures 1A–1D) to high-contrast large targets (2.5°) is initially weaker than either T_1 or T_2, before closely tracking T_1 presented alone.

(B and C) Recordings from two neurons (N2, N3) using smaller (1.25° square), low-contrast targets. As seen in Figure 1D, the receptive field for this stimulus is smaller and at notably lower elevation for T_1 than T_2 (and thus encountered by T_1 250 ms earlier). Under these conditions, the Pair response typically "locks" on to the earlier T_1 and does not switch to T_2, even after T_1 leaves the receptive field completely at that location.

(D–F) Three identical repetitions of large (2.5°), high-contrast targets presented to neuron N2. In the third trial, the Pair response "switches" midway, from T_2 to the response produced by T_1 alone.

(G) Further recording from neuron N2, using smaller (1.25°) targets than in (B). The Pair response initially follows T_1 before switching to T_2.

(H and I) similar behavior is shown in response to large (2.5°), low-contrast targets.

(J and K) Two identical trials using 2.5°, high-contrast targets in neuron N4 (i.e., as in D–F). In this neuron, the stimulus evokes potent responses to both T_1 and T_2 in the early part of the time course. In the second trial (N4, ii), the neuron response to Pair exhibits an onset "delay" before closely tracking T_2.

(L) A similar lag in response to Pair in neuron N3 to the same stimulus.

is evident from consistently small errors (lower plots), compared with the difference between Pair and individual T_1 and T_2 responses. We computed the distribution of such errors across four stimulus combinations (large and small targets, high and low contrast) for this competitive selection model and for several alternative models combining the T_1 and T_2 responses: (1) The average of the observed T_1 and T_2 responses (Figure 4B): we might expect this model to best predict the Pair response if the observations simply reflected neuronal variability from trial to trial. (2) A model for saturating summation of T_1 and T_2 responses (Figure 4C): we might expect the Pair response to best match this model if the two individual responses simply sum (taking into account the potent response to individual targets and the observation that spike rates saturate at $\sim$300 spikes per second). (3) A "maximum" model (Figure 4D) based on the stronger of either the T_1 and T_2 response and (4) the corresponding "minimum" model (not shown): we might expect these models to best predict the Pair response if target selection simply favored the stronger or weaker individual stimulus.

The tightest and most symmetrical error distribution for these model varieties is for competitive selection (n = 72 trials over 9 neurons) (Figures 4E and 4F). Figure 4G shows the linearly weighted sum of signed errors for target pairs with 20° separation (mean ± 95% confidence index [CI], n = 18). Negative errors reflect Pair responses weaker than model predictions and vice versa. Although the four stimulus conditions produce different responses (in both magnitude and time course), as seen in Figure 2, competitive selection consistently provides the best explanation for the activity observed for Pair stimulation, with significantly smaller total errors over all target conditions, compared with every other model (one-way ANOVA, Dunnett's multiple comparison $p < 0.001$, n = 72). The effect size for these comparisons is large (Cohen's *d*, 95% CI): average, 1.3 [0.9, 1.6]; summation, 2.9 [2.5, 3.4]; maximum, 1.7 [1.3, 2.1]; minimum, 1.2 [0.8, 1.5]. Positive bias in errors for the minimum model and negative bias for the maximum model suggests that the Pair response stays tightly bounded by T_1 and T_2, regardless of which is stronger. This is confirmed by the similarity in the division of time that Pair "tracks" T_1 versus T_2 (Figure S3A). Mainly negative errors for the summation model confirm no additive effect between individual responses, even at large separation (Figure S3B). As we decrease target separation to 5°, larger negative errors (Figure S3B) probably reflect lateral inhibitory interactions between targets at earlier stages of visual processing [13].

Discussion

Our data make a compelling case that CSTMD1 reflects competitive selection of one target. We emphasize "competitive," because the attended target is not always the same between trials or even within a trial, as seen in strikingly perfect switches from one to the other (e.g., Figures 2F–2I). Competition is further suggested by rare examples where the activity observed under Pair stimulation initially lags both T_1 and T_2 responses (e.g., Figures 2K and 2L), suggesting initial conflict in the underlying neural network before resolution of competition by a "winning" target. Variability in the actual winner suggests either modulation of the underlying salience of targets over trials (e.g., via local habituation) or a higher-order mechanism of bias [19].

