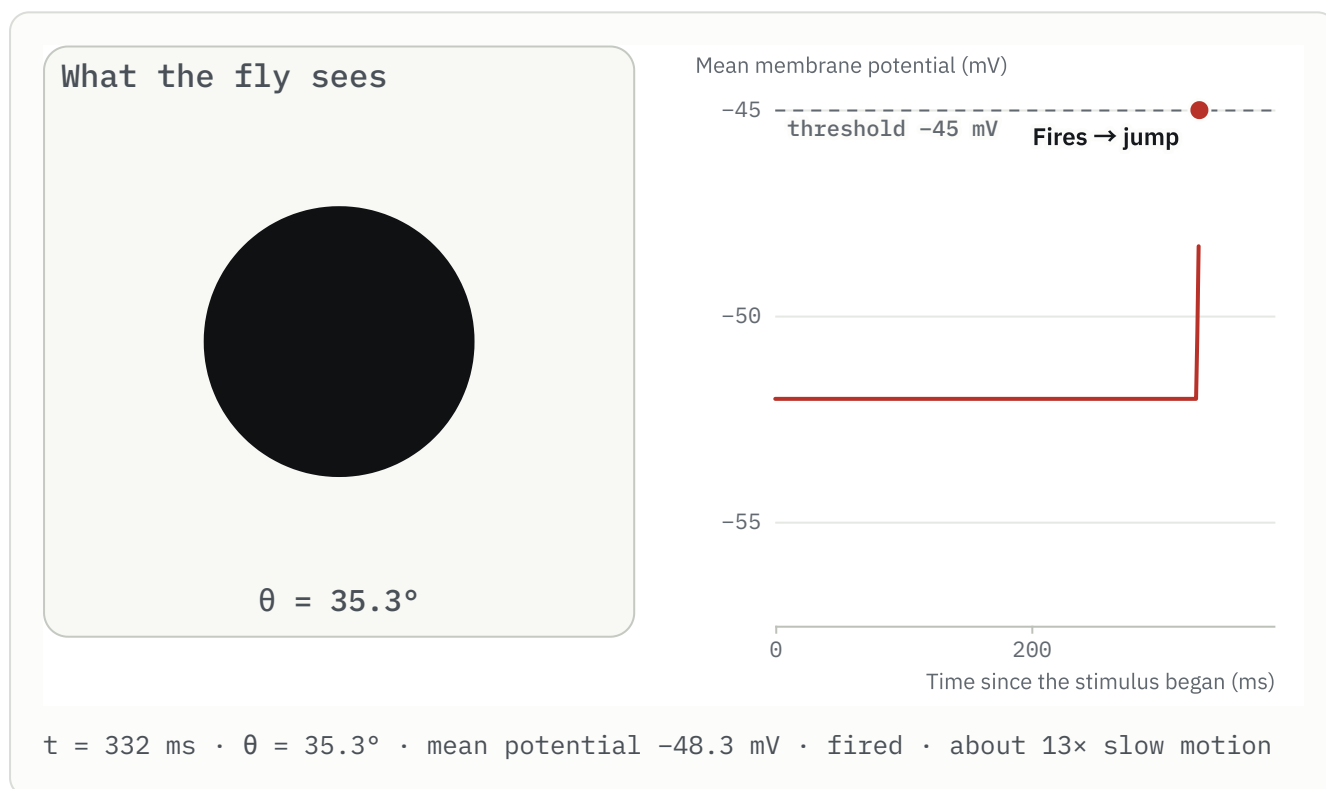


If you scramble a fly's wiring, can it still escape?

When a dark shape rushes at a fruit fly, a neuron in its brain called the **giant fiber** fires and the fly jumps away. This project copied that circuit into a computer, neuron by neuron, from the complete wiring diagram of a real fly. It then checked whether the copy behaves like a real fly, and scrambled its wiring step by step to see whether its response changes.

Ewan Wu • Data: MaleCNS v1.0 connectome (CC-BY 4.0) • Code: MIT license

This is the static PDF edition. The interactive web page:
<https://ewanwu06.github.io/fly-escape-switch/>



The small screen shows what the fly sees, a dark disk coming closer. The chart shows the simulated membrane potential of the giant fibers (the mean of left and right), for the real circuit at an approach speed of $r/v = 40 \text{ ms}$. When the disk spans about 35° , the potential crosses threshold and the giant fiber fires.

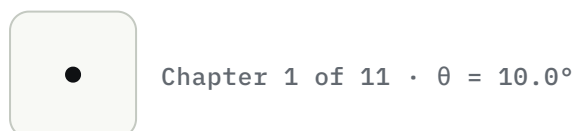
THE ONE-MINUTE VERSION

- **What was done:** the escape circuit, 364 neurons, was built from a real fly's wiring diagram and simulated on a computer.
- **Finding 1:** the virtual circuit reproduced one of four published experimental results: it fires when the shape spans about 34° – 37° .
- **Finding 2:** scrambling the wiring until only 40.6% of it was left intact moved that result by just 0.11° . In this model, as long as each neuron keeps the same number of connections, exactly which neurons they connect to barely affects when the giant fiber fires.
- **But:** the model did not reproduce the other three results, so for those it cannot say whether the wiring matters. Step 2 was also run at only one approach speed.

CONTENTS

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|  9 What it means |  10 Mistakes we caught and corrected |
|  11 Next steps, glossary and references | |

The black disk at the start of each chapter grows as you read, like the approaching shape: from 10° up to 63° .



The question: does the wiring matter?

A **connectome** is a complete wiring diagram of a brain: which neurons exist, which other neurons each one connects to, and how many synapses each connection has. In 2026 researchers released MaleCNS v1.0, the connectome of a male fruit fly's entire central nervous system, as open data that anyone can download.

With a wiring diagram in hand, a natural idea is to run it on a computer and see whether it produces fly behaviour. There are already many demos of "a fly brain playing games". One question is easy to skip,

though. Even if a simulated network can do something, does that ability come from the specific way it is wired, or only from coarser statistics, such as how many connections each neuron has?

A standard control separates the two. It is called **degree-preserving rewiring**. A neuron's number of connections is its "degree". Degree-preserving rewiring shuffles who connects to whom at random, while every neuron keeps the same number of outgoing and incoming connections. If the behaviour survives the shuffle, it did not depend on the specific wiring.

AN ANALOGY

Picture a city's road network. Degree-preserving rewiring reconnects every intersection: each one keeps the same number of roads in and out, but where each road leads changes completely. If traffic still flows as well afterwards, the flow never depended on the original street plan.

