# Behavior–Oriented Approaches to Cognition: Theoretical Perspectives

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## Abstract

Understanding complex behavior requires a multidisplinary effort from the neurosciences, psychology, behavioral biology, and computer science. This paper gives an overview of the current state of theoretical thinking in the field. The focus is on a behavior–oriented approach to cognition, i.e., not so much on the mental representations themselves, but on the behaviors that do require these representations. It is the intention of the paper to support the exchange between the different disciplines involved. Examples of different types of models and explanations are discussed, but no comprehensive review of all relevant work is attempted. In the second part, I collect a number of elements that in my view are essential to a future theory of cognitive behavior.

# 1   Introduction

## 1.1   Perception, Action, and Cognition

The word *cognition* refers to a wide variety of mental processes including attention, recognition of places and objects, planning, reasoning, thinking and language understanding, as well as memory and recollection. Traditionally, these phenomena have been studied in a way motivated by introspection, the focus being on the mental states or representations themselves, rather than on the behavioral functions of cognition.

It is quite clear, however, that like most functions of the brain, cognitive brain functions serve to organize behavior of an organism in its environment. Starting from this notion, a behavior–oriented view of cognition can be developed (see, for example, Terrace, 1985, Vauclair, 1997, and the collection edited by Bekoff and Jamieson, 1996). This view differs from simple stimulus–reaction approaches in that it recognizes the existence of mental representations. However, these representations are introduced into the models only if inevitably necessary to explain observed behavior. The behavior–oriented approach asks:

Q1: What is the simplest mechanism and representation required to explain observed behavior?

Q2: What is the simplest behavior that requires a given type of mental representation?

This view of cognitive behavior (i.e., behavior that relies on mental representations) is very close to the standard view of neuroethology developed for simpler types of behavior. It has been shown that apparently complicated behaviors such as visual orientation and navigation have simple explanations in terms of stimulus and response, stressing the importance of question Q1 above. Since this is particularly true for closed loop behavior, I would like to begin this essay with a brief account of the action–perception view of brain function.

Fig. 1 shows a sketch of the basic action–perception cycle. Feedback from effectors to sensors exists on a number of different levels:

a. *Homoeostasis* is the internal regulation of the organism. It is a feedback loop between effectors and sensors that does not involve behavior. Rather, it is completely internal to the organism and will therefore not be discussed further in this paper.

b. *Acquisitory behavior* is a part of behavior produced to improve the acquisition of information through the sense organs. It closes a feedback loop that involves movements of the organism but normally no changes caused to the environment. Examples include eye movements, active vision, etc.

c. *Interactions with the environment* make up the most complex feedback loop, involving actions that change the environment under sensor control. This includes interactions with other living beings, such as social behavior and communication.

The action–perception view of cognitive brain functions differs in a number of ways from the more traditional one, which is based on the notion of "thinking". First and
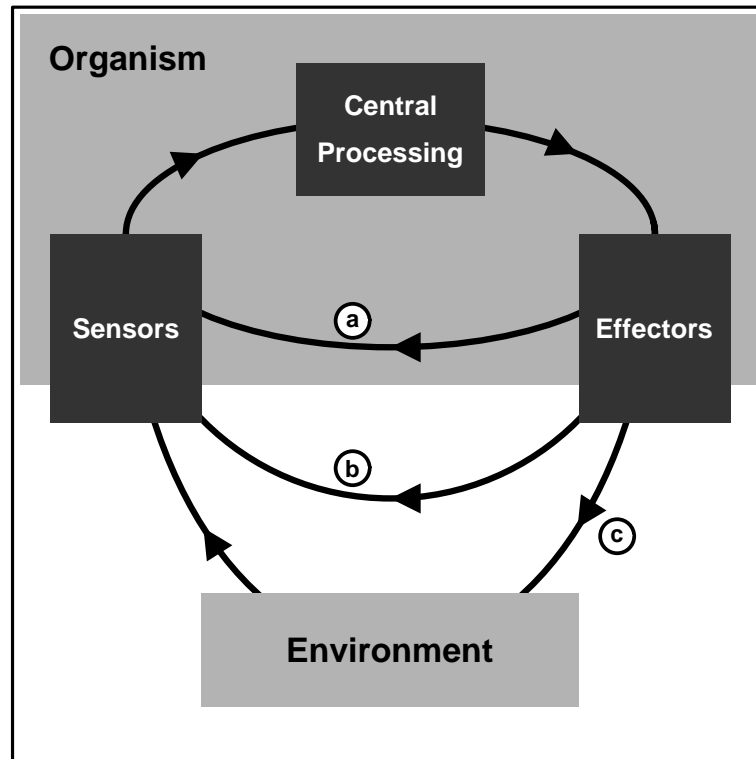
Figure 1: Interaction of an organism's sensors and effectors with each other and with the environment. **a.** Internal regulation or homoeostasis, e.g., of body temperature, blood pressure, etc. **b.** Acquisitory behavior such as eye–movement is a direct feedback path bypassing the environment. **c.** The action–perception cycle proper involves changes to the environment and the monitoring of these changes via the senses.

