



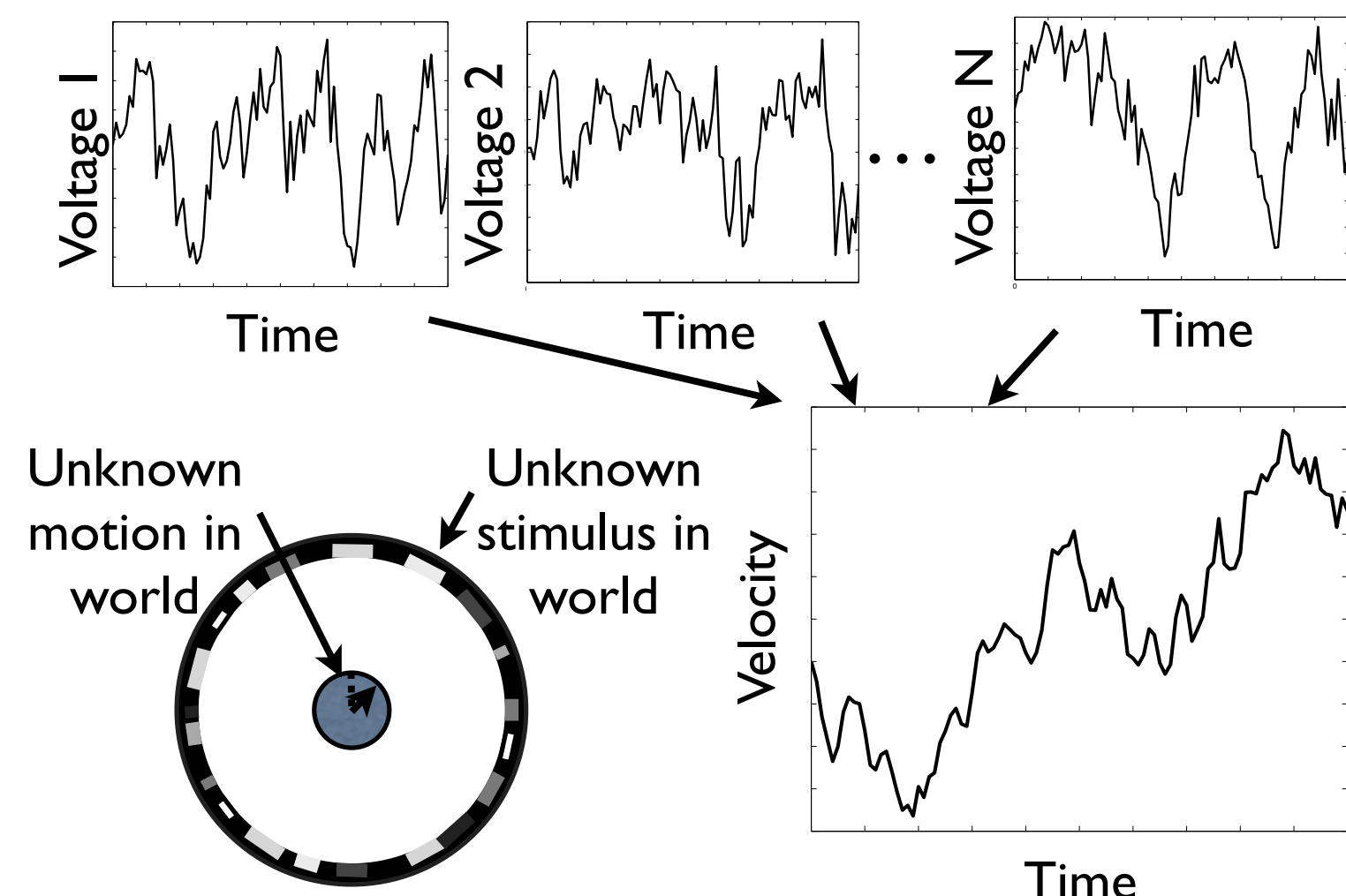
# Of Flies and Men: How Natural Stimulus Correlations Influence Visual Motion Estimation.

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## Visual Motion Estimation and Neural Computation

A major function of the brain is to transform sensory inputs into behavioral outputs. For an animal to do this appropriately, it must infer, or compute, properties of the external world from its neural signals. Across the animal kingdom, animals use vision to help determine their motion through the world. The field that studies how the brain represents and transforms information is called computational neuroscience, and visual motion estimation is a paradigmatic neural computation.

