

Super Bowl, an open platform for visual stimulation of insects

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1 **Abstract**

2 To study how the nervous system processes visual information, experimenters must record
3 neural activity while delivering visual stimuli in a controlled fashion. In animals with a nearly
4 panoramic field of view, such as flies, precise stimulation of the entire visual field is
5 challenging. We describe a projector-based device for stimulation of the insect visual system
6 under a microscope. The device is based on a bowl-shaped screen that provides a wide and
7 nearly distortion-free field of view. It is compact, cheap, easy to assemble, and easy to operate
8 using the included open-source software for stimulus generation. We validate the virtual reality
9 system technically and demonstrate its capabilities in a series of experiments at two levels: the
10 cellular, by measuring the membrane potential responses of visual interneurons; and the
11 organismal, by recording optomotor and fixation behavior of *Drosophila melanogaster* in
12 tethered flight. Our experiments reveal the importance of stimulating the visual system of an
13 insect with a wide field of view, and we provide a simple solution to do so.

14 **Introduction**

15 Neural responses are inherently variable. The visual system is no exception in this respect, as
16 repeated presentations of the same stimulus tend to elicit different neural responses. To
17 decipher the influences of visual stimulation on neuronal responses, experimenters must be
18 able to deliver light to the eye in a controllable and reliable manner. An ideal visual stimulation
19 device would provide precise temporal and spatial control over every retinal photoreceptor cell.
20 In recent years, research on the visual system of insects, in particular that of *Drosophila*
21 *melanogaster*, has produced a rich collection of stimulation devices that take many shapes and
22 forms. Fueled by technological advances, most of them either repurpose devices originally
23 designed for the human visual system [1–6], or are custom-made from highly specialized
24 components [7–11] rendering their implementation almost prohibitively expensive. To tailor a
25 stimulation device to the demands of an insect's visual system, while keeping it versatile,
26 compact and affordable, poses a formidable technical challenge.

27 In contrast to the human eye, the compound eye of *Drosophila* is tiled by hundreds of
28 ommatidia arranged in a hexagonal grid. Each ommatidium of the convex retina collects light
29 from a visual angle of approximately 5° using a miniature lens with an aperture of $16\ \mu\text{m}$ and
30 a focal length of $20\ \mu\text{m}$ [12–15]. These dimensions, for the most part, obviate the need to
31 accommodate, as any object beyond a few millimeters appears at infinity focus. With an inter-
32 ommatidial angle of $\sim 5^\circ$, the spatial resolution of *Drosophila* is low, but the convex geometry
33 of its eyes provides for a nearly panoramic field of view [16,17].

34 Dynamic visual environments for head-restrained insects that allow experimenters to record
35 behavioral and neural responses to visual stimuli are commonplace in insect neuroethology
36 [18]. Relicts of long-gone manufacturing constraints, most displays used to create these virtual
37 environments have either a flat or a cylindrical geometry, neither of which matches the shape
38 of the fly eye. Hence, they all bear at least three limitations: First, they cover only a small
39 fraction of the fly's field of view. Second, the brightness of the display varies across visual
40 space as a function of the viewing angle; and third, distortions in the periphery of the visual
41 field complicate the correspondence between actuator (pixels) and sensor (ommatidia)
42 (Fig 1A–1C). While the latter two can be compensated for by computationally costly pre-
43 adjustment and pre-distortion of the displayed images, the first caveat is unavoidable.

44 Here, we describe an inexpensive projector-based visual stimulation device that caters to many
45 of the demands of the insect visual system. It provides a wide and nearly distortion-free field
46 of view with uniform brightness, but is compact enough to fit under a microscope. The crux of
47 our system lies in the unconventional screen geometry, shaped like a quarter of a football,
48 which simplifies both software and hardware development. Our open-source Python code
49 allows any user with access to a computer and a 3D printer to create a bowl-shaped screen that
50 suites the specifications (i.e. the throw ratio) of their projector. The temporal, spatial and
51 spectral performance of the system can be adjusted, according to experimental requirements
52 and budget constraints by resorting to different commercially available projectors. We provide
53 Python code to generate the screen design and to export it for 3D printing, but also to display
54 a wide repertoire of visual stimuli commonly used by researchers, teachers, and students who
55 study the insect visual system.

56

57 **Results**

58 **Comparing screen geometries**

59 To simulate and quantify the perspective distortions that occur when using different screen
60 geometries, we used a polyhedron as a general, simplified model of the invertebrate compound
61 eye. The screen capture from each projected polyhedron face can be understood as the number
62 of projector pixels required to stimulate a certain fraction of the visual field, for example, one
63 ommatidium or one spatial receptive field of a neuron. To allow direct comparison of different
64 screen geometries, a Goldberg polyhedron containing 272 almost identical faces served as a
65 model observer in front of a flat, a cylindrical, or a bowl-shaped virtual surface.

66 Observing the grid of the polyhedron projected onto a flat surface (Fig 1A), only the hexagon
67 at the center of the visual field appeared undistorted. With increasing distance from the center,
68 the hexagons grew rapidly in surface area and were increasingly distorted. At an angular
69 distance of 50° from the center, hexagonal projections were on average 3.3 times longer and
70 1.9 times wider, after correcting for the hexagon's original aspect ratio; their area increased by
71 a factor of 5.5. On a cylindrical surface (Fig 1B), hexagons remained undistorted along the
72 equator but were subject to heavy distortions along the elevation. At an angular distance of 50°
73 from the center, the average hexagon grew by a factor of 2.9 in elevation and 1.6 in azimuth.
74 The area of a hexagonal projection increased by an average factor of 4.6. The bowl-shaped
75 surface featured no distortion along the elevation and only slight azimuthal distortions in the
76 periphery of the screen (Fig 1C). At an elevation angle of 50° from the pole, the azimuthal
77 distortion factor amounted to 1.2; at 100° from the pole, it was 2.4. The area of the hexagonal
78 projection increased by the same factor of 1.2 at 50° and 2.4 at 100° from the center. Aside
79 from robustness against distortions, a bowl-shaped screen features another advantage: It covers
80 a substantially larger fraction of the visual field compared to a flat or a cylindrical screen of
81 the same surface area. A cylindrical shape would require 44% of the area to cover the same
82 visual field as a flat screen. The bowl-shaped screen can stimulate the same field of view with
83 only 24% of the screen surface.

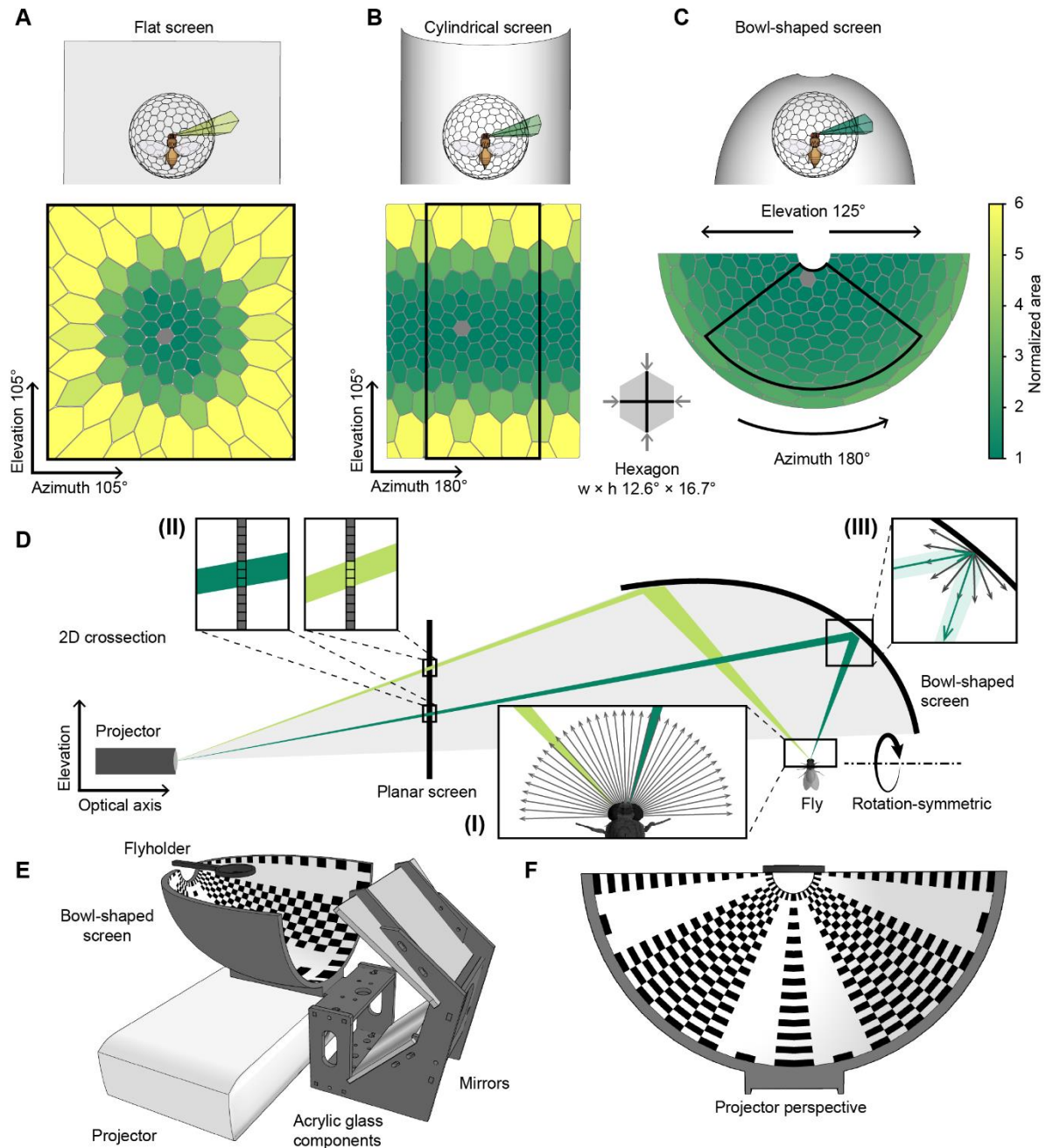


Fig 1: Geometry of the bowl-shaped screen

A-C Renderings of a virtual projection of a hexagonal grid onto a planar (A), cylindrical (B) and bowl-shaped screen (C). The area sizes are normalized to a standard undistorted hexagon at the center. One hexagon corresponds to the visual space covered by approximately nine ommatidia of *Drosophila melanogaster*. **D** Cross-section of the model used to calculate the screen geometry (Equation 3). (I) Spherical photoreceptor arrangement of the fly, assuming a constant inter-ommatidial angle of 5°. (II) Projector designed to produce a uniform illumination and resolution on a planar screen. (III) The shape of the screen and its Lambertian reflection properties guarantee homogeneous spatial luminance distribution across the entire surface. **E** View of the bowl-shaped screen, the mirrors and the projector. **F** Projector perspective of the screen with the necessary equidistant azimuthal projection of the pattern in E.