The control itself is not new. One earlier project ran a single all-or-nothing shuffle on a whole fly brain. This project differs in three ways: it scrambles the wiring in **graded steps**; it targets one small, well-understood circuit; and it first checks that circuit against **published experiments**.

– Go deeper: reservoir computing versus emergence

Many demos treat the connectome as a fixed network and attach a trained "readout" layer on top; the readout is what learns the task. This is called **reservoir computing**. A network that can be trained to do something has not shown that its wiring produces the behaviour. Degree-preserving rewiring separates the two: if a randomly rewired network does just as well, the credit does not belong to the specific wiring.



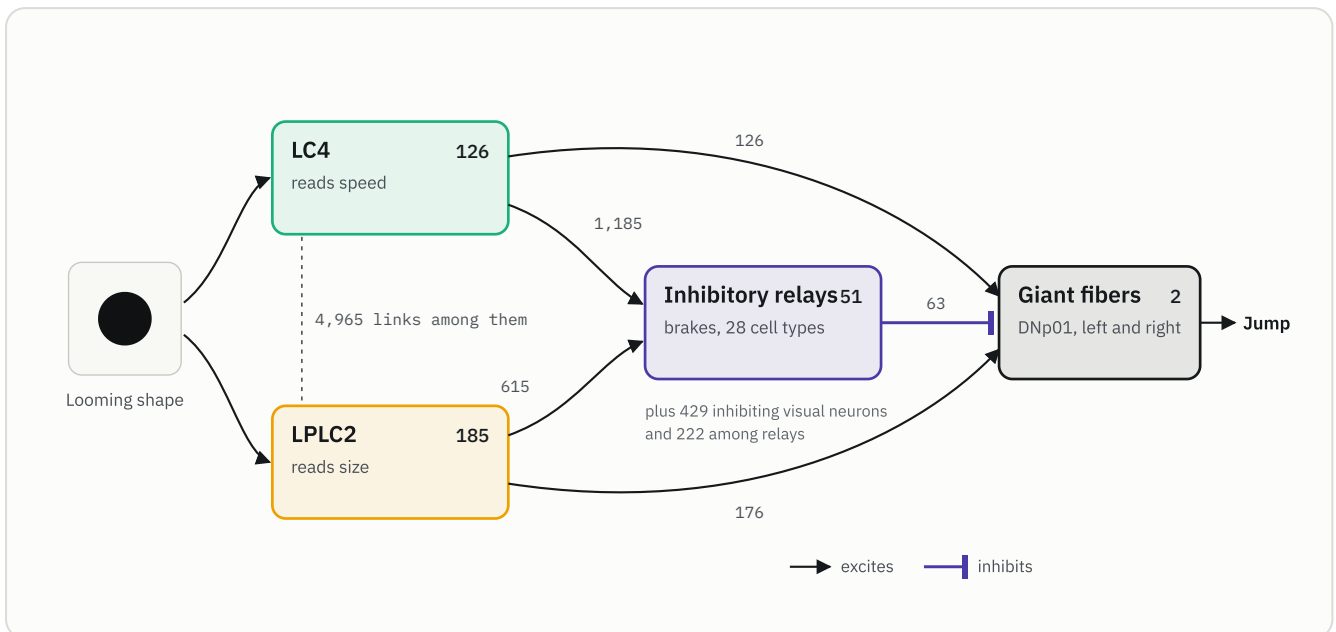
The circuit: the giant fiber escape pathway

Each side of a fly's brain has one **giant fiber** (cell type DNp01). It is a thick, long descending neuron that runs from the brain down to the thoracic ganglia, which control the legs and wings. When it fires, it triggers the fly's fast escape jump.

The circuit's input comes from the eyes. Two kinds of visual neuron send signals to the giant fiber:

- **LC4** responds to how fast something is approaching: how quickly its angular size grows.
- **LPLC2** responds to how large it looks: its angular size itself.

These visual neurons also excite a set of **inhibitory neurons**, which act like brakes and connect back onto the giant fiber. The visual signal therefore reaches the giant fiber by two routes: one presses the accelerator directly, the other goes through the brakes first.



The circuit as extracted from MaleCNS. Arrows $\rightarrow$ are excitatory connections, bars $\dashv$ are inhibitory, and the numbers count connections. The visual neurons are also linked to one another by almost 5,000 connections. Only connections of at least 5 synapses are included.

■ **126** LC4
■ **185** LPLC2
■ **51** inhibitory relays
■ **2** giant fibers
364 neurons

7,784 connections (7,070 excitatory, 714 inhibitory)
95,201 synapses

Was the extraction right?

In 2019, Ache and colleagues counted the LC4 neurons connected to the right giant fiber in a different fly (FAFB, whole-brain electron microscopy of a female). They found **55**. Counting in the male MaleCNS fly also gives **55**, with only 5.7% more synapses (2,580 against 2,442). Different sex, different individual, different dataset, same number. The LPLC2 counts differ more (84 against 108), for reasons not yet known.

