Models of motion detection

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Visual motion detection is one of the most active areas in systems neuroscience today[1,2], and the cellular mechanisms of directional selectivity may soon be understood in unprecedented biophysical detail. Alongside undeniable technical advances such as whole-cell patch-clamp recording and the retinal slice preparation, a major determinant of this recent progress is the conceptual foundation laid almost half a century ago.

Curiously, the story began with two young soldiers during World War II. A biology student, Bernhard Hassenstein, then 21, met a 19-year-old aspiring physicist, Werner Reichardt. In the craziness of wartime, they promised each other that, if they survived, they would do something great together: start the first institute of physics and biology. In 1958 they founded the Research Group of Cybernetics at the Max-Planck-Institute of Biology in Tübingen, Germany. In a congenial collaboration, which still sounds like the goal of every summer school in computational neuroscience, they did a series of elegant experiments, using the optomotor response of the beetle *Cholorphanus* as a behavioral measure. This response is the animal's tendency to follow the movement of the visual surround to compensate for its mistaken perception of self-motion in the opposite direction. The beetle was glued to a rod so it could not move its body, head or eyes relative to the surround, but could express its behavior at decision points by rotating a 'Y-maze globe' under its feet (Fig. 1).

Fig. 1. Tethered *Chlorophanus* walking on the Y-maze globe (from ref. 10).

Their results[3] led to the development of a model for motion detection that became known as the 'correlation-type motion detector', the 'Hassenstein-Reichardt model' or briefly—omitting half the original team—the 'Reichardt detector' (Fig. 2). The core computation in this model is a delay-and-compare mechanism: delaying the brightness signal as measured by one photoreceptor by a low-pass filter and comparing it by multiplication with the instantaneous signal derived from a neighboring location. Doing this twice in a mirror-symmetrical fashion and subtracting the output signals of both subunits leads to a response that is fully directionally selective. The strict mathematical treatment of this model[4] led to many counterintuitive predictions, which nevertheless were experimentally verified in many species' behavior and in many types of neurons (for review, see ref. 5). For example, the model predicted that the response, unlike a speedometer, should not increase continuously with increasing velocity; instead, going beyond an optimum velocity should decrease the response. The model also predicted that the optimum velocity should vary with the pattern's spatial wavelength so that their ratio remains constant.

The theory's influence can hardly be overestimated. It inspired work on motion vision in many animals, including humans. In some cases, filters and parameters of the original model were modified to fit experimental observations[6]. In others, researchers approaching the problem from a different angle arrived at similar solutions, such as the 'motion energy model', which despite a different internal architecture is identical to the original model at its output[7]. Some of these studies became famous under their own name, like the 'Barlow-Levick-model' of motion detection, arising from ex-periments on rabbit retinal ganglion cells[8] that were stimulated, not by smooth motion, but by a sequence of discrete illumination steps in two neighboring locations, in either the preferred or null direction for the cell. Barlow and Levick found that the response to the null direction sequence was significantly reduced compared to the sum of the individual responses, whereas the response to the preferred direction sequence was roughly equal to the sum of individual responses. The authors proposed a veto-mechanism or 'null-direction inhibition' as the basis for direction selectivity. From this study, the historical thread leads to the

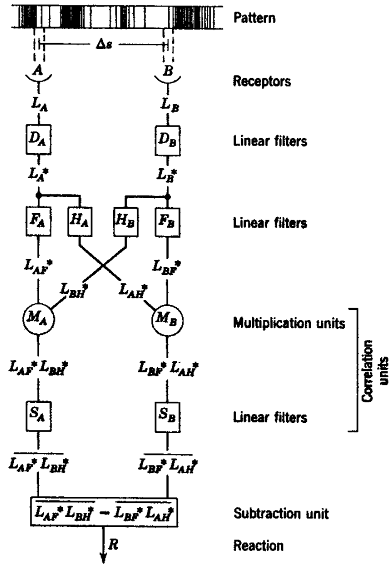

Fig. 2. Correlation-type motion detector (from ref. 4).

proposal that a shunting inhibition is the cellular implementation of the veto operation[9], and from there directly to the current 'pre or post' debate over directionally selective ganglion cells[1].

Thus, the Hassenstein-Reichardt model set the standard for how researchers thought about visual motion detection and how they designed experiments. In a more general sense, it introduced mathematical techniques and quantitative modeling to biology, clearly demonstrating that our intuition does not reach very far; instead we soon reach the point where the 'pen starts getting smarter than the person holding it'. Far beyond the question of whether the particular Hassenstein-Reichardt model is correct or not, this has probably been its most significant contribution to neuroscience.

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