A sign directing to the orient – On visual receptive fields

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A sign directing to the orient – On visual receptive fields*

Helmut Glünder

Traditionally, a neuron's receptive field means a static property although transient stimuli are necessary to measure it: A plea for true spatio-temporal concepts of receptive fields.

Dear Ernst, dear Ingo,

I should like to thank both of you for providing the reason for this splendid symposium and for its organization. I look forward to enjoying many more of such academic Fest-Symposia.

Dear friends and guests,

please allow me to take advantage of today's outstanding occasion and shed some light on a scientific poster that – already some time ago – found a prominent place at the walls of the *Institut für Medizinische Psychologie* here in München. The poster, titled

"Motion processing in the primary visual cortex – Networks and their spatio-temporal receptive fields"

originally has been presented 1997 at the annual Neurobiologentagung in Göttingen and there is an anecdote about it. Among the not too many visitors of this poster was our friend and cybernetically minded colleague Bernhard Ronacher – professor at the Humboldt-Universität zu Berlin. Having studied the poster, he simply stated: You are to display the poster every year. – With this he wanted to express that it takes repetitive stimulation to communicate possible problems with certain textbook knowledge.

In the following, I shall give you quite a personal view of some of the reasons why I think Ronacher was right. Furthermore, I shall present an essential aspect of the work that is displayed on the poster.

But first of all, you may wish to know whether I followed Ronacher's advice. – In fact, there was no need to think about it because the traditional non-profit "Neurobiologentagung" all of a sudden ended being Germany's annual neuroscience meeting.

* Slightly reworked contribution to the Fest-Symposium »Syntopia« on occasion of Ernst Pöppel's and Ingo Rentschler's 60th birthdays in München (28. April 2000)

Introduction

A good deal of confusion in science – especially with interdisciplinary work – results from terms and their associated concepts: Experimentally working scientists use to know what they do, or what they have been doing – at least, as far as it is possible to know what one is doing – but sometimes they are a bit sloppy in the choice of their terms. In contrast, theoretically working scientists often have only a faint idea of experimental details and they rely on their own interpretations of these terms. Occasionally, consequences from perhaps inadequate interpretations are taken up again by experimentalists, and so on and so forth. (In some cases however, the meaning of terms is far from being unambiguous for other reasons …)

Orientation preference of receptive fields

For example, let us take a look at two common descriptors of simple receptive fields in the primary visual cortex: orientation and direction. Both are well defined for those who know how to relate them to classical experiments and their results. In general, a cell's orientation preference is determined by moving a bar or edge pattern across that part of the visual field to which the cell is "looking". Then, the stimulus is moved under different angles across this area of interest and the pattern orientation to which the cell responds best[1] is called its preferred orientation. Stimuli may also be presented flashed or flickered, not moved, but this is a different issue …[2]

1 The number of nerve impulses per time interval commonly serves as the criterion for the neural response, although it has not been shown to be an adequate one

2 According to David Hubel's Nobel Lecture published in 1982, a moving bar – produced by the edge of a glass slide during its insertion to the projector – has been the first effective stimulus for striate cortical neurons (p. 517).

Nowadays, orientation signifies a geometric and static property – specified by angles from the range of 0…180 degrees – hence most neuroscientists – theoreticians included – do recognize orientation selectivity as a basic means for visual form analysis. By the way, it is far from obvious why the visual system is to use a decomposition of patterns according to orientations. Whatsoever, fact is: Orientation describes a static property but orientation selectivity cannot be determined using static stimuli. This is somewhat puzzling, at least for me, and I should like to sophistically rephrase the situation: It appears as if orientation selectivity of cells *per se* has not been measured so far.

There are mainly two ways of dealing with this situation: If we stick with form analysis, we have to admit that it must cope with pattern motion. To my knowledge, there are no elaborated concepts for such kind of form analysis, although the task is appealing. But frankly speaking, is there any need to stick with form analysis? Interestingly, amphibians and reptiles show only quite restricted form vision.[3] So, why not think of orientation selectivity as a means for motion analysis that is well developed in most vertebrates?

Two kinds of direction selectivity

When dealing with visual motion, we are confronted with another term, namely direction selectivity. Electrophysiologists use this term to indicate that back and forth motion of a stimulus evokes different cell responses. However, this is a rather restricted use of the term direction because its general concept is formalized by a vector or pointer – specified by a length (here: speed) and an angle from the range of 0…360 degrees, or – equally well – an angle from the range of 0…180 degrees in conjunction with a sign (plus or minus). Indeed, polarization or sign is what appears appropriate for the characterization of the stimulus: back and forth. Evidently, objects are generally not restricted to move in two directions, why then is the vectorial direction so rarely used as a descriptor for cell responses? As far as I know, this is due to an unfounded experimental convention that says: Firstly, use bar or edge stimuli – because they are simple patterns – and secondly, move them perpendicular to their orientation. Accordingly, the direction of the stimulus movement is determined by its orientation, except for its sign. With this convention, the description by orientation and sign is indeed sufficient. However, we really should become aware of possible implications of this and other silent agreements, for example the restriction to translational fronto-parallel stimulus motion. Why not rotate the bar stimulus to determine a cell's preferred orientation, as proposed by Christoph Zetzsche some years ago? Maybe, the cell response is too small, but did someone really try?

Spatio-temporal receptive fields

Back to my poster: A central motive for its display has been the way receptive fields commonly are visualized, namely by purely spatial arrangements of excitatory and inhibitory subfields. Pretty often, the temporal or motion aspect is not even mentioned, though spatial descriptions are inappropriate for the characterization of visual receptive fields that evidently result from spatio-temporal stimulation.