84 **Screen design and evaluation**

85 The Super Bowl display system consists of an image projector and a screen. Like in any other
86 virtual reality system, the image must be pre-distorted in order to be accurately perceived from
87 the position of the observer. Both the observer and the projector are stationary, which allows
88 us to account for any perspectival distortions in a single step. The correction is not based on a
89 computationally intensive software solution, as is usually the case, but on a specific hardware
90 configuration that uses a precalculated screen geometry at no computational costs. To
91 determine the ideal screen shape, we created models of both the observer and the projector.
92 Here, a sphere with a polar grid served as an approximation of the compound eye, where the
93 optical axis of each ommatidium was represented by a radial vector connecting the center of
94 the sphere with the center of the respective face. Taking advantage of the rotational symmetry
95 of the sphere, we reduced the model of the observer to a two-dimensional cross section
96 (Fig 1D I) (Equation 1). The projector model was simplified to the same extent by considering
97 only two dimensions: one along the optical axis of the projector and a second one along the
98 elevation (Fig 1D). Commercially available projectors are designed to project images with
99 uniform pixel size and uniform luminance onto a planar screen (Fig 1D II) (Equation 2). To
100 guarantee uniform brightness across the visual field of the insect, it is necessary to maintain a
101 constant ratio of pixels (photons) per ommatidium of the convex retina (Fig 1D). A precise
102 correspondence between computer-generated pixels and the retinotopy of the insect visual
103 system can only be established if this ratio is constant across the field of view. We implemented
104 this by intersecting the optical axis vector of each ommatidium along the elevation plane with
105 the modeled photon vector originating at the projector. The trajectory connecting the resulting
106 intersection points defined the screen curvature along the elevation (Fig 1D) (Equation 3). The
107 curvature of the screen along the azimuth was obtained by rotating the trajectory about the
108 polar axis (Equation 4). The resulting concave surface was predicted to be of uniform
109 brightness, from the insect's point of view, provided that the screen surface features diffuse,
110 Lambertian reflectance independent of the incidence angle (Fig 1D III). To achieve this
111 property, and to avoid artefacts caused by a cascade of specular reflection (Fig 2A), we coated
112 the inner surface of the 3D-printed screen with different combinations of white paint and
113 varnish. In order to test the optical properties of the surface, we illuminated square spots
114 ($5^\circ \times 5^\circ$) along the elevation and placed a wide-angle camera (Fusion, GoPro) with a
115 panoramic 360° field of view at the position of the observer to record the reflected light
116 (Fig 2B and 2C). One particular combination of paint and varnish (see Methods) showed

117 virtually no specular reflection along the elevation and was used in all subsequent experiments
118 (Fig 2B and 2C).

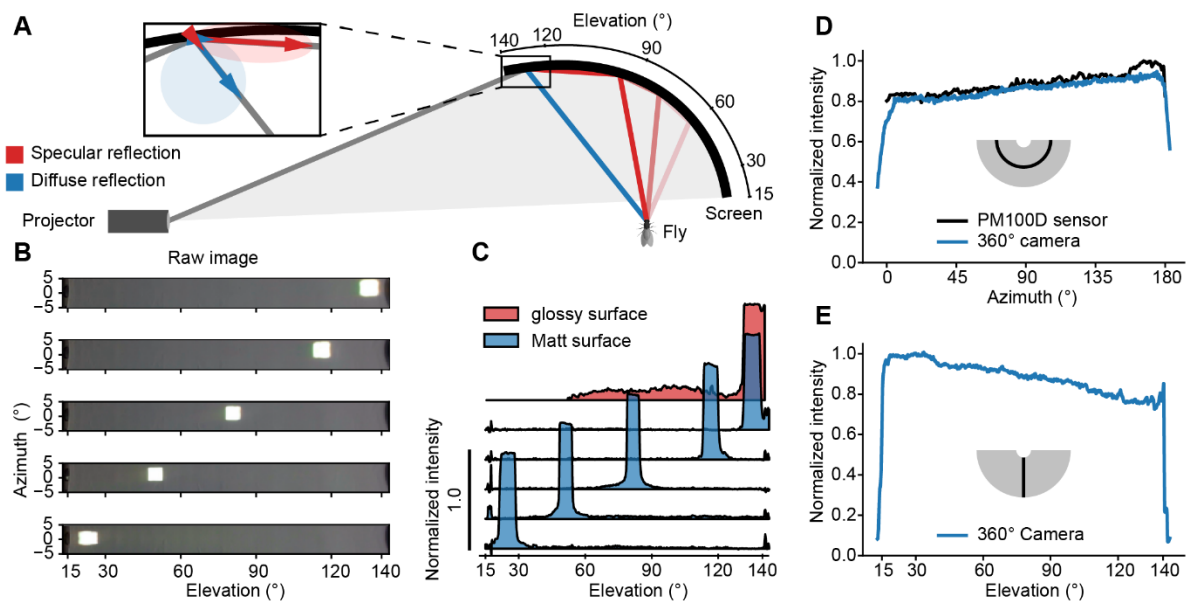


Fig 2: Technical validation of the operating principle

A Overview of Lambertian and specular reflectance properties of the screen surface. The blue vectors describe the diffuse, the red vectors the specular reflection component of an entering light ray. Flat angles of incidence cause a reflective cascade on the screen surface. **B** Raw images of bright rectangular squares displayed at different locations along the elevation. **C** Luminance profile along the elevation of a glossy (red) and a matte (blue) surface. The matte surface was evaluated with bright squares projected onto different locations along the elevation. In contrast to the matte surface, the uncoated, glossy surface showed a pronounced reflection cascade. **D, E** Luminance profiles along the azimuth (**D**) and the elevation (**E**), measured with a 360° camera (blue). Measurements along the azimuth were validated using an optical power meter (black).

119 Luminance measurements from the position of the observer using a rotatable power meter, as
120 well as a 360° camera, corroborated our prediction and revealed a nearly isotropic luminance
121 across the entire elevation of the screen (Fig 2D and 2E). The calculated brightness uniformity
122 (i.e., the lowest luminance reading at any point as a fraction of the highest) amounted to 73%,
123 which is comparable to the uniformity other projectors achieve on a planar screen. For instance,
124 the Texas Instruments DLP® LightCrafter™ projectors 4710 EVM or 3000 EVM, which are
125 used in several stimulation systems, reach about 70% brightness uniformity [1,3,19].

126 The bowl-shaped screen was held in place by a scaffold made of acrylic glass components
127 (Fig 1E). Two mirrors served to reduce the overall size of the set-up, but could be omitted
128 depending on spatial constraints. In the present configuration, the mirrors allowed for the

129 projector to be placed underneath the screen. In contrast to other virtual reality systems the
130 projector is easily replaceable and maintainable, making the system to the largest possible
131 extent independent of the rapid product turn over on the consumer market. We used a standard
132 projector (LG PH510PG) with a native resolution of 1280×720 pixels, a throw ratio of 1.4, a
133 projection offset of 100% upwards, and an intrinsic brightness uniformity of ~90%. The
134 projector had an image refresh rate of 60 Hz and a flicker frequency of 240 Hz, which exceeds
135 the critical flicker fusion frequency of most insects including that of *Drosophila* [20]. Higher
136 refresh rates could be achieved by using projectors like the ViewSonic® M2E (120 Hz) or the
137 Texas Instruments DLP® LightCrafter™ 4500 EVM (400 Hz).

138 **Stimulus design and validation**

139 In order to create an immersive, panoramic virtual reality for the animal, we take the insect
140 observer to be at the center of a fictive unit sphere from where it observes an equidistant
141 azimuthal projection of the sphere. Owing to the special geometry of the screen, this projection
142 is—conveniently— identical to the image that must be displayed by the projector (Fig 1F). In
143 other words, the screen geometry allows the direct projection of a spherical texture. The
144 equidistant azimuthal projection is formally equivalent to a polar-transformed version of an
145 equirectangular projection, the latter of which might be more familiar to the reader, for example,
146 as a Cartesian map of the Earth. These interpretable equirectangular projections served as
147 spherical textures and were chosen as the input format. In order to avoid subsequent
148 interpolation, the projectors polar coordinate system was transformed into the Cartesian
149 coordinate system of the input texture using two precalculated transformation matrices: one for
150 the x- and another for the y-coordinate of each pixel. The size of each matrix, and therefore the
151 runtime, depended on the spatial resolution of the projector. Since the output image size, the
152 transformation matrices, and the input image size were known (and constant) during runtime,
153 we used just-in-time compilation within the JAX (Google) framework to calculate the
154 transformations on the computer's graphics processing unit (GPU). On a standard laptop with
155 a GTX1060 (Nvidia) graphics card, the transformation of a color image of 1280×720 pixels
156 took on average 2-3 ms. Before the transformation, to speed up processing times,
157 equirectangular representations were cropped to the field of view covered by the screen (here,
158 $180^\circ \times 125^\circ$ in azimuth and elevation, respectively) and stimuli with a rotational component
159 were pre-rotated (Fig 3B). To illuminate only the screen and to minimize stray light, a clipping
160 mask was applied, which could be adapted to incorporate additions to the setup, such as time-
161 stamp signals or cameras for monitoring behavior.