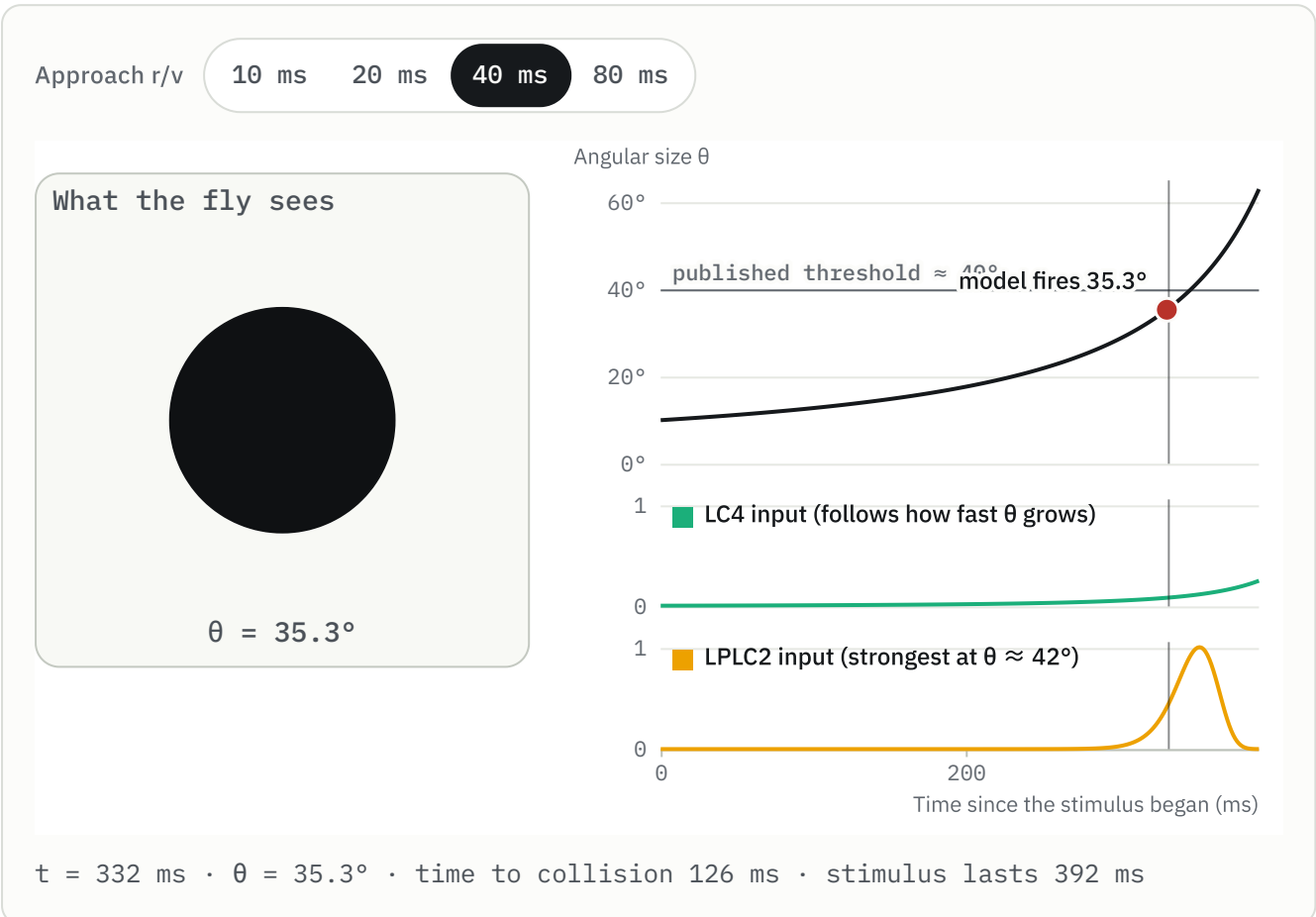
Chapter 3 of 11 · $\theta = 20.6^\circ$

The stimulus: a looming shadow

The usual "threat" in fly experiments is a black disk on a screen that keeps growing, imitating an object on a collision course. How big it looks to the fly is its **angular size** θ : the angle between the object's two edges as seen from the eye.

$$\theta(t) = 2 \cdot \arctan(r / (v \cdot |t|))$$

Here r is the object's radius, v its speed and t the time left before collision. Only the ratio r/v , in milliseconds, sets the pace: the smaller r/v , the faster and more sudden the approach. The published experiments and this project both use 10, 20, 40 and 80 ms, with the disk growing from 10° to 63° .



Pick an approach speed, then drag the time slider or press play. Top: angular size θ over time; the horizontal line is the published firing threshold (about 40°) and the red dot is where the model's giant fiber first fires. Below: the input signals the model feeds to the two kinds of visual neuron.

Notice the shape of the curve: the angle barely moves at first and shoots up only at the very end. ■ **LC4's** input follows how fast the angle grows, so it is strongest at the end, and stronger for faster approaches. ■ **LPLC2's** input peaks when the angle is about 42° , whatever the speed.

– Go deeper: the one part of the model not taken from the connectome

How the visual input is encoded is the model's one explicit assumption, taken from the findings of Ache et al. (2019): LC4's input is proportional to how fast the angle grows, and LPLC2's input is a bell curve centred on 42° . The bell curve's width, $\sigma = 5^\circ$, was calibrated once against the first benchmark, B1, and then frozen. Each visual neuron's input is also shifted by a random offset of up to ± 10 ms, because real

neurons do not fire in perfect lockstep (chapter 10 explains why this step was needed). Everything between the visual neurons and the giant fiber is left to the measured connections of the connectome.



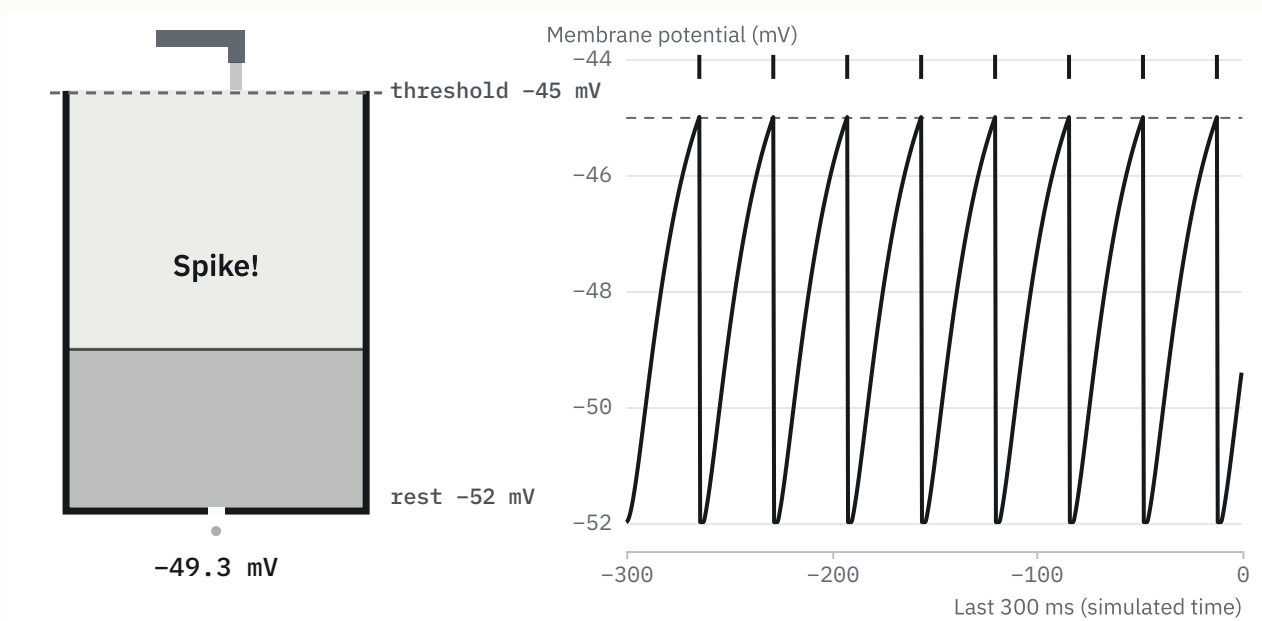
Chapter 4 of 11 · $\theta = 25.9^\circ$

The model neuron: a leaky bucket

Every neuron is simulated with the **leaky integrate-and-fire** (LIF) model. Think of it as a leaky bucket:

- When an upstream neuron fires, water pours in: the membrane potential rises.
- A small hole in the bottom lets water drain away: the potential falls back to rest.
- When the water reaches the mark (the threshold), the neuron fires once, the bucket empties at once, and it rests briefly.