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foremost, it focusses on the functional benefits of cognition, i.e. on the evolutionary advantages they may offer to their bearer; for an instructive example concerning the question of consciousness see Povinelli and Preuss (1995). This implies that action–perception competences are considered as traits, or units of evolutionary adaptation.

A second focus of the action–perception concept of cognition is the notion of information, first of all in the sense of an "informational coupling" (Tembrock 1992) between the organism and its environment. The implied notion of information is more complex than the definition developed in the theory of (technical) data transmission (Shannon 1948, Cover and Thomas 1991) , as will be discussed later. There have been few attempts to formalize this coupling. Von Uexküll (1956) introduced the distinction between the outside world (*Außenwelt*) and the environment (*Umwelt*), i.e., that part of the outside world with which an organism can actually interact. To do justice to the fact that objects are not simply "recognized" by an organism but actually trigger behaviors that relate to or make use of this object, Gibson (1979) developed his notion of the "affordances" of objects.

This paper discusses a number of modelling approaches to cognitive brain function. There are transitional cases between non–cognitive and cognitive behaviors and I will

not worry too much about the distinction. Clear cases of cognitive behavior are characterized by the possibility of planning and choice between alternative actions. They require some kind of mental representation in which planning can be done.

## 1.2 Types of Models and Explanation

Broadly, we can distinguish three types of theoretical approaches, which are not mutually exclusive: (i) neural networks as theories of signal flow, (ii) computational theories based on the notion of information processing, and (iii) closed loop theories that apply control theory to behavior. These approaches relate to different parts of the action–perception circle and are most useful in relation to different experimental paradigms:

**Signal processing and neural network models** describe the signal flow in the nervous system and its plasticity and adaptation. They offer reductionist explanations of how the sensors, effectors, and central nervous systems work. Such models are most useful in (single–cell) neurophysiology, where they can be applied to experimental findings such as receptive field structure or sensory–motor transformations (Arbib 1995).

**Computational theories** focus on the computation necessary to recover information from sensory data or to plan patterns of motor activity that will result in a desired movement ("inverse kinematics"). Starting from some goal that an organism might have, such as reconstructing the distance and three–dimensional shape of objects, the theory describes whether and how this goal can be achieved using the data available. Computational theories address questions like "Is it possible to determine the speed and direction of egomotion from optic flow pattern?" Since computational theories concern competences, not mechanisms, they are most useful in the analysis of behavioral and psychophysical performance (Marr 1982), as well as of the resulting evolutionary fitness (Dusenbery 1992).

**Behavior in closed loop.** Biological cybernetics has long studied behaviors in closed loop, mostly in control or servoing situations, such as course control in flying insects. Biocybernetics and neuroethology combine reductionist explanations in terms of neural networks with the purpose–oriented explanations provided by computational theories. Models involving internal representations and sophisticated forms of learning, however, have only recently begun to become available.