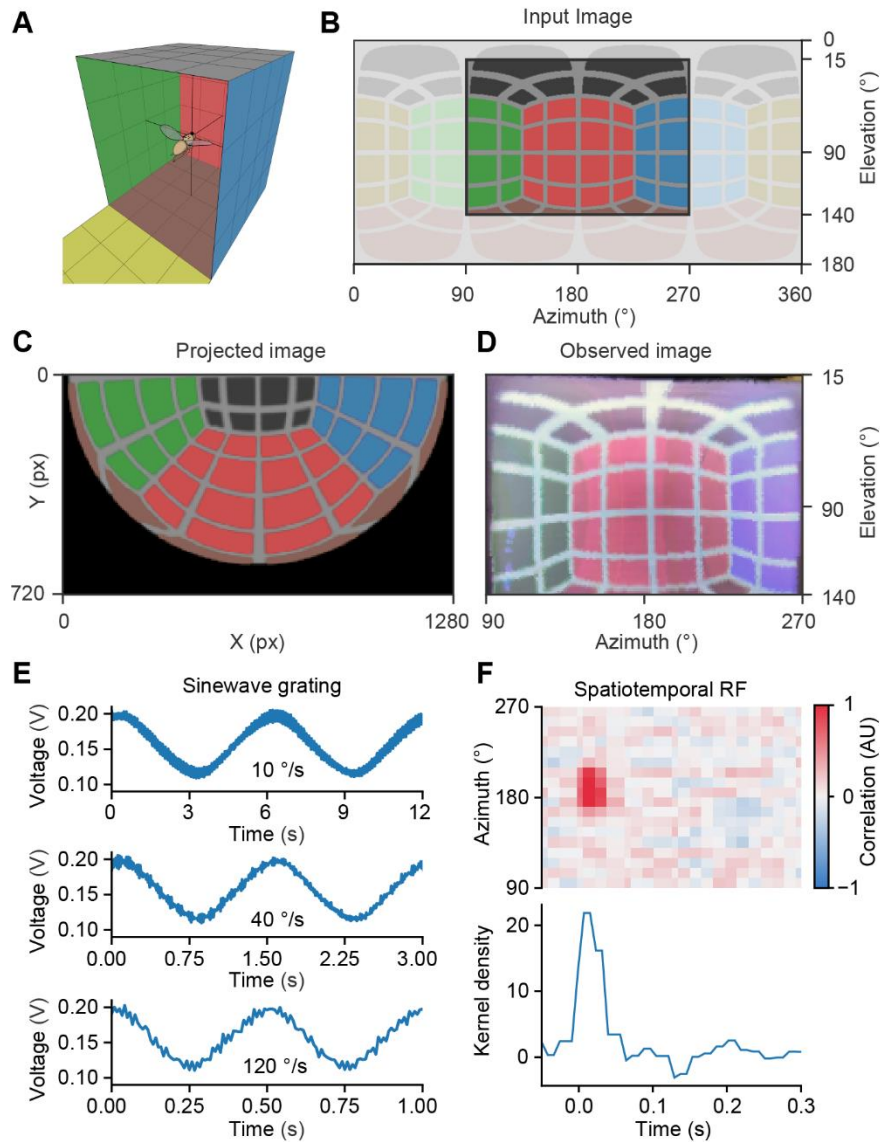


Fig 3: Technical validation of spatial and temporal stimulus control

A 3D view of the fly inside a virtual cube with colored walls. **B** Input image, an equidistant cylindrical projection of the virtual cube. The entire image is shown in light color, the image displayed on the screen is shown in dark color. **C** Image from the viewpoint of the projector to be displayed on the bowl-shaped screen. **D** Captured image of the bowl-shaped screen from the 360° camera in equidistant cylindrical projection, the direct comparison to the dark region in **B**. **E** Sinewave gratings moving across the screen at three different velocities captured by a photodiode and resampled to a framerate of 120 Hz. **F** Spatiotemporal “receptive field” of the photodiode, measured over 8 minutes.

162 To put our stimulation device to a test, we used the panoramic 360° camera. From the position
 163 of the observer, the camera provided a high-resolution equirectangular projection of the entire
 164 screen, which—given correct transformation and alignment—should be identical to the input
 165 image. Comparison between the two allowed for a qualitative assessment of possible image

166 distortions. As an image, we used the panorama from inside a cube with differently colored
167 sides (Fig 3A) and inspected the transformed image at each step in the process chain: the
168 cropped equirectangular projection, which served as the input image (Fig 3B), the projected
169 image (Fig 3C), and the image captured by the panoramic camera (Fig 3D). The cropped input
170 image (Fig 3B) and the observed image (Fig 3D) were virtually identical in terms of their
171 proportions, grid geometry, contrast, sharpness, and field of view. This attests to the accuracy
172 of the transformation and the correct, undistorted display of images on the 3D-printed screen.

173 Time-varying visual stimuli were generated using custom-written software in Python. To
174 assess the temporal performance, rotational stimuli like sine wave gratings moving at various
175 velocities (Fig 3E) and online-generated stimuli such as a discrete white noise stimulus (Fig 3F)
176 were evaluated using a fast photodiode as a fly's proxy. In case of moving sine wave gratings,
177 there were no conspicuous flickers in the down-sampled photodiode signal (<120 Hz), which
178 might be perceived by insects. The amplitude, the frequency and the phases of the signals were
179 identical for all velocities (Fig 3E). Before testing our bowl-shaped screen on real neurons with
180 uncertain temporal filter properties, we measured the temporal precision of our stimulation
181 device by measuring the spatiotemporal “receptive field” of a photodiode for reference. We
182 projected onto the screen a 60 Hz spatiotemporal binary white noise stimulus over a period of
183 8 min. Cross-correlating the luminance at each screen position with the photodiode signal
184 revealed a positive correlation confined to the first 3 frames (50 ms). This sharply tuned
185 temporal receptive field suggests that, over the stimulation period of 8 min, jitter and drift are
186 in the range of ± 1 frame (16.67 ms) (Fig 3F).

187 The bowl-shaped screen makes it possible to stimulate the visual system in an identical manner
188 at various points in space. This is essential, for instance, when spatiotemporal receptive fields
189 of neurons at different spatial locations in the visual system are to be measured precisely. To
190 test the spatial precision of our system, we measured the spatial “receptive fields” of the same
191 photodiode placed at two different locations in the arena (Fig 4A) and corrected the resulting
192 equirectangular image of the receptive field by rotating the position to the undistorted center
193 of the spherical texture (Fig 4B). The result demonstrates that the perspective correction
194 yielded identical receptive field sizes, even in cases where the receptive field was located more
195 than 50° off the center. The occurring deviations of about 8% were below the resolution of the
196 binary white noise grid (Fig 4B).

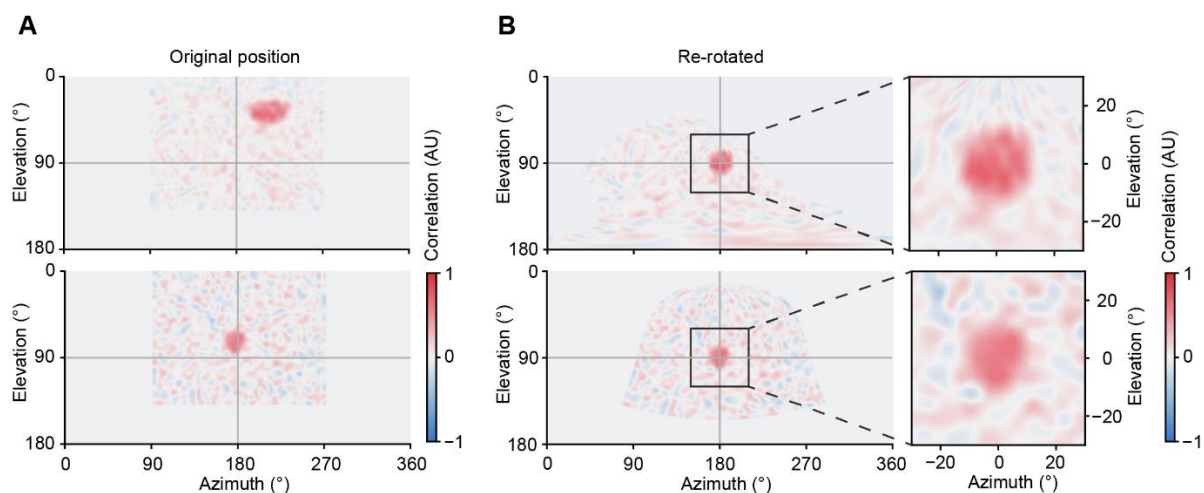


Fig 4: Technical validation of spatiotemporal receptive field measurements

A Equidistant cylindrical projection of the reverse correlation between input white noise and voltage signal of the photodiode. The “receptive fields” are displayed in their original positions. **B** Reverse correlation after rotation to the distortion-free center of the spherical projection map (left) and detailed views of the respective receptive fields after rotation for direct comparison (right).