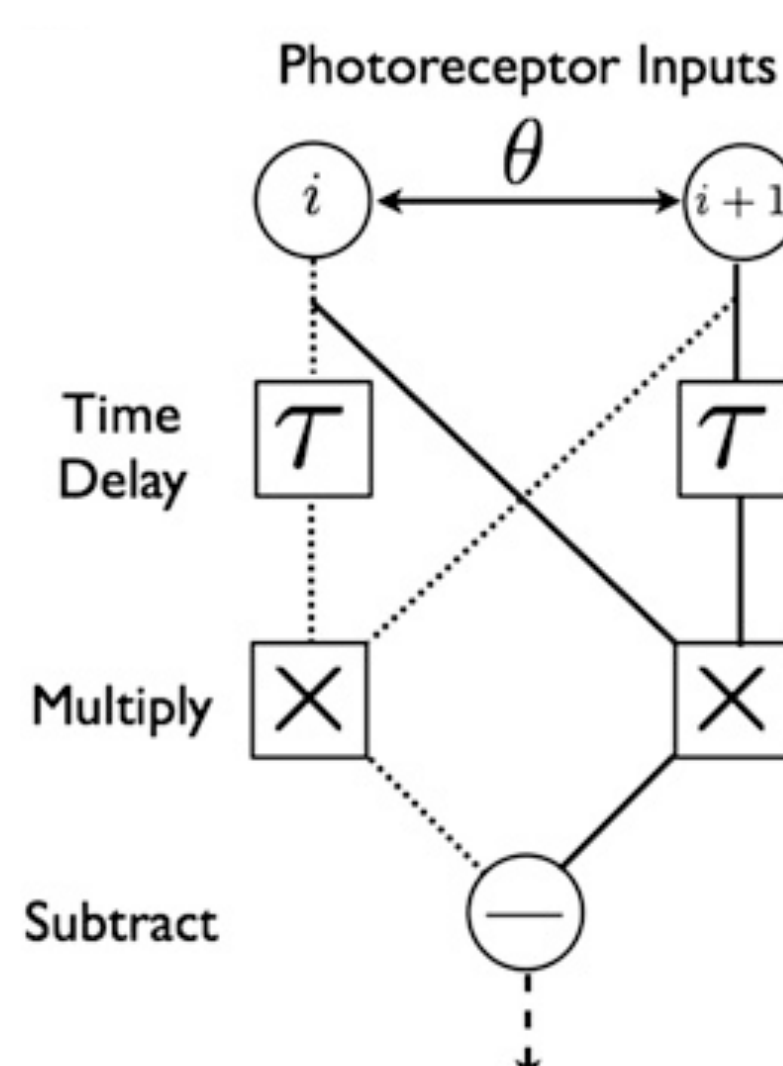


Ultimately, the animal must compute its motion (velocity) using information that was present in its light sensing units, the photoreceptors. How does the brain do this computation?