We previously showed that CSTMD1 still responds robustly to a target even when it is embedded within a high-contrast natural scene containing numerous potential distracters [20]. Taken together with recent evidence that the behavioral state of insects strongly modulates responses of neurons involved in visuomotor control [21], our new data thus suggest a hitherto unexpected sophistication in higher-order control of insect visual processing, akin to selective attention in primates. Perhaps the most remarkable feature of our data is that once the response "locks" onto a target (or following a switch),

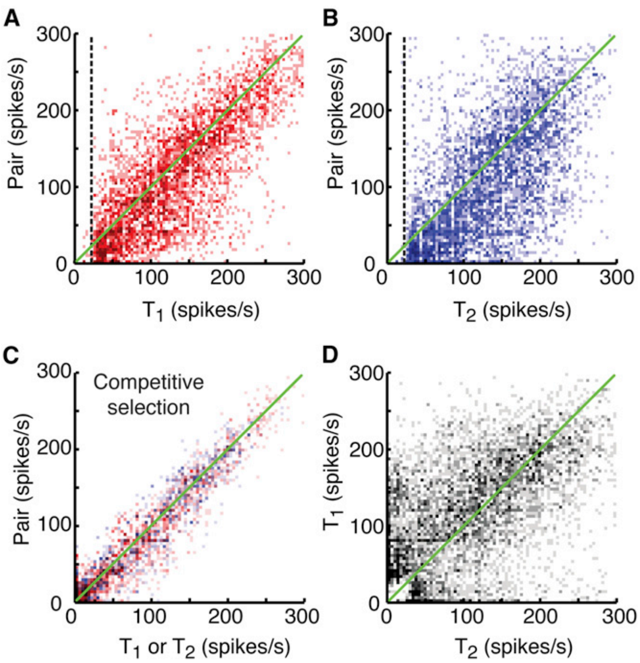

Figure 3. Correlation Analysis Reveals Competitive Selection Underlies the Paired Response

Peristimulus time histograms (25 ms bins) were lightly filtered (Savitzky-Golay [18], 2°, 7 span). Data for further analysis were taken from bins where stimuli were within the receptive field, determined via an inclusion criterion of T_1 or T_2 above a threshold of 1.5 × SD of the spontaneous activity for each cell.

(A and B) Each time point formed density scatter plots for: (A) Pair versus T_1 (r^2 = 0.58) and (B) Pair versus T_2 (r^2 = 0.35). There is a stronger association between Pair and T_1, the trajectory that traverses the receptive field hot spot. Dashed lines show the average inclusion threshold, and the green line is a slope of 1.

(C) We define "competitive selection" as the response of either T_1 (red points) or T_2 (blue points), dependent on which target has the least difference to the Pair response. An r^2 of 0.83 indicates that Pair is highly correlated with either T_1 or T_2 at all times. This value is similar to neuronal variability of a repeated T_1 stimulus (r^2 = 0.81) (see Figure S2).

(D) Weak correlation between T_1 and T_2 (r^2 = 0.27) confirms inhomogeneity in receptive field structure.

the second target exerts no influence on the neuron's response: the distracter is ignored completely (Figures 2B and 2C). This highly accurate encoding of single stimuli is in contrast with competitive selection described for neurons in the primate lateral intraparietal area (LIP) [22] and avian midbrain [23, 24]. These tend to represent relative stimulus salience, with responses still modulated by the strength of distracters outside the receptive field. Our results are more similar to data from primate visual cortex, where responses to stimulus pairs within the receptive field comprising both preferred and antipreferred stimuli tend toward responses for the individual stimulus that the animal attends to [3, 25–27].

Accurate encoding of an "attended" target independent of distracters would be invaluable for control of target pursuit, because it would enable prey tracking amidst swarms of distracters, using the exact same gain in the control loop as in a simpler scenario, where the prey is the sole salient target. We have no direct evidence for where CSTMD1 sits within such a control system or indeed for the hierarchy of underlying mechanisms of competitive selection. The invertebrate brain is a highly coupled neuronal network, with efferent circuitry