Steady input (the tap) 1.80 mV/ms



Firing rate about 27 per second (simulated time) · from rest, one LC4 spike raises the potential by at most about 2.2 mV, against the 7 mV to threshold · 25× slow motion

One model neuron with this project's real parameters, slowed down 25 times. Turn the steady input (the tap), or press the button to have one LC4 neuron fire. With too little input the water settles below the mark and the neuron never fires; above a certain strength it fires regularly, and faster as the input grows.

The numbers are in real units: rest at -52 mV and threshold at -45 mV, so the bucket is only 7 mV deep; the leak's time constant is 20 ms; each synapse contributes 0.275 mV. One LC4 neuron connects to a

giant fiber through about 50 synapses on average, so a single LC4 spike is far from enough: several have to arrive almost together. These parameters are copied from a published whole-brain fly model (Shiu et al., 2024, *Nature*) and were not tuned for this project.

The key point: there is no "escape program" anywhere in the model. How the visual signals add up at the giant fiber is set entirely by the connections and synapse counts measured in the connectome.



Chapter 5 of 11 · $\theta = 31.2^\circ$

Rules first: pre-registration

Before any simulation ran, the study design was written down and committed to version control (git), where every commit carries a timestamp: which results would be tested, with which measures, what counts as a pass, and how each possible outcome would be read. This is called **pre-registration**.

It guards against a common problem: adjusting the standards after seeing the results, so the results look better. After pre-registration, every change has to leave a dated public record that says whether it happened before or after the results were seen.

- Sep 22, 22:54 PLAN WRITTEN d8d510e
Study design pre-registered: hypotheses, measures, analysis plan and how each outcome would be read
- Sep 22, 23:29 RUN 9496a7b
The 364-neuron circuit extracted from MaleCNS
- Sep 23, 10:32 PLAN WRITTEN d53b136
Pass criteria for the four tests (B1–B4) written into code
- Sep 23, 10:48 RUN befb9d5
First test run, which exposed the lockstep problem (chapter 10)
- Sep 23, 11:09 PLAN WRITTEN 0a59501
The fix (input time offsets) written into the design first
- Sep 23, 11:29 RUN d2e9c47
Then B1–B4 re-run
- Sep 23, 15:47 PLAN WRITTEN 9cc0ca4
Step 2 input settings written into the design

- Sep 23, 15:52 RUN 3fa4f26
Graded rewiring run: 100 circuits per dose
- Sep 24, 02:08 PLAN WRITTEN f3e30b5
Gain sensitivity analysis specified in the design first
- Sep 24, 02:15 RUN f2bdc83
Then the gain sensitivity analysis run

Times are as recorded in the git commits.



Chapter 6 of 11 · $\theta = 36.5^\circ$

Step 1: does it act like a real fly?

Four results from published electrophysiology experiments serve as the virtual circuit's "exams", numbered B1 to B4. The pass criteria were written into code and committed before the tests were formally run.

B1

✓ Reproduced

When it fires

Real fly The giant fiber fires when the shape spans about 40° .

Model Fires at 33.7° – 37.2° at all four speeds, inside the 30° – 50° band fixed in advance.

As coded, passes under 6 of 6 random input draws

σ was calibrated on this test, so it is not fully independent. Raise the input gain to 1.2 times or more and the fastest speed falls out of the band.

B2 Not reproduced

Speed versus size

Real fly The faster the approach, the larger LC4's (speed) contribution; LPLC2's (size) stays about the same.

Model No such graded pattern. With LC4 input alone, the giant fibers fire for fast approaches (10 and 20 ms) and do not move at all for slow ones (40 and 80 ms): all or nothing.

As coded, passes under 0 of 6 random input draws

B3 Passes as coded · not reproduced

Silencing LPLC2

Real fly With LPLC2 removed, the giant fiber keeps only its response to speed.

Model With LPLC2 silenced at 40 ms, the giant fiber does not respond at all, so no speed component is left.

As coded, passes under 6 of 6 random input draws

The code only checks whether the response's peak time moves by at least 2 ms. With no response at all, that is met trivially. The registered criterion also requires the right direction; the code never checks it, and the shift runs the wrong way.

B4 Passes as coded · not reproduced

Both eyes together

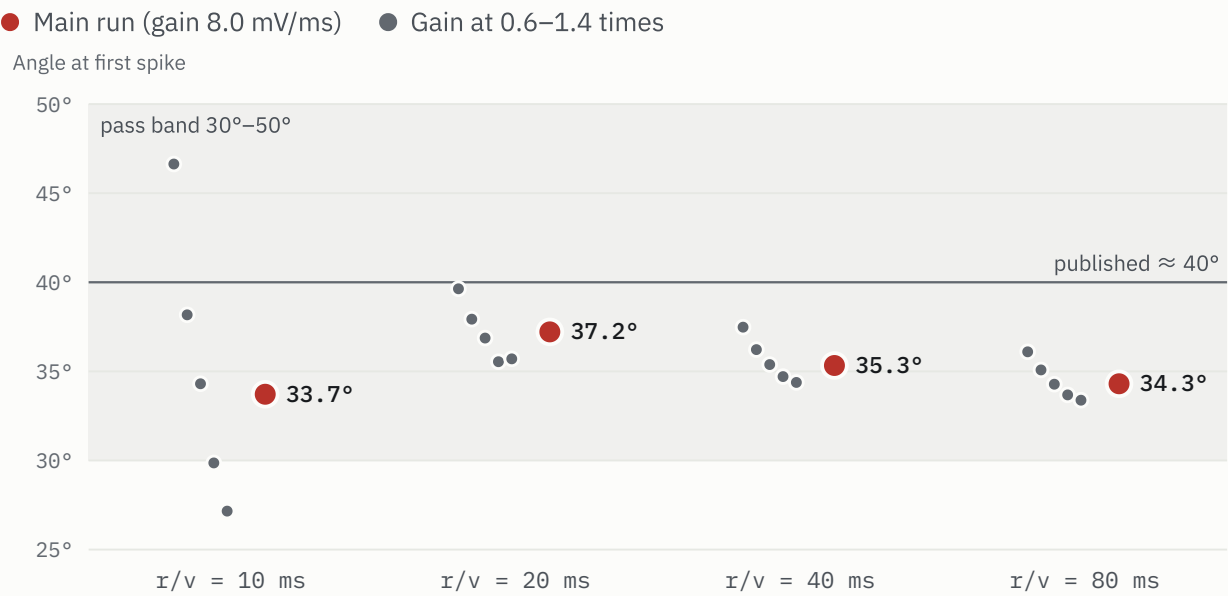
Real fly The response to both eyes at once is smaller than the sum of the responses to each eye alone (sublinear).