## The Reichardt Model for Motion Estimation

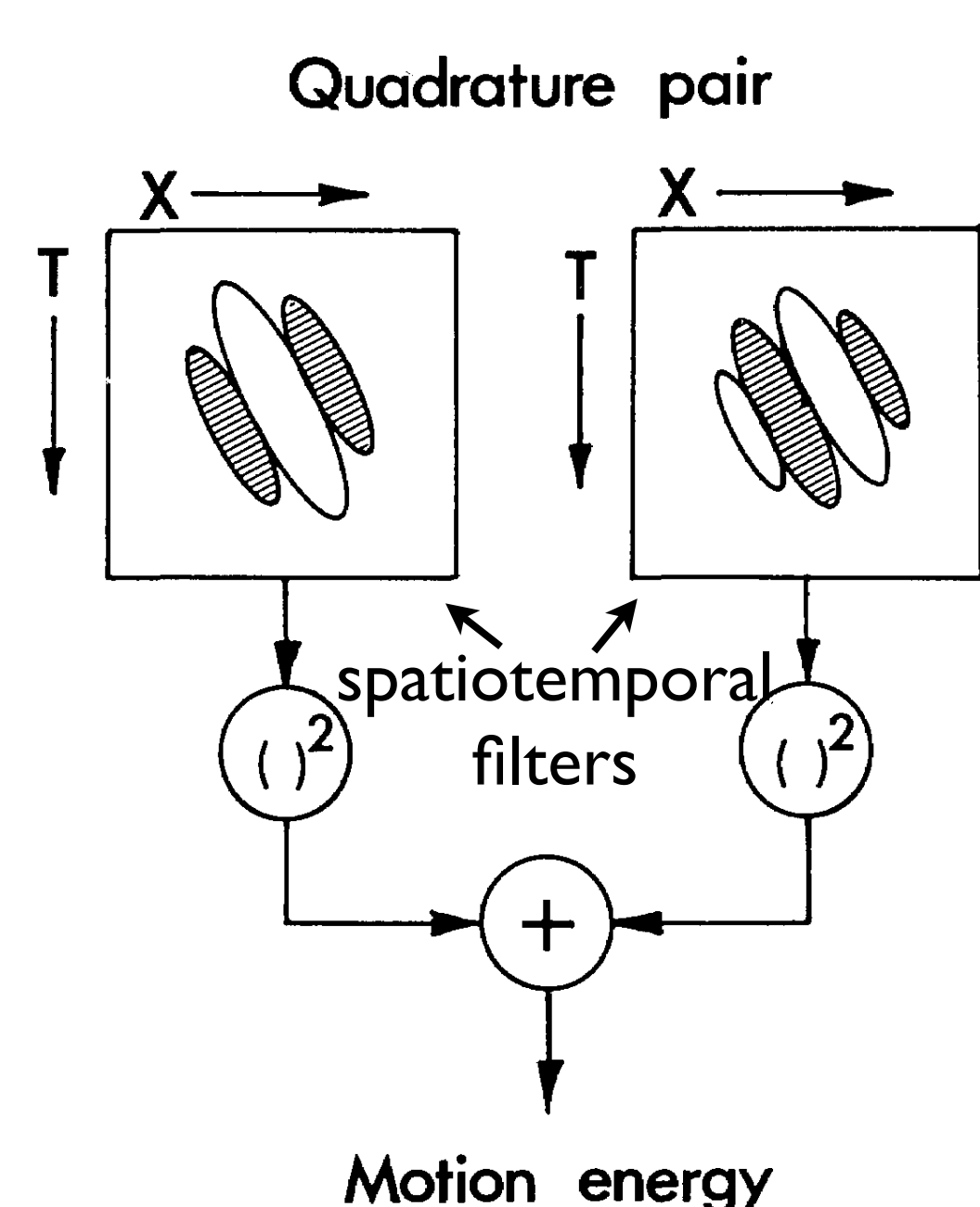
When insects see the world rotate around them, they reflexively counter-rotate to stabilize it, as though the motion was self-motion. Researchers have used this behavioral response to study how insects compute visual motion.

A landmark achievement of this work is the Reichardt correlator model<sup>1</sup>. This model proposes that insects delay and correlate visual signals from two points in space to estimate motion. If the leftward point is correlated with the rightward point at a later time, motion is to the right. If the leftward point is correlated with the rightward point at an earlier time, motion is to the left.



## Motion Perception in Flies and Humans

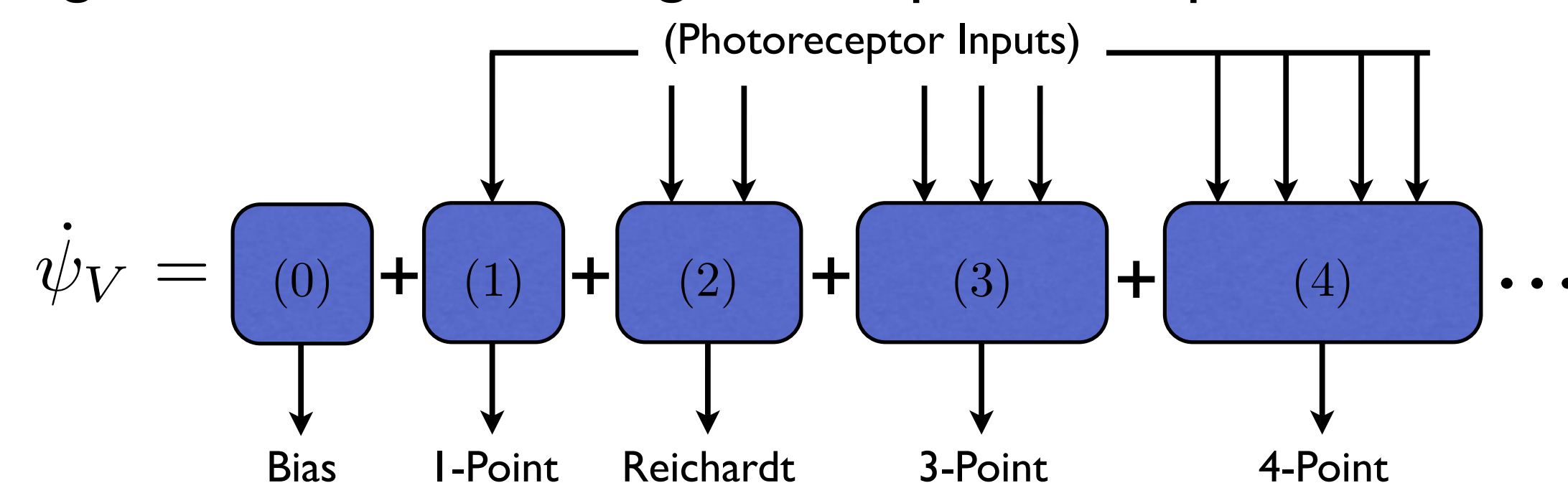
Remarkably, human beings appear to compute visual motion in a similar manner. According to the motion energy model, visual stimuli are spatiotemporally filtered, squared, and summed<sup>2</sup>.



