Attracting the attention of a fly

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Edited by John G. Hildebrand, University of Arizona, Tucson, AZ, and approved March 25, 2011 (received for review February 14, 2011)

Organisms with complex visual systems rarely respond to just the sum of all visual stimuli impinging on their eyes. Often, they restrict their responses to stimuli in a temporarily selected region of the visual field (selective visual attention). Here, we investigate visual attention in the fly Drosophila during tethered flight at a torque meter. Flies can actively shift their attention; however, their attention can be guided to a certain location by external cues. Using visual cues, we can direct the attention of the fly to one or the other of the two visual half-fields. The cue can precede the test stimulus by several seconds and may also be spatially separated from the test by at least 20° and yet attract attention. This kind of external guidance of attention is found only in the lower visual field.

focusing on one source of sensory inputs to the exclusion of others is termed selective attention (1). Attention suppresses part of the incoming sensory information and allows only that from a particular source to be processed further. The need for attention is most obvious in vision because the visual field is often cluttered with many singularities, each one with its special potential significance for the subject. Attention has been compared to a “spotlight” (2) or a “zoom lens” (3). Typically, a human subject is said to shift its attention to a certain location by turning its gaze in that direction, but even without a shift of gaze, it can direct its attention voluntarily to any location in the visual field, as was already observed by Helmholtz (4) in the 19th century. Moreover, visual attention can be steered by external cues even if the subject is not conscious of them (5).

Like in humans, the focus of attention in other animals can also be attracted to arbitrary locations in the visual field. It is revealed by improved visual performance such as higher accuracy, shorter response times, and lower thresholds of neurons in the corresponding projection area of the brain. This property of visual systems has been intensely studied in humans and other mammals (6–8).

Insects can also restrict their behavioral responses to the stimuli in certain parts of the visual field (9), conforming to the operational definition of visual attention above. This property has been studied in flying Drosophila at the torque meter (10, 11). Because flies cannot move their eyes and, at the torque meter, their head and thorax are fixed in space, this preparation is particularly well suited for the study of visual attention. If, for instance, a vertical dark stripe is presented to a fly in a fronto-lateral position and is slowly oscillated around this position, the fly's yaw torque shows a characteristic modulation. During the fronto-to-back movement of the stripe, the fly generates a strong torque response in the same direction as the stimulus motion, whereas during back-to-front motion, the response in the opposite direction builds up much more slowly and the fly generates body saccades against that trend, i.e., toward the side of the stripe. This characteristic asymmetric modulation of yaw torque can serve to reveal the fly's focus of attention. If two stripes are presented, one on the right and the other on the left side of the fly, and coherently oscillated around these positions, the fly will at times show the typical torque pattern that it would generate if only the stripe on the left were presented and at other times the mirror-symmetrical pattern for the stripe on the right side (10). In other words, the response is not the sum of the responses to the single stripes. Sometimes, the fly confines its response to only one of them and ignores the other. Even if surrounded by a slowly oscillating random-dot pattern, the fly occasionally shows this characteristic response pattern in synchrony with the oscillation on the left or right side, as if for a while it was attending to a constellation of dots on that side (10).

Since its discovery in flies, attention has been hypothesized to underlie various behavioral and electrophysiological phenomena (12–16), but no attempts have been made to show that these phenomena correspond to a behavior conforming to an operational definition of attention.

An animal can spontaneously direct its attention to a certain location, but its attention can also be directed experimentally by visual and nonvisual sensory cues. For instance, in the above experiment with a slowly oscillating random-dot pattern, a wiggling vertical stripe on one side or the scent of fermenting banana reaching the fly with a puff of air from one side will prompt the fly to follow the slow oscillation of the panorama on that side (10). In this study, we reinvestigate visual cuing of visual attention and describe some of its properties.

Results

Focusing on Part of the Visual Field. Tethered flies were attached to a torque meter and placed at the center of a light-emitting diode (LED) arena (Fig. 1A). When a dark vertical stripe in the fly's fronto-lateral visual field (height, H = 96°; azimuth, ψo = ±42°) was displaced front-to-back by, for example, Δψ = 30° at 150°/s, flies produced a typical phasic modulation of yaw torque (Fig. 1B, gray area is the time period of front-to-back displacement). In the subsequent period of slow back-to-front motion of the stripe, flies showed no detectable responses. Most phasic responses had the same polarity as the fronto-to-back motion of the stripe (“syndirectional” responses; Fig. 2A, Single). Possibly, flies took the displacement as self-rotation and were trying to correct for it. If two stripes were presented at symmetrical fronto-lateral positions (ψo = ±42°) and one of them was displaced (Fig. 2A, One-of-two), response probabilities were similar to those in the single-stripe experiments.