197 **Electrophysiological validation**

198 To validate the functionality of the Super Bowl in neurophysiological experiments, we
199 performed *in vivo* whole-cell current clamp recordings of medulla intrinsic Mi9 neurons in
200 tethered flies [17]. This experiment requires microscopic access to the brain, while retaining a
201 wide field of view for the experimental animal. We recorded the membrane potentials of Mi9
202 neurons while presenting to the fly a binary white noise stimulus with a solid angle resolution
203 of 2.8° over a period of 5 min. The spatial center of mass of each neuron's receptive field was
204 determined and corrected by inverse rotation as in Fig 4 (Fig 5A). The largest deviations from
205 the center were 38° in azimuth and 41° in elevation (Fig 5A). We estimated the time-averaged
206 spatial receptive fields at two different time intervals (0 to 0.1 s and 0.2 to 0.6 s) and the
207 temporal linear kernel at the center of the average spatial receptive field (Fig 5A). The full
208 width at half maximum was $\sim 10^\circ$ (-3.5° to $+6.5^\circ$) in azimuth and $\sim 10^\circ$ (-5.5 to $+4.5^\circ$) in
209 elevation, at both time intervals (Fig 5A I and Fig 5A II), which is consistent with previous
210 measurements [21]. The temporal linear kernel showed a negative correlation with a kernel
211 density of approximately -7 at 0.05 s and a weak positive correlation with a kernel density of
212 ~ 1 at 0.57 s (Fig 5A). This filter characteristic was absent in the temporal kernel of the
213 photodiode (Fig 3F) speaking for distinct temporal filter properties of the medullary neuron. In
214 addition, we tested a series of commonly used visual stimuli consisting of square-wave gratings

215 and bright and dark edges moving at four different velocities. Unlike the photodiode signal
 216 (Fig 3E), the neurons' membrane potential responses to moving gratings showed a frequency-
 217 and velocity-dependent amplitude modulation (Fig 5B). The responses to moving bright and
 218 dark edges were aligned based on the location of the receptive fields of the respective cells
 219 (Fig 5C). They show step responses of opposite polarity to the stimulus contrast. In summary,
 220 the membrane potentials recorded from Mi9 neurons of flies stimulated using the Super Bowl
 221 screen were consistent with those from an established stimulation device [21,22], with the
 222 difference that the data were acquired across a much wider field of view and with great
 223 temporal precision.

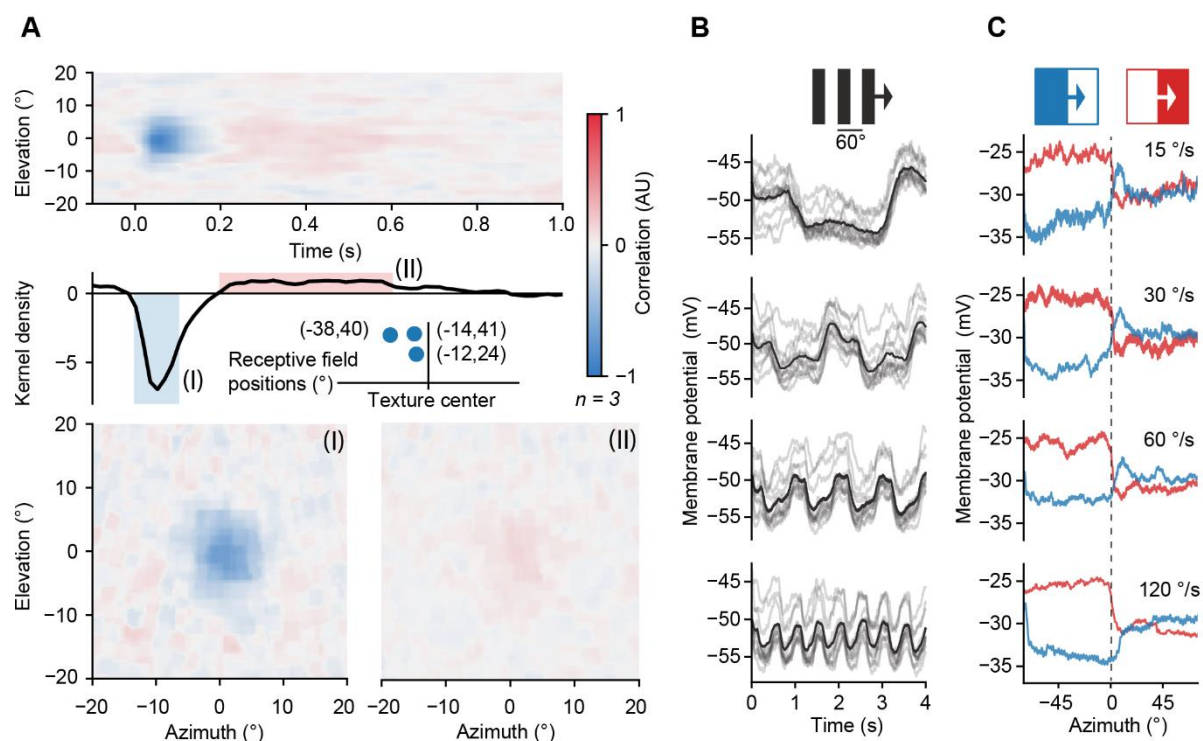


Fig 5: Voltage responses of Mi9 neurons to visual stimulation with the Super Bowl screen

A Average spatiotemporal receptive field of three Mi9 neurons (top), temporal kernel density estimation at the center of the spatial receptive field (center), and relative location and coordinates of the centers of mass of the three receptive fields on the screen (center inset). (I) Time-averaged spatial receptive field in a time interval from 0 s to 0.1 s. (II) Time-averaged spatial receptive field in a time interval from 0.2 s to 0.6 s. **B** Average (black) and single-trail (gray) membrane voltage responses of one Mi9 neuron ($n = 12$ trails) to a 60°-wide horizontal square-wave pattern, moving at four different velocities (15°/s, 30°/s, 60°/s, 120°/s). **C** Exemplary average membrane voltage responses of one Mi9 neuron ($n = 3$ trials) to bright and dark edges, moving at four different velocities (15°/s, 30°/s, 60°/s, 120°/s). Traces were aligned relative to the position of the receptive field.

224 Behavioral validation

225 Besides the voltage responses of individual neurons, the behavior of the fly offers a second
226 level of evidence for proper visual stimulation. The well-studied optomotor and fixation
227 responses of flies [14,23–25] provide clear behavioral readouts for validating the bowl-shaped
228 screen. To observe these types of behavior, we added a tethered flight setup to the bowl-shaped
229 screen (Fig 6A). To quantify the steering direction, a camera was placed above the fly to record
230 the wingbeat envelope as a proxy of the wingbeat amplitude [26] (Fig 6A I). An additional
231 camera, mounted on the side, was used to determine the horizon of the fly (Fig 6A II). The
232 bowl-shaped surface of the screen made it possible to create virtual cylinders with different
233 proportions surrounding the fly (Fig 6A). Like in the microscopic setting, the screen was
234 positioned horizontally, aligned to the fly's horizon, so that the lower hemisphere of the fly's
235 visual field could be stimulated.

236 To evoke an optomotor response, a virtual vertical cylinder, lined by a pattern of vertical stripes
237 that extended from the horizon downward by 36° , was rotated about the yaw axis of the fly
238 head at a velocity of $60^\circ/\text{s}$. Clockwise rotation gave rise to a positive deflection in the difference
239 between left and right wingbeat amplitude, corresponding to a syn-directional steering
240 command. Counterclockwise rotation of the virtual cylinder produced a negative deflection,
241 while a stationary pattern led to no significant change in the wingbeat amplitude difference
242 (Fig 6B). This result is comparable to previous measurements with other visual stimulation
243 devices[14,16,26–32].

244 In contrast to other devices for visual stimulation under the microscope [1,3,7], Super Bowl
245 provides a larger field of view with a homogenous brightness distribution (Figs 2, 6C and 6D).
246 To demonstrate the advantages of the new system, we designed two experiments that would
247 otherwise not have been feasible. In the first experiment, we created a visual virtual
248 environment where the fly is, again, at the center of a rotating hollow cylinder lined by a grating
249 pattern. The wide field of view allowed us to simulate tall and thin as well as wide and flat
250 cylinders without being restricted by the physical size of the screen. Virtual cylinders with
251 diameter/height (d/h) ratios ranging from 0.7 to 10 were rotated clockwise and
252 counterclockwise around the fly at a constant temporal frequency of 2 Hz while we measured
253 the optomotor response of the fly. Trials with different cylinder dimensions and rotation
254 directions were presented randomly and interspersed with stationary patterns. The response
255 was strongest for flat and wide cylinders, which covered a rather small fraction of the field of
256 view, and weakest for a cylinder of equal diameter and height (Fig 6E and 6F). The result of

257 this experiment was unexpected, as the response strength was neither a linear function of the
 258 elevation angle covered by the cylinder, nor a monotonically increasing function of the number
 259 of stimulated ommatidia.