The Reichardt correlator and motion energy model are tightly linked mathematically<sup>2</sup>. Although their implementations differ, both equate motion with correlations across two points in space and time. This commonality shows that certain principles in visual motion estimation apply broadly across species. Thus, researchers can study neural computation in animals with simple brains and retain human relevance.

## A Broader Perspective on Motion Estimation

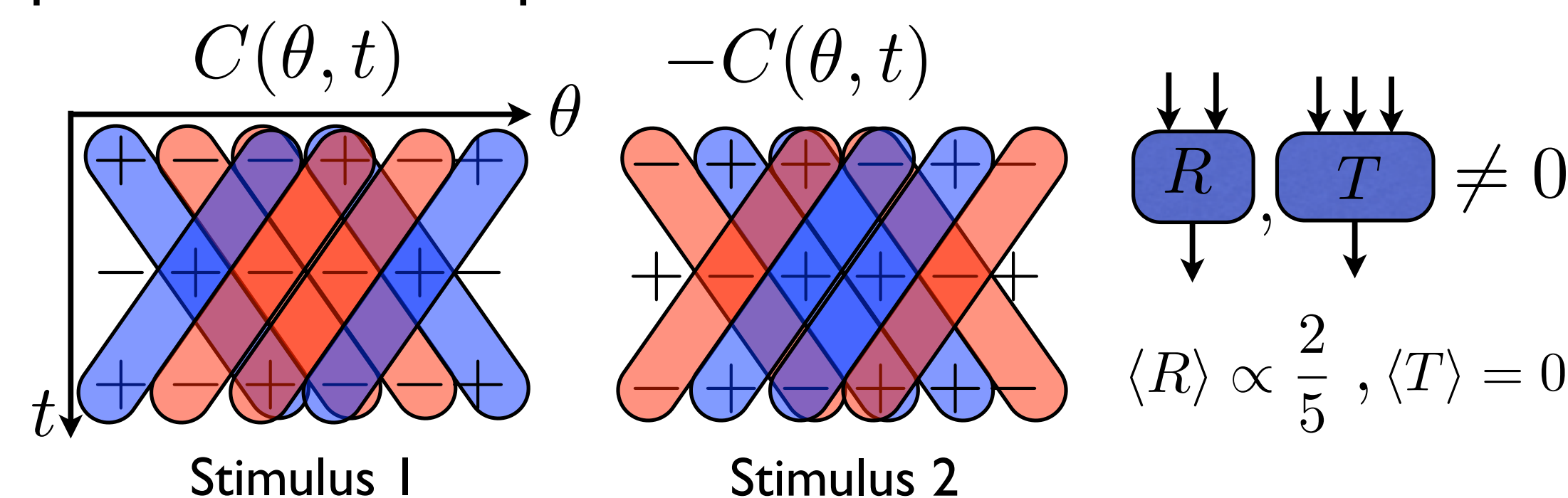
Despite the success of the Reichardt correlator and motion energy model, animals detect motion in stimuli that the models do not. We propose that animals also estimate motion using correlations involving several points in space and time<sup>3</sup>.



Our proposed motion estimator is a sum of multiple terms, each of which infers motion from a particular type of stimulus correlation that is predictive of motion in the natural world<sup>3</sup>.