Model Read one giant fiber at a time, its response to both eyes equals its response to its own eye alone; the other eye never depolarises it. The two eyes simply add.

As coded, passes under 3 of 6 random input draws

The coded measure averages the two giant fibers and stops at the first spike, so what it actually reads is how closely the two fire together. That is where its "sublinear" index of 0.81 comes from.

Only B1 was truly reproduced. For B2 to B4, the model itself does not behave like a real fly, before any wiring is scrambled.



– Show the data table

r/v	Main run	0.6×	0.8×	1.0×	1.2×	1.4×
10 ms	33.7°	46.6°	38.2°	34.3°	29.9°	27.2°
20 ms	37.2°	39.6°	37.9°	36.9°	35.5°	35.7°
40 ms	35.3°	37.5°	36.2°	35.4°	34.7°	34.4°
80 ms	34.3°	36.1°	35.1°	34.3°	33.7°	33.4°

B1: the angular size at the giant fiber's first spike for each approach speed. The grey band is the 30°–50° pass band fixed in advance; the horizontal line is the published value of about 40°. Red dots are the main run; grey dots are the same test with the input gain set to 0.6–1.4 times its value (a gain sensitivity analysis, also specified before it ran).

– Go deeper: B4, one giant fiber at a time

The table shows each giant fiber's maximum depolarisation (relative to rest) before its first spike, from a post hoc check that is not part of the pre-registration; the three runs share one input draw. Each giant fiber responds only to its own eye, and its value with both eyes equals its value with its own eye alone.

Stimulus	Left giant fiber (mV)	Right giant fiber (mV)
Both eyes	6.54	6.63
Left eye only	6.54	0.00
Right eye only	0.00	6.63

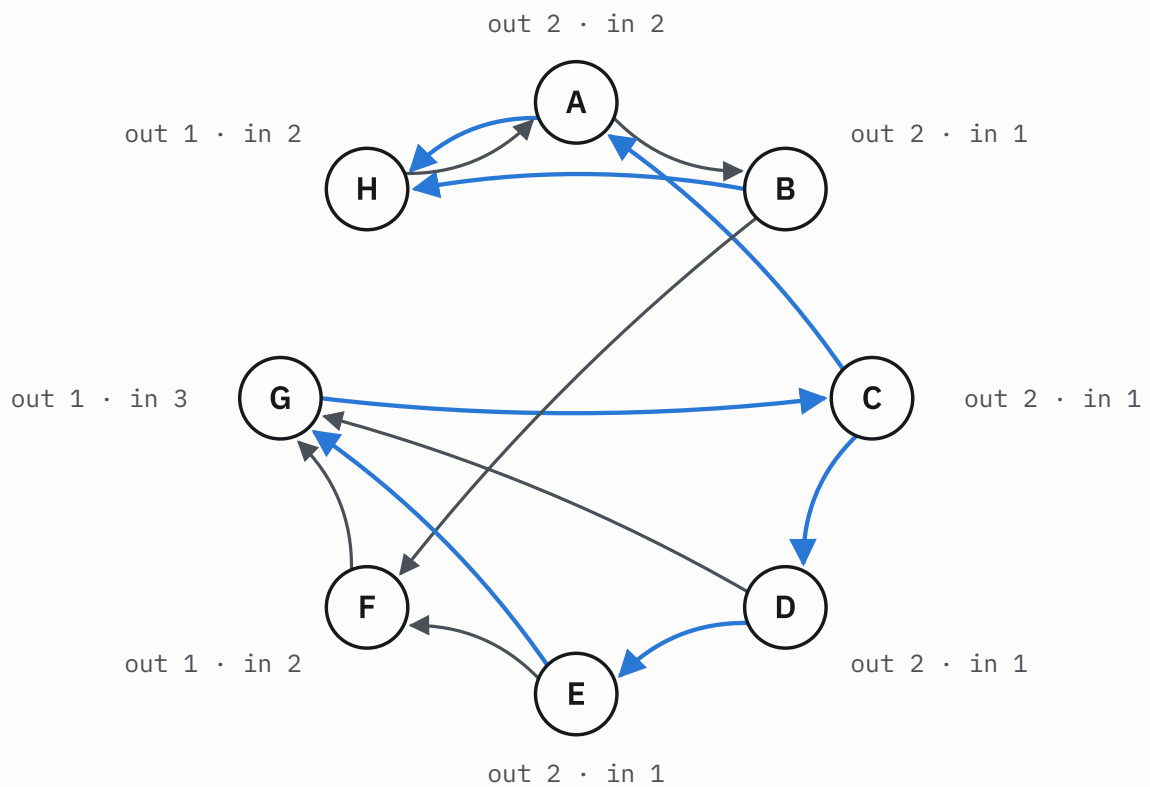
Per-fiber index = both eyes ÷ (left only + right only). Under all 6 random input draws, both giant fibers have a per-fiber index of 1.000.



Chapter 7 of 11 · $\theta = 41.8^\circ$

Step 2: scrambling the wiring

Now for the main question. The wiring is scrambled by **double-edge swaps**: pick two connections $A \rightarrow B$ and $C \rightarrow D$ at random, and turn them into $A \rightarrow D$ and $C \rightarrow B$. Every neuron keeps its number of outgoing and incoming connections, and each connection keeps its synapse count and sign, which travel with the neuron that sends it. Only who connects to whom changes.



Swaps: 6 · original connections kept: 6 / 13 (46%) · last: $E \rightarrow H + B \rightarrow G \Rightarrow E \rightarrow G + B \rightarrow H$

A small example with 8 neurons. Press "Swap once": the two chosen connections light up, then trade targets. The numbers beside each circle (outgoing / incoming connections) never change. Blue marks connections created by swaps, and fewer and fewer of the originals survive.