To test for visual attention, both stripes were simultaneously displaced fronto-back, i.e., the right one moving clockwise, the left one counterclockwise (Fig. 2A, Both). Flies generated yaw torque modulations of either polarity with equal frequencies. The modulations had the same time course as before. If yaw torque would just reflect the vector sum of the motion stimuli in the two visual half-fields, no responses should be found. How-
ever, flies responded as if only one of the stripes was displaced, conforming to the definition of attention above.

Guiding the Focus of Attention. Next, we tried to steer the fly’s focus of attention (FoA) to one or the other visual half-field by using a visual cue. The displacement of the two stripes was preceded by a fast oscillation of one of the stripes (frequency, $f = 10$ Hz; peak-to-peak amplitude, $A_{\text{p-p}} = 4^\circ$; Fig. 2A, Cued). The oscillation stopped at the onset of the displacement. Now, flies responded preferentially with a yaw torque polarity corresponding to the displacement of the stripe on the cued side, whereas the overall response rate was not affected by the cuing. Note that the data exclude the interpretation that the responses to the two-stripes displacements were just the sum of the responses to the single-stripe displacements. In this case, no substantial cuing effect could have been observed (see cuing with single stripe below).

In the single-stripe displacement experiments, no responses and even occasional antidirectional responses were also observed. Their probabilities depended on the details of the experimental setup (see below). In most of the experiments, the bottom of the arena was a black cardboard disk just below the LED panels. If, for instance, the black disk was removed and some of the light of the arena was diffusely reflected by a gray ring and a metal plate underneath, response frequencies in most cases were different. For instance, with the black cardboard disk, the total response rate for the displacements of both stripes was higher ($f_{\text{both}} = 73\%$) than for single-stripe displacements ($f_{\text{single}} = 51\%$; compare in Fig. 2A, Both with Single and One-of-two), whereas with the light gray bottom, response rates were $f_{\text{both}} = 60\%$ and $f_{\text{single}} = 79\%$. These findings indicated that the clockwise and counterclockwise yaw torque modulations in response to the front-to-back displacement of one or two stripes might serve other purposes besides visual course control, such as escape or collision avoidance.

Same Stimulus Leads to Both Yaw Torque and Landing Responses. When both stripes were displaced front-to-back, flies frequently also showed landing responses (Fig. 2B, Both, Cued). They extended all of the legs and lifted the front legs above the head. The synchronous movement of the two stripes was a better releaser of the landing response than a single stripe. In more than one-quarter of all cases the two behaviors, yaw torque and landing response, were generated together. Evidently, for eliciting the landing response, both stripes were effective, whereas in the same event, only one of the stripes triggered the yaw torque modulation. The local stimulus suppression (FoA) was behaviorally selective.

Single stripe displacements elicited landing responses less often (Fig. 2C, Single, One-of-two). Interestingly, if in those cases flies also modulated their yaw torque, they always tried to turn
toward the stripe (syn-directional yaw torque; Fig. 2C). If they generated the two behaviors together, they coordinated them. Naturally, if antidirectional yaw torque modulations were avoidance or escape maneuvers, concomitant landing responses would be inappropriate.

**Cuing Affects Single-Stripe Displacement.** To investigate the cuing effect, we tested whether the FoA could be steered with shorter stripes and at different heights. A single stripe of half the height of the arena (H = 48°; \( \psi_o = \pm 42° \)) was presented at different vertical positions and was displaced front-to-back without a cue (Fig. 3A). If the stripe was presented at an intermediate height (symmetrically above and below the equator; Fig. 3A, Middle Stripe) or in the upper visual field (UVF; Fig. 3A, Upper Stripe), most frequently syn-directional responses were observed. Interestingly, equally frequent syn-directional and antidirectional responses were found if the stripe was confined to the lower visual field (LVF; Fig. 3A, Lower Stripe). This effect was not observed if a bright stripe on a dark background was presented (Fig. 3A, Inverted Lower Stripe). The effect of the inverted contrast (Fig. 3A, Inverted Upper Stripe) is not without precedent. It has been reported that inverting the contrast of the visual scene can change and even invert some of the yaw torque patterns produced by the flies (11).