## Motion Estimation Couples Stimuli and Estimators

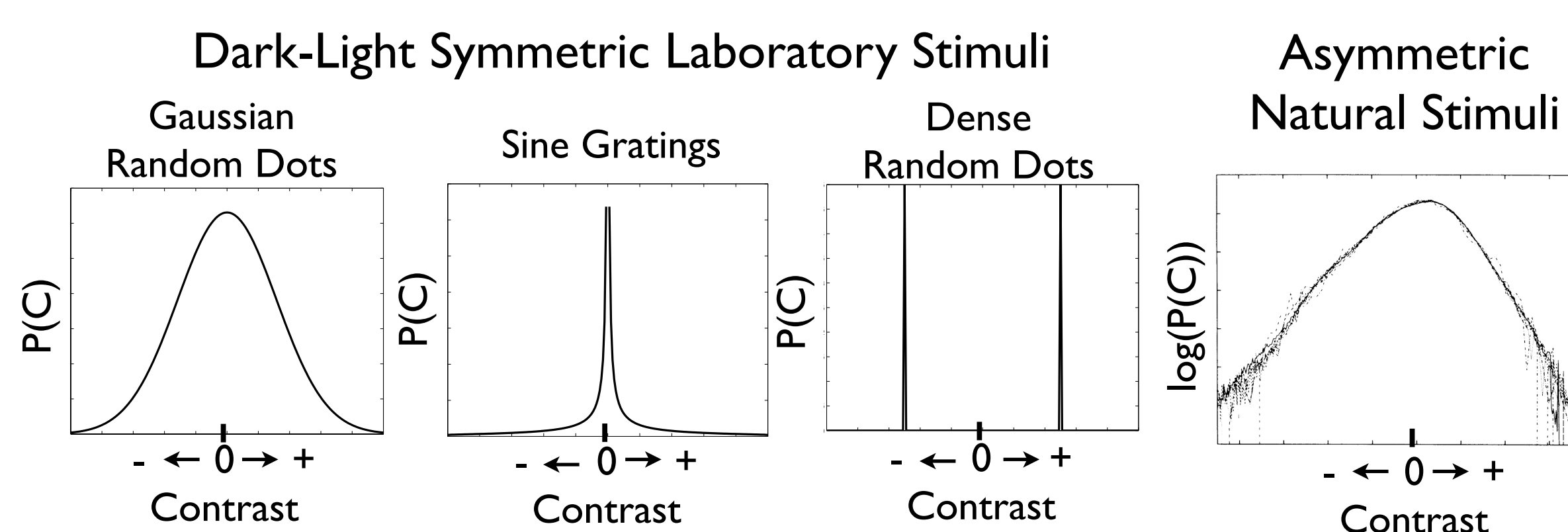
One type of correlation involves three points in space and time. Stimuli where bright and dark are interchangeable cannot detect motion estimates from these correlations<sup>3</sup>, so common experiments do not probe their role in motion estimation.



The spacetime evolution of two moving random dot patterns is diagrammed above. Because motion is rightward, each row is shifted one point to the right relative to the row above it. On average, the Reichardt correlator (R) detects the motion, but the three-point correlator (T) does not. Blue ovals denote patterns that contribute positively to T; red ovals contribute negatively. Each blue oval in Stimulus 1 is canceled by a red oval in Stimulus 2. Even if third-order correlations influence motion estimation, for these stimuli they have no effect<sup>3</sup>.