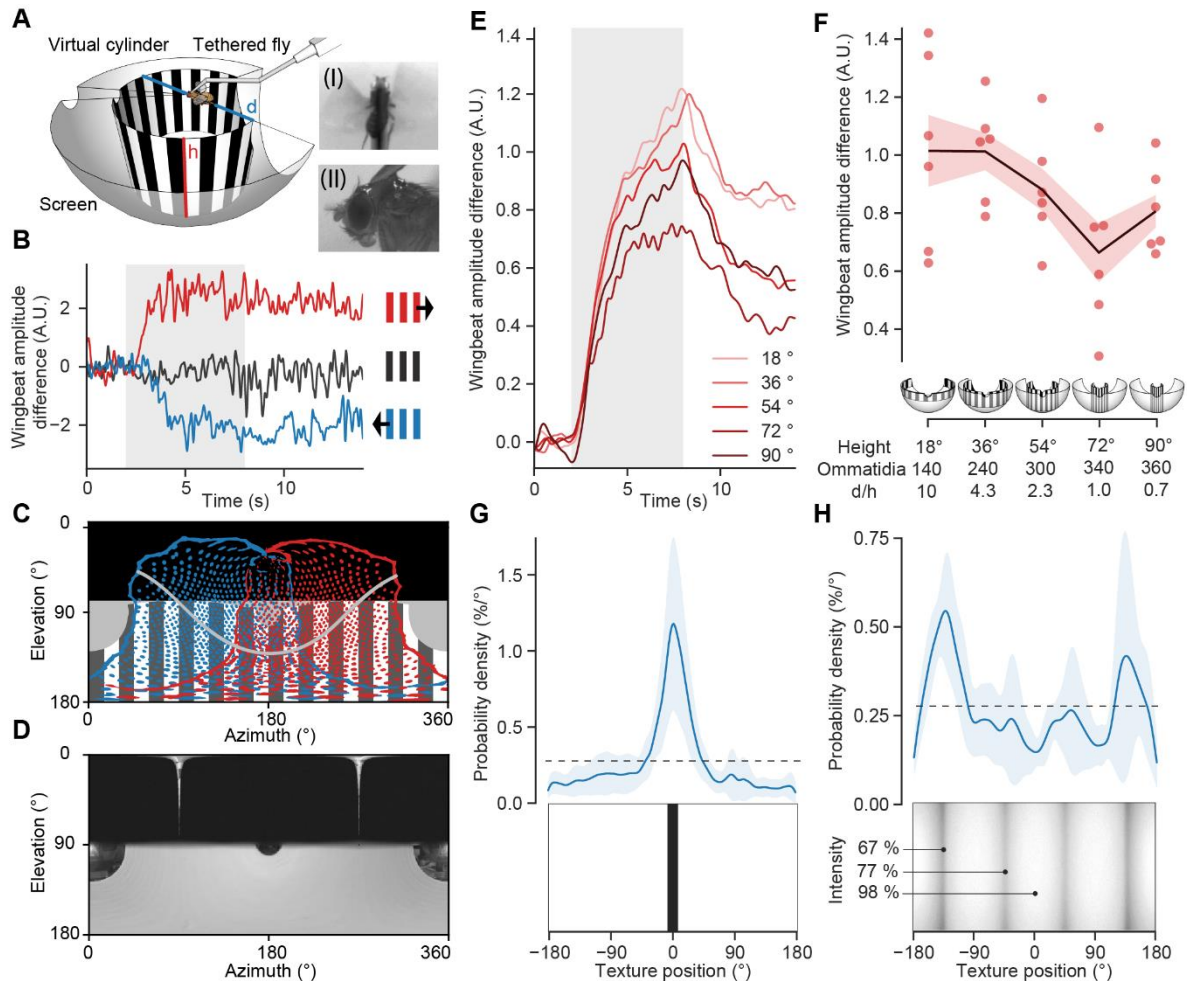


Fig 6: behavioural responses to visual stimulation of the bowl-shaped screen

A View of the tethered flight setup, the bowl-shaped screen and a representation of a virtual cylinder with a height (h) of 54° and a diameter/height (d/h) ratio of 2.3. (I) View from above used to track the wing beat envelope. (II) View from the side used to determine the horizon. **B** Exemplary open-loop optomotor responses to a cylinder with a height of 36° and a spatial grating period of 30° rotating clockwise (red) or counterclockwise (blue) at a velocity of $60^\circ/s$. The gray area indicates the time of stimulation. The black trace corresponds to a stationary grating. **C** Equirectangular projection of the stimulation field (grating) and visual field of the left (blue) and right (red) eye of the fly under microscopic constraints. The field of view was adapted from reference [17] and inclined by 45° to reflect the position of the fly head under the microscope. The black area is obscured by the fly holder. **D** Raw image of the screen brightness distribution measured with an 360° camera from the fly's point of view. The black area is covered by the flat fly holder. **E** Mean rectified wingbeat amplitude difference in response to rotating virtual cylinders of different heights ($n = 6$ flies, 50 trails). The gray area

indicates stimulation duration, the different shades of red correspond to the respective cylinder heights. **F** Time-averaged optomotor responses from E at different cylinder heights ($n = 6$ flies, 50 trials). Red dots, individual flies; solid line, mean; red shading, standard error of the mean (SEM); d/h , diameter/height ratio of the virtual cylinder. The number of stimulated ommatidia was estimated based on reference [17]. **G** Closed-loop bar fixation experiment. Top: Probability of finding a 15° -wide dark vertical bar at a certain position along the azimuth. Solid line, average probability density; shaded area, standard deviation ($n = 6$ flies, 54 trials); dashed line, uniform distribution. Bottom: Representative screen image with central bar. **H** Closed-loop fixation behavior in response to a texture with four dark edges. Top: Average fixation probability (top) relative to the texture (bottom). Solid line, average probability density; shaded area, standard deviation ($n = 6$ flies, 42 trials); dashed line, uniform distribution. The central luminance of two edges was 67%, that of the other two was 77%; the screen luminance in between edges was 98%.

260 The second experiment concerns the influence of dark edges and brightness gradients—
261 undesirable features of many stimulation devices, which our screen is virtually devoid of. Most
262 visual stimulation devices suffer from some form of static brightness gradient. Brightness
263 declines, for example, in the periphery of cylindrical projection screens, or at the gaps where
264 multiple displays connect. If the visual contrast of the experimental stimulus approaches that
265 of the static gradient, experimental artefacts are bound to confound the results. To expose the
266 confounding influence of such subtle gradients, we resorted to the unmatched brightness
267 uniformity and the wide field of view that the Super Bowl screen offers. We rendered an
268 infinitely high cuboid that mimicked an arrangement of four inward-facing screens surrounding
269 the fly. The inner surface of the virtual cuboid was rendered with non-perfect Lambertian
270 properties, resembling real in-plane switching monitors, which produced realistic brightness
271 gradients in the four edges. To test the flies' ability to perceive, and react to, subtle differences
272 in luminance, two of the four edges were rendered marginally darker (67% vs. 77% luminance).
273 In a closed-loop paradigm, the rotation of the cuboid was coupled to the left–right wingbeat
274 amplitude difference of the fly, thus allowing the animal to rotate the virtual cuboid freely.
275 Each fly was first tested with a single dark vertical bar. Consistent with previous results, flies
276 steered toward the bar, keeping it in a narrow range in front of them for most of the time
277 (Fig 6G) [2,7,33]. When facing the cuboid texture, the flies clearly preferred the darker edges
278 (Fig 6H). The mean probability of a halt facing one of the two darker edges was twice as high
279 as the mean probability of a halt facing one of the lighter edges. The implications of this
280 experiment are twofold: First, it demonstrates that flies detect differences in luminance in the
281 range of 10%, which are common when using conventional means of visual stimulation.
282 Second, it demonstrates that these subtle luminance differences are sufficient to bias the
283 animal's behavior.

284 **Discussion**

285 The screen geometry of visual stimulation devices in neuroscience has important implications
286 for the design of experiments and for the acquisition, the analysis, and the interpretation of
287 functional data from the visual system. With a single observer at the center, a cylindrical screen
288 is superior to a flat display, but observer-related perspective distortions remain. Super Bowl
289 provides a virtual spherical texture, displayed on a bowl-shaped screen, free from projection-
290 related distortions, which are otherwise difficult to control. The bowl-shaped screen covers a
291 much larger fraction of visible space with far fewer distortions than commonly used visual
292 stimulation devices. Unlike systems with rear-projection screens [1,3,6,10], it is not affected
293 by light bleeding artefacts caused by subsurface reflections and scattering in the screen material.
294 The peculiar geometry of the screen also facilitates image transformations, and bypasses the
295 need for computationally expensive matrix calculations.

296 All crucial system components, including the screen, can be 3D printed. The overall cost of the
297 system depends on the type of projector used, providing the user a maximum of cost control.
298 The system is compact enough to allow for the recording of neural responses and animal
299 behavior under a microscope (Figs 1E and 7A). The distance of the projector and the size of
300 the screen can be adjusted to the needs of the experiment, for example, by incorporating a
301 spherical treadmill to create an immersive virtual environment for walking flies (Fig 7).
302 Alternatively, depending on the physical requirements, the screen can be trimmed and only a
303 subset of it can be stimulated selectively (Fig 7B). The system was designed to be easy to
304 manufacture and assemble. The provided software generates vector graphic files that are
305 readable by a broad range of programs and can be used as a design basis for 3D printing and
306 laser cutting. The processes of filling, painting and varnishing the screen are crucial to achieve
307 Lambertian surface properties and an even brightness distribution, but they require neither
308 special equipment nor special practical skills. Projectors with identical throw ratios can be
309 exchanged seamlessly, making it easy to incorporate the latest technological advances in spatial
310 and temporal resolution.