The similar frequency of syn-directional and antidirectional responses to the displacement of a single stripe in the LVF raised the question whether cuing would affect this frequency. For reasons to be explained in the experiment of Fig. 4, we chose the arrangement of stripes shown in Fig. 3B (height of each stripe, H = 28°). As in Fig. 3A (Lower Stripe), syn-directional and antidirectional responses to the displacement of only the stripe in the LVF were about equally frequent (Fig. 3B, Not cued). Now, if the stripe in the LVF was oscillated before its displacement, the marked prevalence of syn-directional responses was restored (Fig. 3B, Cued). This change in response frequencies shows that cuing not only can steer the FoA of the fly but also can influence directly or indirectly the fly’s evaluation of the significance of the test stimulus.

**Cuing Operates Exclusively in the LVF.** In the next experiment, four stripes of equal height (H = 28°) were presented to the fly (Fig. 4). Two stripes were always placed at the same azimuth (\( \psi_o = \pm 42° \)), one in the LVF, and the other in the UVF. Upper and lower stripes were separated by a 40° vertical gap. First, only the lower two stripes were displaced (Fig. 4A). As seen previously, flies generated equally often clockwise and counterclockwise yaw torque responses. Next, only the upper stripes were displaced (Fig. 4B), and again flies responded equally often in both directions. Now, the cue was presented. If one stripe in the LVF (Fig. 4C; upper stripes were stationary) was oscillated before the displacement of both the lower stripes, flies responded more often with the yaw torque polarity corresponding to the cued side showing that the attention could be guided by the cue. Intriguingly, when the cue was presented in the UVF (Fig. 4D), flies did not show more frequent responses to the cued side (only upper stripes were displaced). These results indicate that the cue could guide the attention only in the LVF. To see whether there was a cross-talk between the LVF and the UVF, the cue was presented in the LVF, whereas the stripes in the UVF were displaced (Fig. 4E) or vice versa (Fig. 4F). In none of these cases flies showed more frequent responses to the cued side. So, the cue could only guide the attention when both the cue and the displacements were presented in the LVF.

**Cuing Is Equally Effective at All Lateral Positions.** To further characterize the steering of the FoA, some of the conditions of its occurrence were investigated. Because the UVF seemed not to contribute to the phenomenon, experiments were confined to only the LVF with two dark stripes of H = 48°. First, the stripes were presented at various positions between \( \psi_o = 0° \) and \( \psi_o = \pm 90° \) (Fig. 5). Although without any cue the responses to the two sides remained almost equally frequent (Fig. 5, ccw, cw), the total response frequency decreased as the stripes were placed further apart. Guidance was observed for a wide range of stripe positions (\( \psi_o = \pm 30° \) to \( \pm 90° \)). At \( \psi_o = 14° \), the guidance effect was small and not significant, maybe because this position fell into the range of binocular overlap or because the stripe that was not cued was close enough to the cued stripe to be reached by the spotlight of attention (Fig. 5).

**Cuing Effect Lasts Longer Than 2 Seconds.** In an attempt to find how long the guidance effect lasts, the cue and the displacements were separated in time. The delay between the presentation of the cue and the displacements was varied from 0.5 s to 5 s (Fig. 6A). During the intermission, the two stripes remained visible but stationary. The efficiency of the cue diminished as the delay increased. The cue attracted the attention significantly to its side even after a delay of 2 s, whereas its effect was no longer significant at a delay of 5 s (Fig. 6A). Interestingly, if the two stripes disappeared after the oscillation for 0.8 s and reappeared just before displacement, the cuing effect was abolished (Fig. S2).

**Cuing and Test Stimuli Can Be Spatially Separated.** To find the spatial extent of the cuing effect in guiding the attention, the oscillating stripe was presented at variable positions, from \( \psi_o = \pm 22° \) to
ψ₀ = ±60°, whereas the positions of the displacements remained constant at ψ = ±42° (Fig. 6B). In this experiment, two extra stripes (H = 48°; in the LVF) appeared at the time of the cue presentation at the indicated positions. One of these stripes oscillated and then both disappeared. This event was followed by the normal test i.e., the displacement of the stripes at ψ₀ = ±42°, which were always visible. The guidance of attention was not compromised by the appearance or disappearance of the additional pair of stripes and irrespective of the distance of the cue from the displaced stripes, the guidance was equally effective at all of the positions tested (ψ₀ = ±22° to ±60°; Fig. 6B).