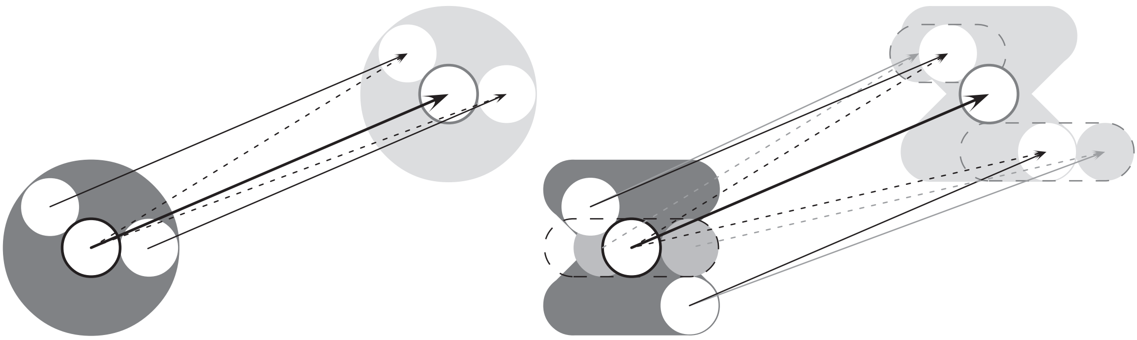
Visual motion analysis means to bridge the crucial computational gap between a set of elementary and inevitably ambiguous local motion measurements on the one side[4] and the behaviorally relevant object trajectory on the other. Only very few promising approaches are known and one of them is proposed on my poster. It is based on inhibition and excitation between neighboring motion vectors,[5] not neighboring points or regions. Two highly simplified figures may illustrate the principle. They can be regarded as an attempt to visualize spatio-temporal receptive fields, although I still don't know how to draw motion …

The mechanisms that are presently proposed to serve the detection or measurement of visual motion in vertebrates also respond to flashed or flickered bars – but not always as well

3 "The frog does not seem to see or, at any rate, is not concerned with the detail of stationary [static; HG] parts of the world around him. He will starve to death surrounded by food if it is not moving." (Lettvin *et al.* 1959, p. 1940)
As far as it is known, motion analysis precedes form analysis in amphibians and reptiles in the sense that the latter is founded on the former, and there are good reasons (e.g. microsaccades) to assume that the same holds true for species with well-developed cortical vision

4 Because velocity is defined by the differential $\vec{v} = \mathrm{d}\vec{r}/\mathrm{d}t \approx \Delta\vec{r}/\Delta t$, it is inherently local. The fundamental problem associated with elementary measurements of pictorial motion has already been known in ancient times: It is impossible to determine the true velocity of a pattern, if the investigated region is small compared to the inverse curvature of the pattern structure in this region. Consequently, a pattern's motion must be determined from several independent local measurements, e.g. by the mechanism proposed by Glünder and Lehmann (1992)

5 These vectors are not the desired unique motion vectors but spatio-temporal coincidences of moving pattern points. They can be detected by tuned bilocal units that are defined by their spatial $\Delta\vec{r}$ and temporal Δt intervals and that are similar to those proposed by Hassenstein and Reichardt in 1956



Two examples of spatio-temporal receptive fields visualized by arrows that originate from the dark regions (region of origins: RoO). To activate a cell, two conditions must be met: (1) An object point must be present at the RoO-center at time t and at the center of the region of destinations (RoD; light gray) at time $t + \Delta t$. (2) The pattern in the RoO at time t must equal that in the RoD at time $t + \Delta t$. This behavior can be achieved, if the basic activation by correspondence (1) (fat arrow) is supported by the correspondences (2) (thin black arrows) and if the centrally diverging correspondences (dashed black arrows) neutralize this support by inhibition. Condition (2) can be relaxed by use of the scheme shown on the right hand side where solid gray arrows indicate slightly deviating correspondences. This scheme however, requires oriented RoO (here: hourglass-shaped).

The fat arrows indicate the motion direction and speed to which a cell is tuned. While object points that move the same distance in parallel (solid black arrows) support a cell's activity, motion in deviating directions (dashed arrows) are of inhibitory influence. It turns out – and here you must believe me – that the simple scheme on the left hand side is too rigid and does not allow for acceptable motion analysis, except in very special cases. However, if one restricts the excitatory vectors to those originating from a region that is shaped like an hourglass and if one tolerates deviations from collinearity and equal speed (right hand side), then the analyses become much more convincing. In other words, this kind of motion analysis demands for orientation selectivity, but in a sense that fundamentally differs from the usual.

Confusion

I should like to conclude with two apparently altered concepts that cannot be ascribed to scientific corruption: Originally, the meaning of orientation was "pointing to the orient", in the way the apse of a church points to the orient. Therefore, orientation has had today's meaning of direction. To confuse things further, the German translation of direction usually is "Richtung" that derives from the verbs "richten" or "zurichten" which mean, to make parallel or in-line. Hence, this term has had today's meaning of orientation. To now infer that both terms exchanged their meanings would be premature: The German *Duden* Dictionary explains the verb "sich orientieren" (to orient) as "eine Richtung suchen" (to look for the right direction). Similarly, the *Longman* Dictionary of Contemporary English tells us that orientation means position or direction …

From this and many more – mostly interdisciplinary – confusions I have learned what is nicely expressed by the verse of the Münchner poet Eugen Roth titled "Feingefühl" (sensitivity or delicacy):

„Ein Mensch sieht ein – und das ist wichtig:
Nichts ist ganz falsch und nichts ganz richtig."

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