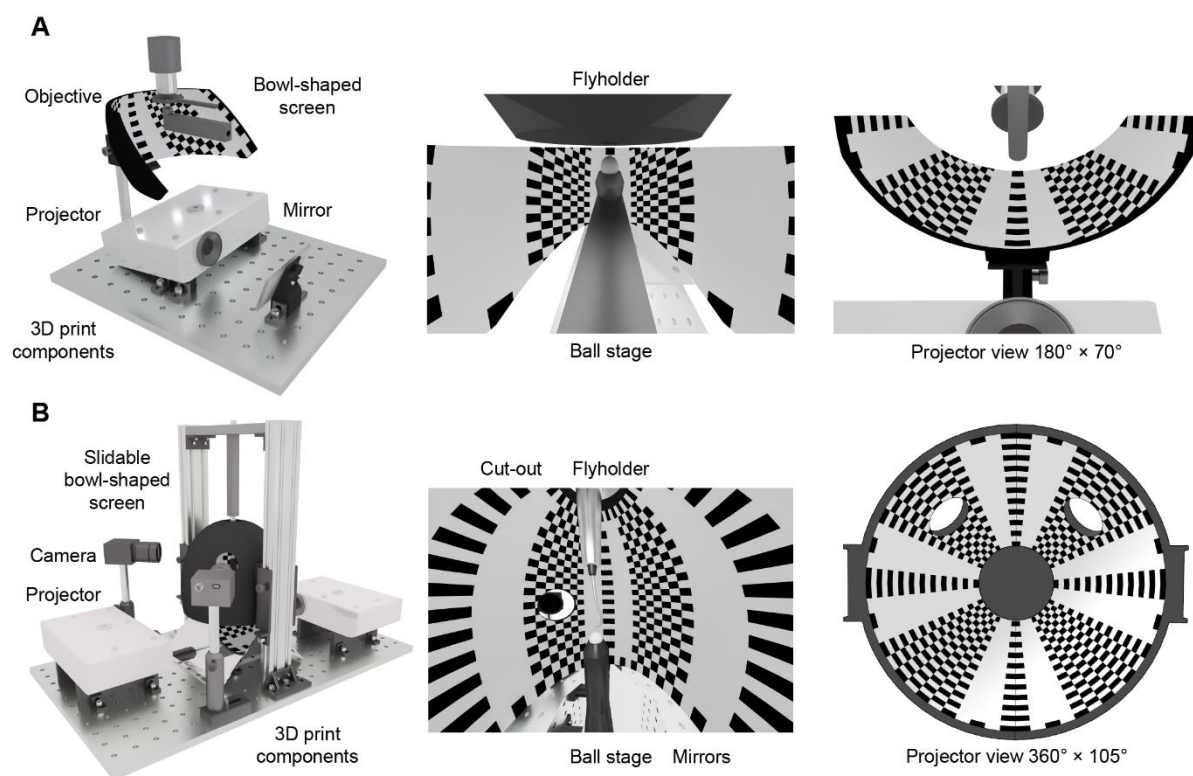


Fig 7: Application concepts of the bowl-shaped screen

A 3D rendering of a tethered walking behavior set-up, which also provides microscopic access to the brain. The field of view of the screen was designed in a way which enables closed loop bar fixation experiments, while recording neuronal activity. **B** 3D rendering of a tethered walking behavior setup, which creates an immersive virtual world around the fly. The system requires two projectors and allows tracking cameras to be installed at various locations using cut-outs.

311 The software for stimulus generation (https://github.com/borstlab/super_bowl_screen) enables
312 researchers to create visual stimuli and entire visual environments. Accurately transformed
313 projector output can be generated based on input from a game engine, a video, or a simple
314 numeric array. The comparatively low computational demands of the software and fast online
315 image transformations allow for the system to be used in closed-loop virtual reality settings
316 that require fast response times. The performance can be increased if the calculation is carried
317 out directly in a graphics library, like the Open Graphics Library (OpenGL).

318 Projector-based systems are compatible even with noise-sensitive electrophysiological
319 experiments such as whole-cell patch clamp recordings (Fig 5). Local sources of
320 electromagnetic noise, like the power supply unit or the projector itself, can be easily shielded.
321 Some projectors can be operated in battery-powered mode, which increases the versatility even
322 further.

323 Obtaining accurate measurements of the spatiotemporal receptive fields of neurons is
324 challenging when using flat or cylindrical screens for at least three reasons: First, because
325 receptive fields located at the periphery of the screen are subject to distortions, which lead to
326 an overestimation of receptive field sizes (Fig 1A and 1B). Second, brightness and contrast
327 tend to decline toward the periphery of a conventional screen. Together with perspective
328 distortions, this reduces the correlation between luminance changes at each pixel and changes
329 in neural activity, entailing longer acquisition times. Third, the surrounds of peripheral
330 receptive fields are often obscured by the bezel. Therefore, it is common practice to include in
331 the analysis primarily neurons with a receptive field at the center of the screen, which
332 introduces a spatial picking bias and reduces the amount of analyzable data.

333 To investigate mechanisms of contrast normalization, especially the contribution of the visual
334 surround on a neuron's receptive field [22,34,35], it is necessary to control luminance and
335 contrast precisely across as much of the visual surround as possible. While the brightness of
336 rear-projection screens [1,3,6,10] and conventional LED displays [5] depends on the viewing
337 angle and requires adjustment at the cost of dynamic range, the bowl-shaped screen features
338 nearly uniform brightness (Fig 2) and only minimal perspective distortions (Fig 1A–1C). This
339 allows for precise measurements of receptive fields of visual interneurons on a spherical map
340 (Figs 4 and 5A), without the need for post-hoc corrections, as is the case when using cylindrical
341 or flat screens.

342 The extensive field of view covered by the Super Bowl screen (Fig 6C) opens up new
343 experimental possibilities, a glimpse of which we provided in a series of behavioral
344 experiments (Fig 6). They revealed a counter-intuitive relationship between the extent of the
345 visual stimulus and the strength of the optomotor response (Fig 6E and 6F), which underscores
346 the truism that the sum of all visual inputs rarely predicts the behavior of animals with a visual
347 system as complex as that of the fly [36]. To those who seek to discover the neuronal
348 mechanisms by which the fly estimates distance or height, an immersive virtual environment
349 system, like ours, is essential.

350 Uniform, well-controllable screen brightness, on the other hand, is a prerequisite for any study
351 of perceptual decision-making; especially when operating close to psychophysical threshold,
352 where subtle luminance differences start to matter. Using a closed-loop experiment, where the
353 experimental animal was trapped inside a virtual cuboid, we showed that the fly perceived fine
354 distinctions in brightness, comparable those at the edges of conventional screens, and
355 consistently chose to approach the darker edges (Fig 6H).

356 A visual system with an almost panoramic field of view, like that of *Drosophila*, should be
357 stimulated with an immersive, distortion-free screen if we shall begin to understand its
358 neurobiology. Although spherical wide-field displays have been used in behavioral
359 experiments [10], Super Bowl is the first system that can stimulate an extensive field of view
360 while recording nervous activity under a microscope.

361 **Materials and Methods**

362
363 Assembly instructions and a user manual for the Super Bowl screen are available at
364 https://github.com/borstlab/super_bowl_screen and supporting videos are available at
365 <https://www.youtube.com/playlist?list=PLcB8ZWnb7EzSwOxb3ipZU5DP4hZYWpbc6>.

366 367 **Analytical solution of Super Bowl screen geometry**

368 In two dimensions, the position of the fly is assumed to be at the center of the coordinate
369 system, $POS_{Fly} = \begin{bmatrix} 0 \\ 0 \end{bmatrix}$, and the position of the projector at a distance d_{proj} , i.e.

$$370 \quad POS_{Proj} = \begin{bmatrix} d_{proj} \\ 0 \end{bmatrix}.$$

371 The throw ratio r_{throw} and the aspect ratio r_{aspect} are constants and can be summarized to
372 $r = r_{throw} \cdot r_{aspect}$. A projection offset of 100% (i.e.: upward projection) is required. The
373 elevation angle α with $0 < \alpha < \pi$ in radians is used to parameterize the curvature of the
374 bowl.

375 The viewing direction of each facet of the fly eye is defined as

$$\overrightarrow{Fly}(\alpha) = \begin{bmatrix} \cos(\alpha) \\ \sin(\alpha) \end{bmatrix}; \quad (1)$$

376 and the projecting direction of the projector is given as

$$\overrightarrow{Proj}(\alpha) = \begin{bmatrix} 1 \\ \alpha/\pi r \end{bmatrix} + \begin{bmatrix} d_{proj} \\ 0 \end{bmatrix}; \quad (2)$$

377 The two vectors intersect at point X, which has the coordinates:

$$\vec{X}(\alpha) = d_{proj} \frac{\alpha}{\alpha - \pi r \tan(\alpha)} \begin{bmatrix} 1 \\ \tan(\alpha) \end{bmatrix}; \quad (3)$$

378 The vector $\vec{X}(\alpha)$ determines the curve of the bowl-shaped screen along the optical axis and
379 one axis perpendicular to it. To parametrize the surface area in \mathbb{R}^3 , a second variable $\beta = \beta \in$
380 \mathbb{R} , $0 < \beta < 2\pi$ is needed for the azimuth. The surface S of the bowl-shaped screen is then
381 given by the outer product:

$$\vec{S}(\alpha, \beta) = d_{proj} \frac{\alpha}{\alpha - \pi r \tan(\alpha)} \begin{bmatrix} 1 \\ \cos(\beta) \\ \sin(\beta) \end{bmatrix} \cdot \begin{bmatrix} 1 \\ \tan(\alpha) \\ \tan(\alpha) \end{bmatrix}^T. \quad (4)$$

382 **Modeling and 3D-printing**

383 The screen shape along the elevation axis was calculated using a custom-written script in
384 Python v.3.7 (Python Software Foundation), using NumPy v.1.21.5, SymPy v.1.10.1, and
385 Cairo v.1.16.0, based on the projector- and user-dependent input variables, such as distance,
386 throw ratio, resolution, and field of view (https://github.com/borstlab/super_bowl_screen).
387 Here, we specified a field of view ranging from 15° to 140° along the elevation axis. The
388 automatically generated scalable vector graphics (SVG) file was imported into the computer-
389 aided design program SketchUp (Trimble), where a 180° rotational extrusion along the optical
390 axis of the path generated the final screen shape as a 3D surface mesh. After adding mounting
391 connections to the drawing, a surface tessellation lattice (STL) file was exported for 3D
392 printing. The screen was printed from black polylactide using fused filament fabrication on a
393 Replicator 3D printer (UltiMaker). Comparable results were achieved using acrylnitril-
394 butadien-styrol-copolymer on a Makerbot Method X (UltiMaker) or tough 2000 resin on a
395 stereolithography-based Form 2 3D printer (Formlabs). Use of the latter significantly reduced
396 the need for post-processing. Where a 3D printer is not available, online services such as Hubs
397 (www.hubs.com), Materialise (www.materialise.com), Shapeways (www.shapeways.com), or
398 Sculpteo (www.sculpteo.com) can be used to create the screen at competitive prices. Grooves
399 in between filaments were filled using 2K General Purpose Body Filler (3M) to create a smooth
400 texture. The surface was sanded using silicon carbide sandpaper with (grit 400) and painted
401 with three layers of white paint (585036, Dupli Color). To reduce specular reflection and
402 associated artifacts, a final layer of matte varnish (Matt varnish 850, Marabu) was applied
403 which is a critical step to achieve near-Lambertian reflective properties.