**Different Cuwing Stimuli.** What kinds of sensory stimuli are suited to guide visual attention? An exhaustive answer to this question would exceed the scope of this study, but in a couple of pilot experiments, we asked whether visual motion was essential for cuing. Like the test stimulus, the A_p-p = 4° oscillation of the stripe used in the experiments so far, is a fast directional-motion stimulus (11). We wondered whether nonmoving visual cues would also be effective. In the first experiment, one of the stripes was flickered (flicker frequency f = 5 Hz; H = 48°; ψ₀ = ±42°) before both stripes were displaced as the test. The flicker attracted the attention to its side as effectively as the 10-Hz oscillation.

In a final experiment, vertical columns of LEDs were placed at ψ₀ = ±42° and -42° in front of the dark stripes spanning the whole height of the arena as in the experiment of Fig. 2 (H = 96°; δ = 10°) and one of the columns was flickered at 2 Hz. The LEDs emitted white light at >10 times the intensity of the green LEDs of the arena. Flies responded with the characteristic torque modulation to the displacement of the stripes but surprisingly, with this massive cue before the displacement, no guidance effect was observed. The overall response frequency and the dynamics of the individual responses, were not altered, indicating that the flickering LED column did not hamper the visibility of the displacement on its side. These observations indicate that highly salient stimuli may override the attention system.

**Discussion**

We have established a solid experimental approach to visual attention in *Drosophila* showing that the fly can temporarily restrict some of its behavioral responses to a certain location in the visual field (FoA) and that the FoA can be guided to different locations by external stimuli. We have started to characterize this system. An earlier account of the basic phenomenon (10) had not been fully conclusive because the cuing stimuli were presented during the test, leaving as alternative interpretation an interaction of the cuing and test stimuli. The present paradigm avoids this ambiguity. Moreover, it is robust and should lend itself to the genetic dissection of the neuronal and functional architecture of visual attention.

The simultaneous front-to-back movements of the two stripes at symmetrical positions on the right and left side of the fly, one rotating clockwise, the other counterclockwise, do not annihilate each other’s stimulatory effects for yaw torque. The fly behaves as if only one stripe had been displaced. Formally, the operational definition of visual attention, the temporary restriction of a behavioral response to a certain location in the visual field (FoA), would be met by this phenomenon. However, such an effect could be explained just by a mutual inhibition of the central pattern generators (CPGs) for right and left turns. The one triggered first would suppress the other. In fact, a network preventing the simultaneous activation of these two CPGs might well exist. However, visual attention serves more than just preventing the simultaneous activation of antagonistic motor patterns. It enables the organism to deal with the visual features in its surroundings one at a time and according to their salience and putative behavioral significance.

This parcellation of the visual field is what we find in the present experiments. The FoA and its external steering reveal one aspect of this internal choice process. The cue attracts the FoA to the location of the cue. At the time of the test, the oscillations have ceased but the FoA persists. A direct interaction of the cuing and test stimuli can therefore be excluded.
A major finding of this study is the marked functional difference between the LVF and the UVF. With the cues tested, we could only guide the attention in the LVF. Moreover, in the LVF, syn-directional and antidirectional responses to the displacement of a single stripe (Fig. 3A, Lower Stripe) occurred equally often. Inverting the contrast of the stripe changed these response frequencies close to those found in the UVF (Fig. 3A, Inverted Lower Stripe) but had no effect on the response frequencies in the UVF. What ecological roles the specific response frequencies play is a matter of speculation. Intuitively, during flight, the guidance of attention would be more important in the LVF for a fly as most of the objects of interest like food and landmarks are in the LVF while flying. Moreover, bigger insects (like robber flies and dragonflies) that predate on *Drosophila* generally attack from below. It will be interesting to try out other cues and to find out whether these differences between the LVF and UVF are the same during walking. These LVF and UVF differences in *Drosophila* are not an exception. In humans and nonhuman primates, it has been shown that some visual attributes are differentially processed in the LVF and UVF (19, 20) and that the attentional resolution is finer in the LVF (21).

Whether effective cueing of some kind will eventually be found for the UVF remains open. Because antidirectional yaw torque responses to unilateral test stimuli as well as directional yaw torque responses to bilateral test stimuli are also observed in the UVF (Fig. 3A and 4), this part of the visual system may be no more “hard-wired” than the LVF. Cuing in the UVF may just follow different rules and require different stimuli.