How much the wiring is scrambled is set by the **dose f**: number of swaps = $f \times \text{number of connections} \div 2$. At $f = 1$ each connection is touched once on average. Because the picks are random, though, some connections are picked several times and others never, so about 41% of the original connections survive.

Dose f on the right

0.05

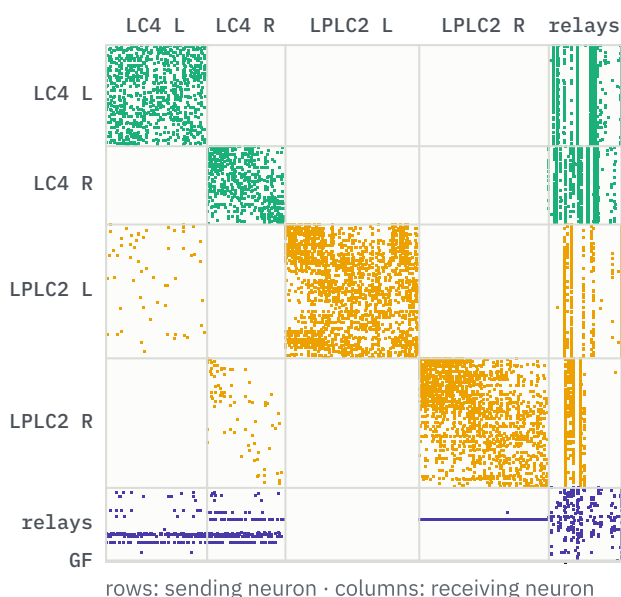
0.10

0.25

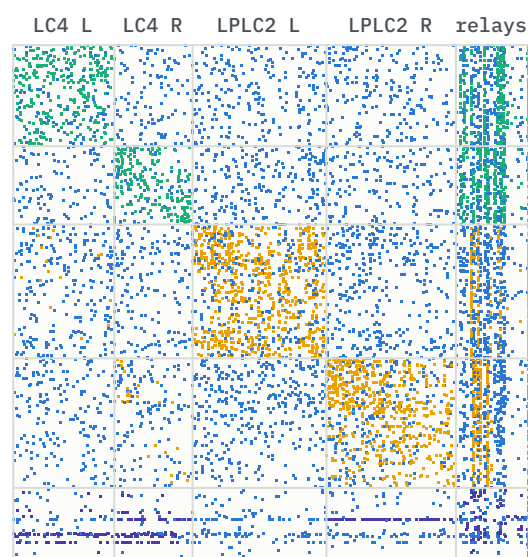
0.50

1.00

Real circuit



A rewired example: f = 1.00, 40.3% kept



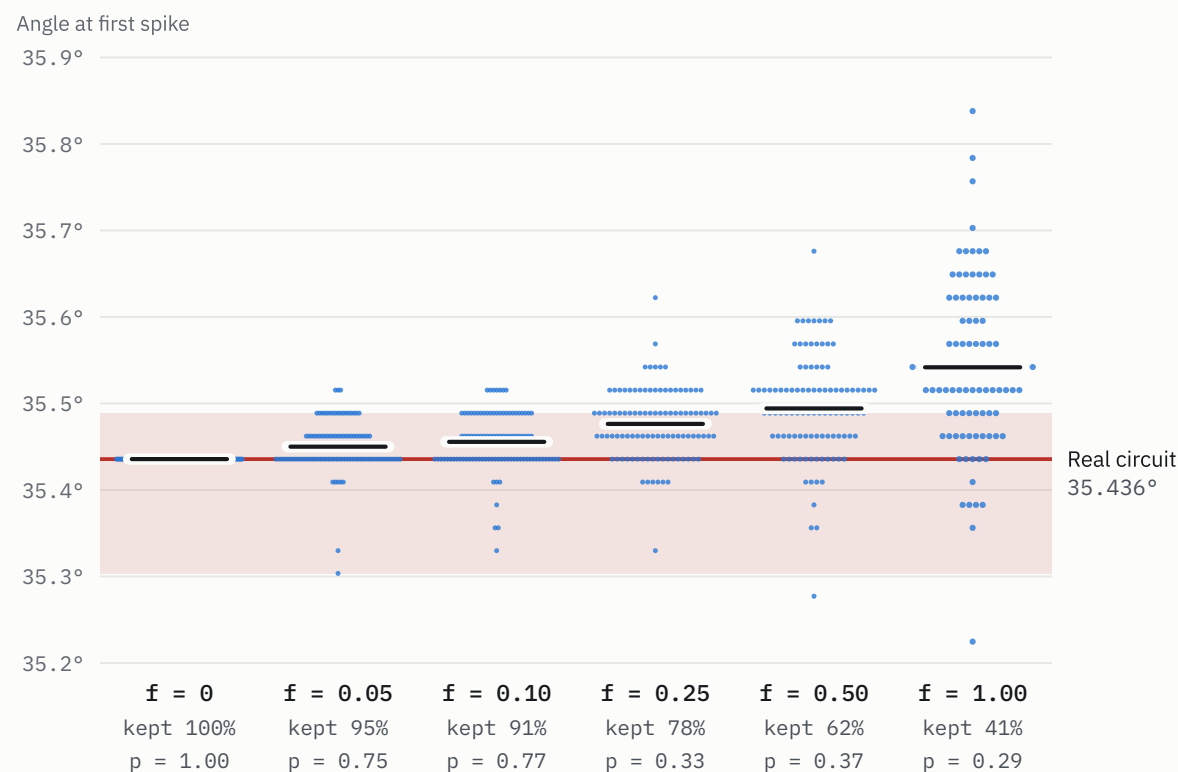
Right: $f = 1.00$ · 7,784 connections, kept intact: 40.3%, new: 4,644 · every neuron keeps the same out- and in-counts as on the left

Left: the real circuit's connectivity matrix, 364×364 cells. Each row is a neuron sending connections, each column a neuron receiving them; each dot is one connection, coloured by the sender's type. Right: one rewired example of the same circuit (pick the dose), with connections created by the rewiring in blue. The dots move, but not one row or column changes its count. Hover over either matrix to compare the same row and column.

The experiment: at each of 6 doses ($f = 0, 0.05, 0.10, 0.25, 0.50, 1.00$), 100 rewired circuits were generated and all were simulated with the same input at one approach speed ($r/v = 40$ ms). The question is whether the real circuit's response stands out among those 100.