404 **Assembly**

405 The dimensions, the distances and the optical light field of the projection geometry, and the
406 design of the fly holders, were based on the vector graphic of the beam path (created in the
407 previous step). In order to minimize the overall dimensions of the system, we installed two
408 planar metal-coated mirrors (ME8S-G01 - 8", Thorlabs) perpendicular to each other and at a
409 45° angle relative to the projector (Fig 1E). Screen, projector, and mirrors were mounted on a
410 frame made of matte black acrylic glass which was manufactured using a laser cutter (Speedy
411 360, Trotec). If a laser cutter is not available, the frame can also be 3D-printed, ordered from
412 on-demand fabrication services (see above), or manufactured by conventional means in a
413 workshop.

414 **Stimulus generation**

415 Custom-written software in Python v.3.7 was used to generate visual stimuli, as well as to
416 control their timing. For ease of use, stimuli were created using the NumPy v.1.21.5 package.
417 Rotating textures were generated using just-in-time compilation using the JAX package
418 (Google), to increase performance. The projection function was also based on the JAX package.
419 Images were processed and presented using the OpenCV v.4.6.0 package and stimulus timing
420 was implemented using the built-in time module of Python. After initialization, the software
421 operated in a loop, which was run periodically with a stimulus-dependent rate of 80 to 120
422 frames per second. In each iteration, the input texture was recalculated (or rotated) based on
423 the elapsed time. The resulting texture was then transformed, masked and displayed by the
424 projector. This procedure continued until the stop time point was reached. The entire procedure
425 was processed in one thread; multithreading was not required, but would lead to additional gain
426 in speed.

427 The white noise stochastic stimulus used to determine the receptive fields, was updated online
428 at a rate of 60 frames per second. The individual pixels corresponded to a visual solid angle on
429 a virtual equirectangular cylindrical texture. For example, using a solid angle of 5° , the field of
430 view of the arena was divided into 36×28 pixels grid and the updating stimulus was displayed
431 over 8 minutes. The intensities of the individual pixels were drawn randomly and were either
432 0% or 100% of luminance. Using a sliding reverse correlation, the impact of each stimulating
433 pixel on the signal was reconstructed. Each reconstructed image thus corresponded to an
434 equidistant cylindrical projection of the receptive field.

435 **Luminance measurements**

436 To measure luminance profiles across the screen, we took two different approaches. First, we
437 used a PM100D optical power meter (Thorlabs), whose sensor aperture was placed at the
438 position of the observer. The angle of incidence was kept constant by rotating the sensor about
439 its axis using a servo motor (RS-2, Modelcraft) and a gimbal tracking the position of a square
440 spotlight along the azimuth of the screen. In addition, we placed a 360° camera (Fusion, GoPro)
441 with a resolution of 3000×3000 pixels at the position of the fly and took a photo of the scene.
442 To obtain temporal high-speed measurements, we used a 5-mm photodiode (L-7113GC,
443 Kingbright) as a light sensor and acquired the voltage-signal generated by the photodiode using
444 a 12-bit digital oscilloscope (WaveRunner HRO 66 Zi, LeCroy).

445 **Evaluation of screen geometries**

446 To visualize the effect of screen geometry on the ratio of pixels per ommatidium, we generated
447 computer-aided designs of a flat [2–4], a cylindrical [1,5], and a bowl-shaped screen (this
448 paper). In place of the insect, we added a Goldberg polyhedron model of the observer. The
449 polyhedron contained 260 hexagonal faces of equal area ($\pm 1\%$) and, like any Goldberg
450 polyhedron, 12 pentagonal faces, each of which with an area of approximately 66% of that of
451 the largest hexagon. On average, one hexagonal face covered a solid angle of 14° , equivalent
452 to the angle covered by ~ 9 ommatidia of *Drosophila melanogaster*, a necessary approximation,
453 given that Goldberg polyhedron cannot assume any arbitrary number of faces. Twenty of the
454 hexagonal faces were regular, the rest were irregular hexagons with aspect ratios ranging from
455 0.87 to 1.07.

456 The edges of the faces were projected radially onto the screen surfaces, using the open-source
457 physically-based render engine LuxCoreRender (<https://luxcorerender.org>). The resulting
458 renderings were vectorized and analyzed in Python v.3.7.13. Hexagonal projections were
459 color-coded based on their screen surface area relative to that of a central, undistorted
460 projection. To allow for a rigorous comparison between the different structures, a field of view
461 covering 105° in azimuth and elevation was considered for all screen shapes (Fig 1A–1C). For
462 visualization purposes, we used an orthographic view of the flat screen and a flattened
463 orthographic projection of the cylindrical screen. Additional perspective distortions that would
464 occur in the cylindrical setting under real projection conditions were neglected. The projection
465 of the bowl-shaped screen was already a perspective projection, which did not require
466 additional image distortion.

467 **Fly husbandry**

468 *Drosophila melanogaster* were cultivated on a standard agar medium containing cornmeal, soy,
469 molasses and yeast under a 12 h–12 h light–dark cycle at 25°C and 60% humidity. All
470 experiments were carried out on female flies bearing at least one wild-type allele of the *white*
471 gene. Wild-type Canton-S flies were used for behavioral experiments and flies of the genotype
472 $P\{R48A07-p65.AD\}attP40$, $P\{10XUAS-IVS-mCD8::GFP\}su(Hw)attP5$; $P\{VT046779-$
473 $GAL4.DBD\}attP2$ were used to visualize Mi9 neurons during patch clamp experiments.

474 **Patch clamp recordings**

475 Whole cell patch clamp recordings were performed *in vivo* as recently described [21]. Female
476 flies were cold-anesthetized 2-24 hours after eclosion and fixed with soft thermoplastic wax on
477 a custom-made polyoxymethylene mount. The dorsal part of the head was submerged in
478 solution (pH 7.3) containing 5 mM TES, 103 mM NaCl, 3 mM KCl, 26 mM NaHCO₃, 1 mM
479 NaH₂PO₄, 1.5 mM CaCl₂, 4 mM MgCl₂, 10 mM trehalose, 10 mM glucose and 7 mM sucrose
480 (280 mOsM, equilibrated with 5% CO₂ and 95% O₂) and the left optic lobe was exposed by
481 surgically removing cuticle, adipose tissue, and trachea using a stereomicroscope (S8 APO,
482 Leica). Green-fluorescent somata were visually identified under an Axio Scope.A1
483 epifluorescence microscope (Zeiss). Patch pipettes (15–20 MΩ) were pulled from borosilicate
484 glass capillaries using a PC-10 micropipette puller (Narishige) and targeted to the somatic cell
485 membrane through a small incision in the perineural sheath. The pipette solution (pH 7.3)
486 contained 10 mM HEPES, 140 mM potassium aspartate, 1 mM KCl, 4 mM MgATP, 0.5 mM
487 Na₃GTP, 1 mM EGTA and 10 mM biocytin (265 mOsM). Membrane voltage signals were
488 recorded at room temperature (21–23°C) using a MultiClamp 700B amplifier (Molecular
489 Devices), low-pass filtered, and sampled at 10 kHz. Voltage data were corrected for the liquid
490 junction potential and analyzed using custom-written software in Python v.3.7. The resting
491 potential was determined to be the most negative membrane potential recorded in the absence
492 of any holding current. Cells with a resting membrane voltage more depolarized than –25 mV
493 were excluded from further analysis.

494 **Tethered flight behavior**

495 Female flies were cold-anesthetized two days after eclosion and attached to the tip of a needle
496 at head and thorax using light-curing dental glue (Sinfony Opaque Dentin). The flight position
497 was adjusted relative to the screen based on one camera on the side (Flir Chameleon3 CM3-
498 U3-13S2C) and one camera above (Flir Flea3 FL3-U3-13S2M). The horizon of the fly eye was
499 levelled before the start of each experiment; only flies with a well-aligned head ($\pm 5^\circ$) were
500 included. Left and right wingbeat envelopes were recorded from above by acquiring images
501 (656 × 524 pixels) of the tethered flying fly at 120 Hz and 8.3 ms exposure time. To minimize
502 processing times and to enable behavioral experiments in closed loop, a digital wingbeat
503 analyzer, analogous to a previous study [26], was implemented. Images were background
504 subtracted and analyzed using two image masks covering the left and the right wingspan,
505 respectively. The ratio of the mean pixel values of the two masks served as an indirect measure

506 of the wingbeat amplitude and, thus, of the yaw torque [23,26,30]. Possible differences in
507 illumination were compensated by weighting each mask individually. Wingbeat analysis
508 (~8 ms) and image generation (~5 ms) were performed in sequence and completed within
509 approximately 13 ms. The total closed-loop lag amounted to approximately 30 ms and was
510 determined by the projector. The loop speed can be increased significantly by executing
511 wingbeat tracking and image generation in two separate processes. This is particularly useful
512 in combination with projectors that support higher frame rates.

513 **Optomotor responses**

514 The virtual cylinders were lined by a vertical grating with a bar width of 15° and a height as
515 specified (Fig 6E and 6F). Each stimulus phase was 14 seconds long, of which the first two
516 were used as reference, followed by 6 seconds of stimulation and a 6-second-long post-
517 stimulation period. Each trail consisted of three stimulus phases (clockwise, counterclockwise
518 and static) in which the pattern was moved at $60^\circ/\text{s}$ in the respective direction or remained
519 static. Cylinders of different diameter/height ratios and clockwise, counterclockwise and static
520 phases were presented in random sequences. In open-loop experiments, the wingbeat amplitude
521 signals were down sampled to 50 Hz, lowpass filtered with a symmetrical gaussian kernel
522 ($\tau = 0.4$ s) and the signals from the two sides were subtracted (left–right). The average wingbeat
523 amplitude during the first two seconds, in the absence of visual motion, was taken as a baseline
524 reference and subtracted from the signal. To obtain the total response strength of each fly,
525 responses during clockwise and counterclockwise trials were rectified and averaged (Fig 6E).
526 Time-averaged responses for each stimulus condition (Fig 6F) were calculated by averaging
527 the wingbeat amplitude difference over a 6-s period starting two seconds after stimulus onset.