It should be stressed at this point that biological science has to seek two types of explanations. The first is the reductionist type shared with physics; it is reflected in neural network models. The second, purpose–oriented or evolutionary type, however, is just as important: why does an organism need to get a certain piece of information from its environment and how can it achieve this task? This type of explanation is covered by computational theory, but only on a small scale. For instance, computational theory states that the perception of stereoscopic depth requires the determination of binocular disparities. The larger question of what type of depth information is used and for what

behavior, has to be answered on another level, i.e., based on the fitness value of this competence.[1]

# 2    Examples

In this section, I give examples of different modelling purposes and the associated types of insight or explanation. As always, models have to be adjusted to the question that is to be answered. Levels of complexity range from phenomenological descriptions as a prerequisite of proper modelling to the self–organization of behavior.  Not all of them deal with cognition in a strict sense. However, the examples illustrate modelling techniques that can be useful in modelling cognition proper as well.

Clearly, in this discussion I do not claim to give a complete review of modelling approaches. Rather, I focus on some instructive examples. For more comprehensive sources to modelling approaches in neurobiology, the reader is referred to Arbib (1995), Gazzaniga (1995) or Landy and Movshon (1991).

## 2.1    Phenomenological models

This section is concerned with examples of casting data into mathematical descriptions. This is a subject related to descriptive statistics and function fitting.  The examples presented here, however, are rather more complicated.  The underlying idea is that appropriate mathematical descriptions of data facilitate a deeper understanding of the mechanisms involved. We mention two examples, concerning quantitative anatomy and the entire action–perception loop.

**Quantitative Anatomy.**   Anatomical data about the nervous system is increasing at a rapid pace, calling for structured descriptions and data bases.  These can be useful just to organize the data, but may also lead to more realistic neural network models.  One recent example of quantitative anatomy is the analysis of the connectivity of cortical areas presented by Young et al. (1995).  They applied a multi–dimensional scaling technique to anatomical connectivity data and found that primate visual cortical areas are organized in two clusters broadly in line with the well–known dorsal and ventral processing streams.  Other examples of quantitative anatomy include mapping functions describing retinotopic organization of the visual cortex (Schwartz 1980, Mallot 1985) or the modelling of dendritic arborizations by Markov chains (Schierwagen 1988).

**Dynamics of action–perception coupling.**   The dynamics of the coupling of action and perception can be modelled with ordinary differential equations (e.g., Schöner 1991).  For example, if a subject is standing in front of a periodically moving wall, a postural oscillation can be observed that is dynamically coupled to the movement of the wall. This coupling can be studied by varying or disturbing the oscillation of the wall and measuring the subject's reactions.  Using a differential equation to describe

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[1]Following Tinbergen's famous introduction to his 1951 book "The Study of Instinct", there are actually four types of explanation sought in behavioral biology.  These are physiology, ontogeny, phylogeny, and ecology.

the coupling is purely phenomenological, i.e., it does not imply mechanisms for the perception of the wall's movement or for the generation of the postural sway. A clean description of the data, however, is needed if possible mechanisms are to be inferred.

The notion of dynamic coupling between input and output has been applied mostly to periodic phenomena such as oscillating rooms, gaits, or the tapping of a finger in response to acoustically presented rhythms. More recently, it is also implemented in autonomous robots (e.g., Beer 1995).

## 2.2    Receptive Fields

The most important coding scheme in the nervous system is "labelled line coding". Information about a stimulus is represented by the specificities of the neurons reacting to it, rather than by properties of the excitation itself (amplitude, repetition rate, etc.). The specificities of a neuron, i.e. the set of stimuli it reacts to, can be thought of as a "label". This label is called the neuron's receptive field.