## Optimal Motion Estimation Minimizes Errors

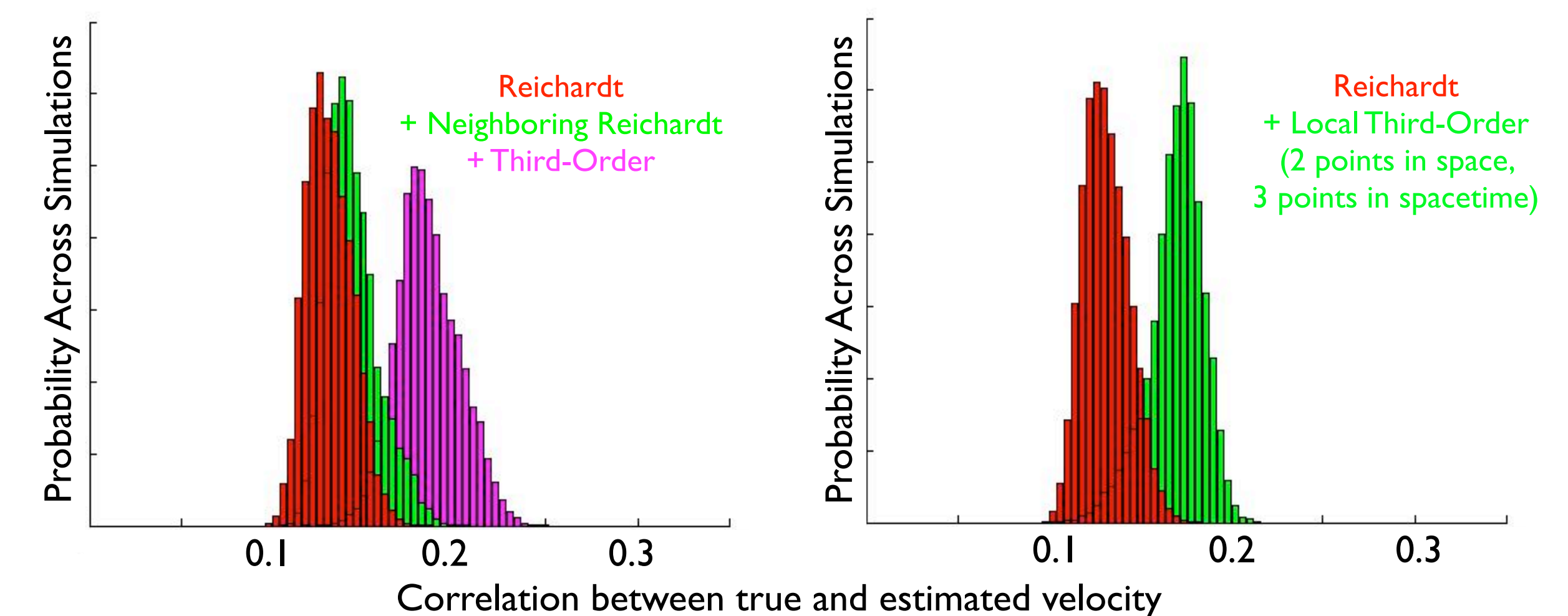
We hypothesize that evolution has built a near optimal motion estimator in the brain<sup>3,4</sup>. Which strategy is optimal depends on statistical properties of the visual world. Unlike most laboratory stimuli, natural images are asymmetric between light and dark<sup>5</sup>.



Above, we plot contrast probability distributions for several common stimuli. Positive contrasts are bright. Our theory shows how the contrast asymmetry of natural stimuli permits third-order correlations to signify motion in natural setting<sup>3</sup>.

## Estimating the Motion of Natural Images

Natural images are not random and have many complex correlations. By simulating and estimating motion with natural images<sup>6</sup>, we show that third-order estimators improve estimation accuracy.



## Exotic Motion Estimation in Flies and Humans

A central prediction of the theory is that animals should perceive complex stimulus correlations as motion<sup>3</sup>. Consistent with this prediction, recent studies show that humans report perceiving certain third-order and fourth-order correlations as motion<sup>7</sup>. Because each stimulus lacks two-point correlations, the Reichardt correlator and motion energy model do not detect any signature of motion in these stimuli. The experimental results thus imply that complex correlations influence motion perception. We are now testing whether these stimuli induce behavioral effects in flies that are consistent with motion perception. Such a result would facilitate studies on the neural basis of the computation.

## Conclusions

1. Visual motion estimation is a canonical neural computation.
2. Previous work suggests that both insects and humans estimate motion using simple two-point stimulus correlations.
3. We propose that animals also use more complex stimulus correlations to estimate motion.
4. Even if third-order correlations are used for motion estimation, they wouldn't be detected by classic experiments.
5. The motion of natural images can be better estimated if third-order correlations are included in the estimate.
6. Humans perceive complex correlations as motion. Our fly experiments will help to assign a neuro-computational basis to this computation.

## References

1. Hassenstein and Reichardt (1956). *Z Naturf*, 11b:513-524.
  2. Adelson and Bergen (1985). *J Opt Soc Am A*, 2:284-299.
  3. Fitzgerald et. al. (2011). *Proc Natl Acad Sci USA*, 108:12909-12914.
  4. Potters and Bialek (1994). *J Phys I France*, 4:1755-1775.
  5. Ruderman and Bialek (1994). *Phys Rev Lett*, 73(6):814-817.
  6. van Hateren and van der Schaaf (1998). *Proc. Bio Sci*, 265(1394):359-366.
  7. Hu and Victor (2010). *J Vision*, 10(3):1-16.
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