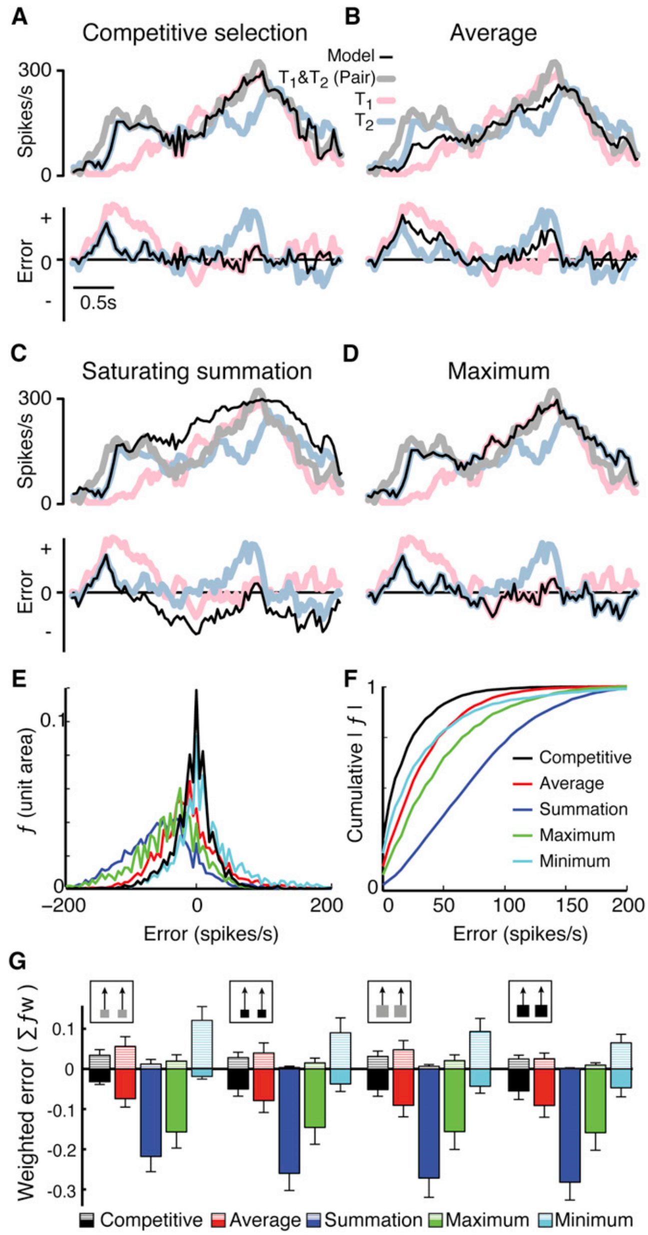

Figure 4. Competitive Selection More Accurately Matches Paired Responses than Alternative Models

(A) An example of CSTMD1 response (upper) to T_1 (red), T_2 (blue), or Pair (gray) and a model for competitive selection (black line) based on the actual value of either T_1 or T_2 that most closely resembles Pair. The lower plots show errors between observed Pair and either model (black), T_1 (red), or T_2 (blue). Negative errors represent Pair responses below model predictions.

(B–D) This is the same as for (A) but where the model is: (B) the average of T_1 and T_2, (C) summation of T_1 and T_2 followed by a saturating nonlinearity (see text), or (D) maximum of T_1 or T_2.

(E and F) (E) Frequency histograms and (F) cumulative frequency (unsigned) of all errors (normalized to unit area, n = 72). The narrowest error distribution is for competitive selection, with 91% of the data within an error less than 50 spikes per second.

(G) Linearly weighted errors (mean ± 95% CI) for the four target conditions. In each, competitive selection matches the Pair response with least errors, centered on zero (n = 18).

projecting to even the most distal levels of sensory processing [28]. CSTMD1 itself is a high-order efferent neuron, with its major dendritic input in the midbrain. The axon traverses the brain to contralateral arborizations coincident with the inputs of its mirror symmetric counterpart and a second set of extensive arborizations over the contralateral optic lobe [12, 29]. This morphology, in conjunction with the inhibition by targets presented in the contralateral visual field (Figures 1A and S1B; [13]), suggests a form of interhemispheric gating control by the competitively selected inputs.

It is possible, then, that CSTMD1 reflects the output of exogenous (bottom-up) attention mediated via a competitive process occurring at a lower level in the STMD pathway. However, we cannot rule out the possibility that target selection reflects a top-down, endogenous attention process. We recently showed that CSTMD1's response builds up slowly over hundreds of ms when single targets move along long trajectories [29, 30]. This slow facilitation could represent "arousal," as also observed in locust anticollision neurons [31]. Alternatively, it may resemble enhanced responses in primate visual cortex once attention is directed to a single stimulus [32, 33]. The rare cases where Pair initially lags both T_1 and T_2 responses (e.g., Figures 2K and L) may thus be analogous to recent data from primate area V4, where pattern selectivity for a "sought-after" target builds 40 ms after selectivity for "hardwired" features, such as color, shape, or orientation [34].

Our finding of a process analogous to selective attention in primates is particularly exciting because insects have proved to be powerful tools for "circuit-busting" neuronal computations in biological motion vision [35], inspiring substantial breakthroughs in computational models with diverse applications [36–38]. Insect preparations are amenable to physiological and pharmacological intervention in vivo, with major progress also now being made via selective genetic knockdown, at least in fruit flies [39, 40]. Nevertheless, our experimental preparation offers some disadvantages compared with preparations such as the awake, behaving monkey. Intracellular recordings require immobilization of head movements, preventing our dragonflies from directing gaze toward attended targets (overt attention) during experiments. Such fixation head movements have certainly been observed during free-flight pursuit of prey, using high-speed video techniques [41]. Controlled, endogenous focus on a particular area or feature (selective attention) in primate models functions via interaction with neuronal circuits of reward, memory, and sensory-motor coupling [42–44]—all of which have analogous circuitry in the invertebrate brain [21, 45, 46]. Although we have yet to find a way to train or reward dragonflies for covertly attending to a specific location, we may be able to manipulate the "attended" target more explicitly by carefully controlling the presentation order and initial location of the target and distracters in future experiments.

Supplemental Information

Supplemental Information includes three figures and Supplemental Experimental Procedures and can be found with this article online at http://dx.doi.org/10.1016/j.cub.2012.11.048.

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