Vertical axis **Zoomed in** Inside B1's band

● Rewired circuits (100 per dose) — Mean of the rewired circuits — Real circuit
Real circuit's own spread (6 input draws)



— Show the data table

Dose f	Original kept	Rewired mean	SD	Real	p
0	100.0%	35.436°	0.000°	35.436°	1.000
0.05	95.1%	35.450°	0.031°	35.436°	0.752
0.10	90.5%	35.456°	0.034°	35.436°	0.772
0.25	78.2%	35.476°	0.041°	35.436°	0.327
0.50	61.9%	35.494°	0.060°	35.436°	0.366
1.00	40.6%	35.542°	0.093°	35.436°	0.287

Each column shows the angular size at first spike for the 100 rewired circuits at one dose (blue dots); the short line marks their mean. The red line is the real circuit, and the pale red band is how much the real

circuit itself varies across 6 different random input draws. Under each column: the share of original connections kept, and the p-value. Switch to "Inside B1's band" to see how small these differences are next to the pass band.

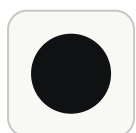
The result

- None of the **24 tests** (6 doses × 4 measures) was significant. The smallest p-value was 0.287, far above the usual 0.05 threshold.
- The more the wiring is scrambled, the more the mean angle at first spike does creep up, but by at most **0.11°**. That is less than the real circuit moves when it simply gets a different random input (0.19°).
- Every rewired circuit still fires, and all of them fire well inside B1's 30°–50° band.

– Go deeper: all 24 p-values

A p-value is the probability of seeing a difference at least this large if the real circuit were just an ordinary member of its 100 rewired neighbours. After Benjamini–Hochberg correction for multiple comparisons none is significant, and none falls below 0.05 even uncorrected. At $f = 0$ the "rewired" circuits are identical to the real one, so $p = 1$. The four measures are not independent (angle at first spike and peak time move almost in lockstep), so the 24 tests amount to far fewer than 24 independent ones.

Measure	$f = 0$	$f = 0.05$	$f = 0.10$	$f = 0.25$	$f = 0.50$	$f = 1.00$
Angle at first spike	1.00	0.75	0.77	0.33	0.37	0.29
Peak response time	1.00	0.75	0.77	0.33	0.37	0.29
Maximum depolarisation (in fact reads synchrony)	1.00	0.74	0.75	0.88	0.67	0.55
Whether it fires	1.00	1.00	1.00	1.00	1.00	1.00

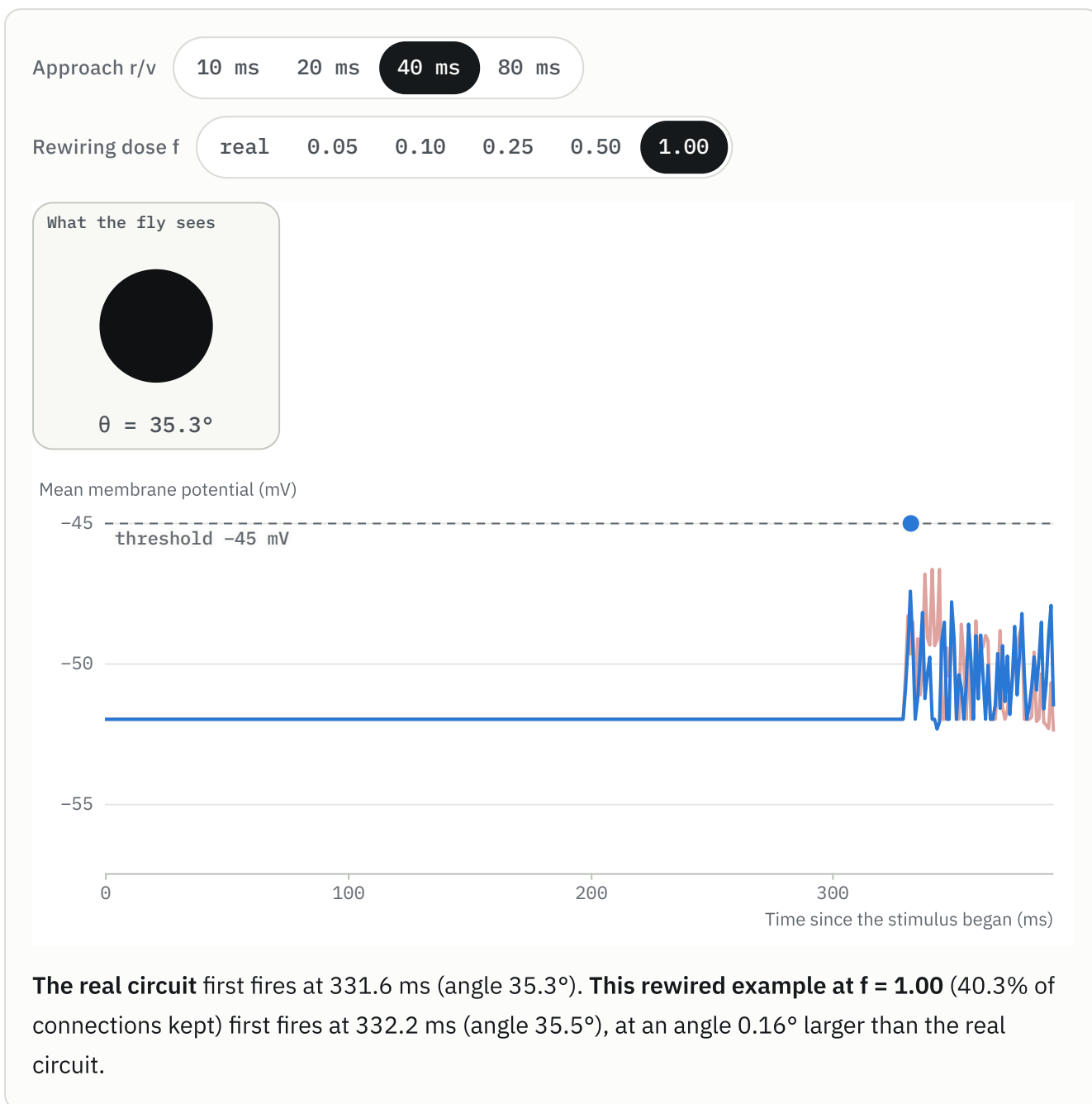


Chapter 8 of 11 · $\theta = 47.1^\circ$

Try it yourself

These are the simulation's raw traces. Pick an approach speed and a rewiring dose to see how the two giant fibers' mean membrane potential changes over time. Hover to read values, or press play, and the small screen shows what the fly sees at that moment. Each dose shows one rewired circuit as an

example, the same one shown in the matrix above; the statistics are in the previous chapter. The random input here is a different draw from the previous chapter's, so the real circuit's numbers differ from those by a few hundredths to tenths of a degree.