Visual attention has been postulated to play an essential role in visual pattern recognition at the torque meter (22). As the fan-shaped body is involved in pattern recognition (23) and is thought to represent visual space (24), one might search there for a neuronal substrate of visual attention.

To our knowledge, visual attention in an insect has not previously been subject to a systematic account. It will be interesting to compare this system to visual attention in mammals. Given the basic need for attention in complex visual systems, it is too early to even speculate whether the attention systems in mammals and insects coevolved or have a common phylogenetic origin.

Materials and Methods

**Flies.** Wild-type flies of the strains Canton S (CS) or Berlin (WTB) were reared on standard corn meal-molasses medium at 25 °C and 60% relative humidity under 14 h/10 h light/dark cycle. CS flies were used in the experiments unless otherwise mentioned. For tethering, individual female flies (2- to 3-d-old) were briefly immobilized by cold anesthesia. A triangular-shaped holder made of copper wire (0.05-mm diameter) was positioned by using a micro-manipulator between the fly’s head and thorax. Dental composite (3M ESPE Silflow, DO3) was used to glue the hook to the fly. The composite was polymerized with a 10-s pulse of blue light from a LED dental curing light source (distance < 0.5 cm). Flies were then kept in separate chambers supplied with sucrose and water for a day before the experiment.

**Setup.** A cylindrical arena made of 180 × 48 green LEDs was used to present the visual stimuli. If not otherwise stated, a circular disk of black cardboard was positioned at the lower edge of the LED panels, forming the floor of the arena. For a “bright bottom,” the fly could see a ring of gray plastic underneath the arena (on which the arena rested) and, ±6 cm further down, a gray metal plate (floor) diffusely reflecting some of the light of the LEDs.

Control of the sequence of pattern presentation and timing of the experiments was accomplished by custom-made software written in C++ on a Linux environment (by Andreas Eckart). Flies were clamped with their triangular copper wire holders to a small metal clip that was attached to a torque meter. While doing so, the flies were positioned in the center of the LED arena (Fig. 1A) in an otherwise dark room. Yaw torque of the stationary flying flies was digitalized (resolution 12 bit) and recorded on the controlling computer’s hard disk at a sampling frequency of 100 Hz. These torque data were later evaluated by using Microsoft Excel. All experiments were carried out under open loop conditions, i.e., the yaw torque responses of the flies were only recorded and had no retroactive effect on the stimulus itself.
Stimulus Conditions. Stripes used in all of the experiments were 6° wide (three vertical columns of LEDs) unless otherwise mentioned. For the test of visual attention, two stripes were presented in the fly's fronto-lateral visual field at symmetrical positions with respect to the fly's longitudinal body axis. Stripes were displaced by $\Delta \psi = 30^\circ$ with fast front-to-back motion of $150^\circ/s$ and then moved back slowly to the initial positions at $20^\circ/s$. For cuing, one of the stripes was oscillated before the displacement with a frequency of 10 Hz and a peak-to-peak amplitude $(A_{p-p})$ of $4^\circ$. Unless otherwise mentioned, the stationary starting positions of the stripes were at $\psi_0 = \pm 42^\circ$. A typical experimental frame without a cue had the following sequence: presentation of stationary stripes at the initial position $\psi_0$, for 5 s, displacement over $\Delta \psi = 30^\circ$ for 0.2 s, stripes returning back to $\psi_0$ in 1.5 s. In a typical experiment involving cue presentation, the following sequence was used: stationary stripes presented at $\psi_0$, for 5 s, cue presentation for 5 s, displacement over $\Delta \psi = 30^\circ$ for 0.2 s, stripes returning back to the initial position $\psi_0$ in 1.5 s. This sequence was repeated eight times for the same fly, if the fly did not stop flying. Responses to the fast front-to-back displacement were readily recognizable (steep rising phase in one or the other direction and somewhat slower decline). A response was scored when the yaw torque modulation in response to the front-to-back displacement was $> 10 \times 10^{-10}$ Nm and started within 40–200 ms after the onset of the displacement (Fig. 1B). The response was called syn-directional when the steep rising phase of the same polarity as the front-to-back displacement. When it was of the opposite polarity, it was called antidirectional. Syn-directional and antidirectional responses as well as the responses to bilateral displacements had all about the same dynamics and remained similar in all of the cases whether there was a cue present. For the experiments of Fig. 5, the stationary positions of the stripes were varied from $\psi_0 = 0^\circ$ to $\psi_0 = \pm 90^\circ$. In the experiments with temporal delays between the cue and the displacements (Fig. 6A), the stripes were visible already during the delay before their displacement. Here, a response index was defined as $RI = (p(s) – p(0))/p(s) + p(0))$, with $p(s)$ being the probability of the response toward the cued side and $p(0)$ the probability of the response away from the cued side. Both WT strains, CS and WTB, were tested in these experiments. Data from both WT strains were pooled because they did not show any significant differences. For the spatial separation of the cue from the displacement (Fig. 6B), during cue presentation two extra stripes appeared at variable positions. These stripes had the same size as the displaced stripes. The stripes to be displaced were always presented at $\psi_0 = \pm 42^\circ$. For the flickering stripe as the cue, just like the oscillating stripe, one of the stripes that was later displaced, was flickered at 5 Hz. For flickering, the corresponding LEDs of the arena were switched on and off. The white LED column was not completely opaque and was narrower (column width $= 3^\circ$) than the width of the dark stripe ($\delta = 10^\circ$) in this experiment on the display such that the latter was easily visible on both sides of the LED column. In the experiments of Fig. S3, four stripes were presented always while only one was ever displaced at any given time. The cuing duration was 3 s in these experiments.