At least in primary sensory areas, the excitation of neurons usually depends strongly on the position of the stimulus in the visual field. This dependence can be described by a spatio–temporal weighting function $\varphi$ specifying the contribution of each stimulus point to the neuron's activity by a linear summation of the form:

$$e(t) = \int_{-\infty}^{t} \int \varphi(\mathbf{x}, t - t')s(\mathbf{x}, t')d\mathbf{x}dt'. \tag{1}$$

Here, $e$ denotes the excitation of the neuron and $s$ is the stimulus, e.g., a spatio–temporal image intensity. The weighting function $\varphi$ is often modelled by a Gaussian, differences of Gaussians, or Gabor–functions (see von Seelen 1970, Adelson and Bergen 1991, Mallot and Giannakopoulos 1996). While the excitation is always a scalar entity, both receptive field and stimulus function can be more complicated. In the analysis of optic flow, for example, two–dimensional vector fields of local motions are considered as input. In this case, neurons have been found that are specific to large patterns of velocity vectors corresponding to specific motions of the observer (Krapp and Hengstenberg 1996, Lappe et al. 1996). Let us denote the current velocity field (sensory input) as $\mathbf{v}(\mathbf{x})$ and the expected velocity field for some egomotion as $\Phi(\mathbf{x})$. A receptive field selective for that egomotion can be modelled by the equation

$$e = \int (\Phi(\mathbf{x}) \cdot \mathbf{v}(\mathbf{x}))d\mathbf{x}, \tag{2}$$

where ($\cdot$) denotes the dot product. Other examples of vector quantities are given by Adelson and Bergen (1991).

A further extension of this idea is the modelling of receptive fields as matched filters for some stimulus property (see Horridge 1992). Using the framework of radial basis functions from approximation theory (Poggio and Girosi 1990), receptive fields can be modelled by equations of the form

$$e = G(\|\mathbf{s} - \mathbf{t}\|). \tag{3}$$

Here, $\mathbf{s}$ is a multi–dimensional feature vector forming the input to the neuron; in Eq. 2, it corresponds to the entire velocity field $\mathbf{v}(\mathbf{x})$. The "center" $\mathbf{t}$ is the stimulus to which
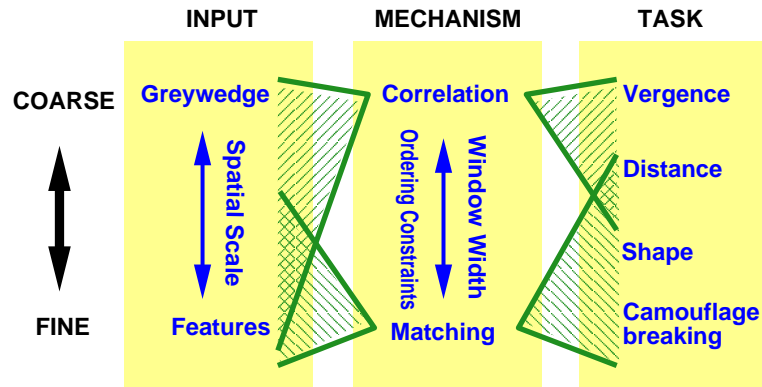
Figure 2: Hypothetical modularization of stereopsis in terms of input, mechanism, and purpose; for explanation see text. From Mallot (in press).

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the neuron is tuned. The scalar function $G$, usually a Gaussian, is a decreasing radial function transforming the difference between $\mathbf{s}$ and $\mathbf{t}$ into the output activity. Matched filter neurons of this type have been used in models of pattern recognition (Poggio and Girosi 1990, Edelman 1993) and optimization (Durbin and Mitchison 1990). If both input and center are normalized by $\|\mathbf{s}\| = \|\mathbf{t}\| = 1$, Eq. 2 becomes a special case of Eq. 3 with $G(x) := 1 - x^2/2$. In the general case, Eq. 3 includes a normalization nonlinearity not present in Eq. 2.

The relation of these receptive field models to behavior is that they characterize highly specialized "matched filters" capable of carrying out what seem to be rather more complicated tasks. Consider for example the computation of heading or self–rotation from optic flow. It might appear that sophisticated reasoning were required to do this. However, a set of matched filters of the form of Eq. 2 tuned to different heading vectors and rotation axes and combined into a population code suffice to do this job (Krapp and Hengstenberg 1996). Similarly, simple networks of tuned neurons (Eq. 3) achieve orientation–invariant object recognition (Poggio and Girosi 1990, Perrett et al. 1992, Logothetis et al. 1994).