The trace is the mean of the left and right giant fibers' membrane potentials. After the first spike both fire and reset repeatedly, so the mean jumps up and down.



What it means

Before the experiment ran, the design listed three possible outcomes and how each would be read. Here is where the results fell:

Outcome	Reading fixed in advance	Lands here
Real circuit passes, rewired ones do not	The specific wiring is needed (structure specificity)	none
Rewired circuits pass too	Keeping each neuron's number of connections is enough	B1
The real circuit itself fails	A negative result: connectome + LIF cannot explain these responses	B2 B3 B4

What it shows

- In this model, for when the giant fiber fires, keeping each neuron's number of connections is enough; exactly where they lead barely matters.
- A real connectome plus a standard simplified neuron model reproduced only one of four experiments. That is a useful negative result in itself: a wiring diagram alone is not enough.

What it does not show

- It does not show that a real fly's wiring is unimportant. Step 2 ran at one approach speed (40 ms), one random input draw and one input gain.
- The scrambling is gentle: each neuron keeps its connection counts, synapse counts and signs, and even the strongest dose leaves about 41% of the original connections in place.
- For B2 to B4 the model itself failed, so it cannot say whether the wiring matters for them.
- The model has known simplifications: no electrical synapses (electron-microscopy connectomes cannot see them, and the giant fiber's links to its downstream motor neurons are mostly electrical); no computation inside LPLC2's dendrites; about 1,000 other inputs to the giant fiber left out (about 673 excitatory and 361 inhibitory); and an "eye" that is only a formula.



Mistakes we caught and corrected

Research is rarely right the first time. This project records every correction in public and notes whether it came before or after the results were seen. A few examples:

Before the re-run

Too tidy to be real

In the first run, the 311 visual neurons received almost identical input and fired in perfect lockstep, like a parade. The giant fiber jumped from rest past threshold in a single step, and several measures read zero in every condition, so nothing could be tested. The fix, a random time offset for each visual neuron, was written into the design and committed first; only then was the test re-run.

Before any test ran

A normalisation that erased the answer

LC4's input was first normalised separately within each approach speed, which pinned every speed's peak to 1. That erased exactly what B2 tests: for the fastest approach the LC4 signal should be 8 times stronger than for the slowest. It was switched to one shared reference before any test ran.

After all results

A measure that was really reading synchrony

The final review found that the "maximum depolarisation" measure averages the two giant fibers and stops as soon as either one fires. Once one fires first, it reads how closely the two fire together, not how large the response is. That is where B4's "pass" came from. The registered verdicts were not re-scored; the report states what they actually mean and adds a per-fiber check labelled post hoc.

After all results

A reference with the wrong label

The "55 LC4 neurons" used to validate the extraction were first labelled as hemibrain counts. They actually come from Ache et al.'s 2019 reconstruction in the FAFB dataset, a paper that predates the hemibrain's release. An explanation built on the wrong label was withdrawn with it. The numbers themselves did not change.

Disclosed after all results

A scan that left no record

The input gain is the factor that turns the visual signal into input current. Before it was fixed, a gain $\times \sigma$ scan was run while working out why the whole circuit was silent. It glimpsed some B1 outcomes, was stopped, and its results were not kept. This was disclosed after all results were in. A re-check also found that the rule written down for the gain gives 7.0 (or 6.0), not the 8.0 actually used. A gain sensitivity analysis, specified before it ran, was added: B1 passes at 0.6–1.0 times the gain and fails at 1.2 and 1.4 times.



Chapter 11 of 11 · $\theta = 63.0^\circ$

Next steps, glossary and references

Tests that could come next

- Run the rewiring at all four approach speeds (so far only 40 ms).
- Repeat Step 2 with several random input draws, other input gains and other values of σ .
- Register, in advance, a per-fiber measure over the whole stimulus and re-test B2 and B4 with it.
- Try other kinds of scrambling: one that does not carry synapse counts along with each neuron, or one that respects the wiring rules between cell types.
- Improve the model itself until the real circuit passes B2 to B4, with a new pre-registration written first so that nothing is tuned after the results are seen.

Glossary

Connectome

A brain's complete wiring diagram: every neuron, and every connection between them with its synapse count.

Neuron, synapse

A neuron is a cell that carries signals; a synapse is a contact point where one neuron passes a signal to another. Two neurons are often joined by dozens of synapses.

Membrane potential, spike

The membrane potential is the voltage across a neuron's membrane, in mV. When it reaches threshold the neuron sends a brief electrical pulse, a spike.

LIF	Leaky integrate-and-fire: a neuron simplified to a leaky bucket that fires and empties when full.
Giant fiber (DNp01)	One descending neuron on each side of the fly; when it fires, the fly makes a fast escape jump.
LC4, LPLC2	Two kinds of visual neuron: LC4 responds to approach speed, LPLC2 to an object's size.
Inhibitory relay	A neuron excited by the visual neurons that in turn inhibits the giant fiber, like a brake. There are 51 here.
Angular size θ, r/v	Angular size is the angle an object takes up in the eye; r/v , radius over speed, sets how fast it approaches.
Degree, degree-preserving rewiring	A neuron's degree is its number of connections. Degree-preserving rewiring randomises where connections lead while keeping every neuron's degree fixed.
Dose f	How much the wiring is scrambled: $\text{swaps} = f \times \text{number of connections} \div 2$.
Pre-registration	Writing down, before seeing any results, what will be tested, what counts as a pass and how outcomes will be read.
p-value, BH correction	A p-value measures how likely a difference this large would be by chance alone. When many tests are run together, a correction such as Benjamini–Hochberg keeps chance from passing as a finding.
Reservoir computing	Using a fixed network as a "reservoir" and training only an attached readout to do the task.

References

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2. Klapoetke, N. C., et al. (2017). Ultra-selective looming detection from radial motion opponency. *Nature*, 551, 237–241.
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Every number on this page is read directly from the project's committed result files. The example circuits in "Try it yourself" and in the Step 2 matrix were regenerated with the project's own code and checked bit for bit against the committed results.

Connectome data from the MaleCNS v1.0 dataset, HHMI Janelia Research Campus FlyEM project, in collaboration with the University of Cambridge, MRC Laboratory of Molecular Biology, and Google Research. Licensed under CC-BY 4.0.

Web: ewanwu06.github.io/fly-escape-switch · PDF: English · 中文

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