Statistical Analysis. Because some data were not normally distributed (Kolmogorov–Smirnov test), Wilcoxon Matched Pairs test for dependent pairwise comparisons was used to test the frequency of response to one side (for e.g., the “cued” side) against the frequency of response to the other side (for e.g., the “not-cued” side). The one-sample Wilcoxon Signed Rank test was used to compare the response frequencies with a random value (for landing response). $P$ value $< 0.05$ was taken as significant.

ACKNOWLEDGMENTS. We thank Tom Collett for interesting comments on the manuscript and Konrad Oechsner and Andreas Eckart for technical support. This work was supported by Sonderforschungsbereich 554 (to R.W. and M.H.). P.S. was supported by a grant of the German Excellence Initiative to the Graduate School of Life Sciences, University of Wuerzburg.
Supporting Information

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SI Results

After observing the equally strong cuing effects with various spatial separations of the test and the cue, we wanted to check whether the focus of attention is as wide as one visual half-field or whether attention can be differentially allocated to locations within one half-field as well. So, we presented four stripes (H = 40°) at $\psi_0 = \pm 24°$ and $\psi_0 = \pm 74°$. Each time only a single stripe was displaced front-to-back. First, the stripe at $–24°$ was displaced and the rest of the stripes remained stationary. Flies almost always responded syn-directionally (Fig. S3A). Then, either the same stripe at $–24°$ (Fig. S3B) or the stripe at $–74°$ was oscillated before displacement at $–24°$ (Fig. S3C). The trend of the response frequencies did not change in both the conditions. Next, we displaced the stripe at $–74°$ and the flies responded with the same frequency syn- and antidirectionally (Fig. S3D). When the same stripe at $–74°$ was oscillated before the displacement, flies started responding more syn-directionally (Fig. S3E). However, cuing at $–24°$ did not result in more syn-directional responses for the test at $–74°$ (Fig. S3F).

Fig. S1. Steering of the focus of attention, as in Fig. 2A, for the n = 17 flies evaluated for the landing response in Fig. 2 B and C. *P < 0.05, **P < 0.01. Error bars are SEM.

Fig. S2. Discontinuity in the display of the cue and the test stripes abolishes the cuing effect. When the test stripes are presented after 0.8 s of the disappearance of the cue, the cuing effect is abolished (Upper) but when the test stripes are continuously visible after the cue presentation, the cuing effect persists (Lower). n = 27. ***P < 0.001. Error bars are SEM.
Fig. S3. Spatial extent of the focus of attention is smaller than one lower visual half-field. Attention can also be guided within one lower visual half-field. When a stripe is displaced at a more frontal azimuth (±24°), flies always respond syn-directionally (A). When the same stripe is cued and then displaced (B) or another more laterally placed stripe (at ±74° in the same half-field) is cued before the more frontal stripe’s displacement (C), flies similarly respond more syn-directionally. However, when the more lateral stripe is displaced flies generate equally frequent syn-directional and antidirectional responses (D). Cuing this same stripe before its displacement results in significantly more frequent syn-directional responses (E), whereas cuing the other stripe in the same half-field does not (F). n = 49. **P < 0.01, ***P < 0.001. Error bars are SEM.