528 **Fixation behavior**

529 At the beginning of each experiment, flies were allowed to accustom and become familiar with
530 the closed loop system over a period of at least 5 minutes. During this phase, the weights of
531 left and right wingbeat signals were determined and balanced, to prevent any unwanted rotation
532 bias in slightly tilted flies. The feedback gain was set individually for each fly during this phase
533 so that the fly was able to achieve rotation speeds of 0- $140^\circ/\text{s}$ with its wingbeat amplitude.
534 Once set, the gain was kept constant for all subsequent experimental conditions and trails. One
535 trail of a fixation experiment consisted of initializing a texture at a random yaw position. Flies
536 were then able to rotate the texture freely for 60 s during which the wingbeat amplitude
537 difference was coupled to the yaw position of the texture. Each fly was subjected to both types

538 of visual environment: a single vertical bar (Fig 6G) and the interior of an infinitely high cuboid
539 (Fig 6H); trails were identically for both types of experiment. The position data of each trail
540 was resampled to 50 Hz, and a probability density function was calculated for each trail
541 independently. The individual trials of each fly were averaged to compute the fly's fixation
542 response.

543 **Acknowledgements**

544 We thank B. Zuidinga for help with fly husbandry and behavioral experiments and L. Fenk for
545 discussions.

546 **Funding**

547 The Max Planck Society. Support for SP, LNG and AB. Horizon 2020 programme under the
548 Marie Skłodowska-Curie Action MOVIS (grant agreement no. 896143). Support for LNG.

References

1. Arenz A, Drews MS, Richter FG, Ammer G, Borst A. The temporal tuning of the *Drosophila* motion detectors is determined by the dynamics of their input elements. *Curr Biol*. 2017;27: 929–944. doi:10.1016/j.cub.2017.01.051
2. Bahl A, Ammer G, Schilling T, Borst A. Object tracking in motion-blind flies. *Nat Neurosci*. 2013;16: 730–738. doi:10.1038/nn.3386
3. Creamer MS, Mano O, Tanaka R, Clark DA. A flexible geometry for panoramic visual and optogenetic stimulation during behavior and physiology. *J Neurosci Methods*. 2019;323: 48–55. doi:10.1016/j.jneumeth.2019.05.005
4. Loesche F, Reiser MB. An inexpensive, high-precision, modular spherical treadmill setup optimized for *Drosophila* experiments. *Front Behav Neurosci*. 2021;15: 689573. doi:10.3389/fnbeh.2021.689573
5. Reiser MB, Dickinson MH. A modular display system for insect behavioral neuroscience. *Journal of Neurosci Methods*. 2008;167: 127–139. doi:10.1016/j.jneumeth.2007.07.019
6. Hindmarsh Sten T, Li R, Otopalik A, Ruta V. Sexual arousal gates visual processing during *Drosophila* courtship. *Nature*. 2021;595: 549–553. doi:10.1038/s41586-021-03714-w
7. Isaacson M, Ferguson L, Loesche F, Ganguly I, Chen J, Chiu A, et al. A high-speed, modular display system for diverse neuroscience applications. *bioRxiv* 2022; 08.02.502550. doi:10.1101/2022.08.02.502550
8. Kócsi Z, Murray T, Dahmen H, Narendra A, Zeil J. The Antarium: A reconstructed visual reality device for ant navigation research. *Front Behav Neurosci*. 2020;14: 599374. doi:10.3389/fnbeh.2020.599374
9. Perkel JM. How remouldable computer hardware is speeding up science. *Nature*. 2021;600: 348–349. doi:10.1038/d41586-021-03627-8
10. Williamson WR, Peek MY, Breads P, Coop B, Card GM. Tools for rapid high-resolution behavioral phenotyping of automatically isolated *Drosophila*. *Cell Rep*. 2018;25: 1636-1649.e5. doi:10.1016/j.celrep.2018.10.048
11. Supple JA, Varennes-Phillit L, Gajjar-Reid D, Cerkvenik U, Belušič G, Krapp HG. Generating spatiotemporal patterns of linearly polarised light at high frame rates for insect vision research. *J Exp Biol*. 2022;225: jeb244087. doi:10.1242/jeb.244087
12. Stavenga DG. Angular and spectral sensitivity of fly photoreceptors. II. Dependence on facet lens F-number and rhabdomere type in *Drosophila*. *J Comp Physiol A*. 2003;189: 189–202. doi:10.1007/s00359-003-0390-6
13. Stavenga DG. Angular and spectral sensitivity of fly photoreceptors. I. Integrated facet lens and rhabdomere optics. *J Comp Physiol A*. 2003;189: 1–17. doi:10.1007/s00359-002-0370-2

14. Götz K. Optomotorische Untersuchung des visuellen Systems einiger Augenmutanten der Fruchtfliege *Drosophila*. *Kybernetik*. 1964;2: 77–92.
15. Borst A, Groschner LN. How flies see motion. *Annu Rev Neurosci*. 2023;46: 17–37. doi:10.1146/annurev-neuro-080422-111929
16. Heisenberg M, Wolf R. *Vision in Drosophila*. Berlin, Heidelberg: Springer Berlin Heidelberg; 1984. doi:10.1007/978-3-642-69936-8
17. Zhao A, Gruntman E, Nern A, Iyer NA, Rogers EM, Koskela S, et al. Eye structure shapes neuron function in *Drosophila* motion vision. *bioRxiv* 2022; 12.14.520178. doi:10.1101/2022.12.14.520178
18. Dombeck DA, Reiser MB. Real neuroscience in virtual worlds. *Curr Opin Neurobiol*. 2012;22: 3–10. doi:10.1016/j.conb.2011.10.015
19. Xiao N, Xu S, Li Z-K, Tang M, Mao R, Yang T, et al. A single photoreceptor splits perception and entrainment by cotransmission. *Nature*. 2023;623: 562–570. doi:10.1038/s41586-023-06681-6
20. Miall RC. The flicker fusion frequencies of six laboratory insects, and the response of the compound eye to mains fluorescent ‘ripple.’ *Physiol Entomol*. 1978;3: 99–106. doi:10.1111/j.1365-3032.1978.tb00139.x
21. Groschner LN, Malis JG, Zuidinga B, Borst A. A biophysical account of multiplication by a single neuron. *Nature*. 2022;603: 119–123. doi:10.1038/s41586-022-04428-3
22. Drews MS, Leonhardt A, Pirogova N, Richter FG, Schuetzenberger A, Braun L, et al. dynamic signal compression for robust motion vision in flies. *Curr Biol*. 2020;30: 209–221.e8. doi:10.1016/j.cub.2019.10.035
23. Götz KG. Flight control in *Drosophila* by visual perception of motion. *Kybernetik*. 1968;4: 199–208. doi:10.1007/BF00272517
24. Poggio T, Reichardt W. Nonlinear interactions underlying visual orientation behavior of the Fly. *Cold Spring Harbor Symposia on Quantitative Biology*. 1976;40: 635–645. doi:10.1101/SQB.1976.040.01.059
25. Von Fermi G, Richardt W. Optomotorische Reaktionen der Fliege *Musca domestica*: Abhängigkeit der Reaktion von der Wellenlänge, der Geschwindigkeit, dem Kontrast und der mittleren Leuchtdichte bewegter periodischer Muster. *Kybernetik*. 1963;2: 15–28. doi:10.1007/BF00292106
26. Maimon G, Straw AD, Dickinson MH. Active flight increases the gain of visual motion processing in *Drosophila*. *Nat Neurosci*. 2010;13: 393–399. doi:10.1038/nn.2492
27. Borst A, Bahde S. Comparison between the movement detection systems underlying the optomotor and the landing response in the housefly. *Biol Cybern*. 1987;56: 217–224. doi:10.1007/BF00365216

28. Fenk LM, Kim AJ, Maimon G. Suppression of motion vision during course-changing, but not course-stabilizing, navigational turns. *Curr Biol*. 2021;31: 4608-4619.e3. doi:10.1016/j.cub.2021.09.068
29. Fenk LM, Avritzer SC, Weisman JL, Nair A, Randt LD, Mohren TL, et al. Muscles that move the retina augment compound eye vision in *Drosophila*. *Nature*. 2022;612: 116–122. doi:10.1038/s41586-022-05317-5
30. Tammero LF, Frye MA, Dickinson MH. Spatial organization of visuomotor reflexes in *Drosophila*. *J Exp Biol*. 2004;207: 113–122. doi:10.1242/jeb.00724
31. Haikala V, Joesch M, Borst A, Mauss AS. Optogenetic control of fly optomotor responses. *J Neurosci*. 2013;33: 13927–13934. doi:10.1523/JNEUROSCI.0340-13.2013
32. Blondeau J, Heisenberg M. The three-dimensional optomotor torque system of *Drosophila melanogaster*: Studies on wildtype and the mutant optomotor-blind H31. *J Comp Physiol*. 1982;145: 321–329. doi:10.1007/BF00619336
33. Fenk LM, Poehlmann A, Straw AD. Asymmetric processing of visual motion for simultaneous object and background responses. *Curr Biol*. 2014;24: 2913–2919. doi:10.1016/j.cub.2014.10.042
34. Matulis CA, Chen J, Gonzalez-Suarez AD, Behnia R, Clark DA. Heterogeneous temporal contrast adaptation in *Drosophila* direction-selective circuits. *Curr Biol*. 2020;30: 222–236.e6. doi:10.1016/j.cub.2019.11.077
35. Pirogova N, Borst A. Contrast normalization affects response time-course of visual interneurons. Coleman MJ, editor. *PLOS ONE*. 2023;18: e0285686. doi:10.1371/journal.pone.0285686
36. Matsliah A, Yu S, Kruk K, Bland D, Burke A, Gager J, et al. Neuronal “parts list” and wiring diagram for a visual system. *bioRxiv*; 2023;10.12.562119. doi:10.1101/2023.10.12.562119