## 2.3   Computational Theory and Neural Networks: Stereopsis

An example of the use of computational theories of competence is stereoscopic, or binocular depth perception. Starting with the seminal work of Julesz (1971), this field is part of what led to the formulation of the concepts of "early vision" and "computational theory" (Marr 1976, see also Marr and Poggio 1979). With his random-dot stereograms, Julesz showed that stereoscopic depth can be perceived from disparities (left–right position differences) of single image points even if the image appears to be a meaningless noise–pattern under monocular inspection.

Let us denote the images seen by the left and right eye as $I_l(\mathbf{x})$ and $I_r(\mathbf{x})$, respectively. The problem of stereopsis can then be formulated in the following way: given

these two images, find a (vector–valued) function $\delta(\mathbf{x})$ such that

$$I_l(\mathbf{x} + \frac{1}{2}\delta(\mathbf{x})) \equiv I_r(\mathbf{x} - \frac{1}{2}\delta(\mathbf{x})). \tag{4}$$

The components of $\delta(\mathbf{x})$ are called the horizontal and vertical disparities of the stereogram $(I_l, I_r)$ at point $\mathbf{x}$. The points $\mathbf{x} + \frac{1}{2}\delta(\mathbf{x})$ in the left and $\mathbf{x} - \frac{1}{2}\delta(\mathbf{x})$ in the right image are said to be corresponding points.

One way to solve Eq. 4, and the main focus of early computational theories, is to find individual correspondences. This leads to the so–called correspondence problem of stereopsis, which consists in finding local features in the left and right half-images depicting the same object or texture element in the three–dimensional scene. If such corresponding image features are found, depth can easily be inferred by triangulation. Psychophysical demonstrations of the correspondence problem include the double–nail illusion (Krol and van de Grind 1980) as well as the wallpaper illusion and the related autostereograms (Tyler and Clarke 1990).

The advantage of computational theories for behavioral neuroscience is that they can be readily tested in psychophysical and behavioral experiments. Marr and Poggio (1979), in particular, formulated a list of critical predictions about stereo psychophysics that have been tested in experiments afterwards. These experiments led to some adjustments of the original theory. For example, Marr and Poggio formulated a "uniqueness constraint" that might help solve correspondence. It states that each feature in a stereogramm should participate in one correspondence pair only. In experiments with multiple double–nail stimuli, Weinshall (1991) was able to show that the uniqueness constraint is not strictly enforced in human vision. As a consequence, several depth values can be assigned to a single image point, leading to the perception of transparency. Transparency is not modelled by the formulation of stereopsis given in Eq. 4.

Another prediction of correspondence–based stereopsis is that images must contain salient and localizable features, since disparity is measured as the difference in position of corresponding features. Bülthoff and Mallot (1988) and Arndt et al. (1995) have shown that stereopsis also occurs in images void of localizable features, i.e., in smooth intensity profiles. This result indicates that in addition to a correspondence–based stereo mechanism, whose existence is proven by Julesz' random–dot stereograms, an intensity–based mechanism exists which is able to exploit still–poorer image information. A likely mechanism of intensity–based stereo is inter–ocular correlation (Mallot et al. 1996a), which has been suggested for other aspects of stereo processing as well (Cormack and Riddle 1996, Mallot et al. 1996b). In terms of Eq. 4, this means that the average value of $\delta$ is estimated by minimizing $\int (I_l(\mathbf{x} + \overline{\delta}) - I_r(\mathbf{x} - \overline{\delta}))^2 d\mathbf{x}$ subject to $\overline{\delta}$.

In parallel to the computational theory of stereopsis (for a review see Jenkin et al. 1991), neural network theories of cooperating, disparity–tuned neurons have been developed (Julesz 1971, Marr and Poggio 1976, Blake and Wilson 1991, DeAngelis et al. 1995). These models represent both interocular correlation and correspondence selection, correlation by the excitation of disparity–tuned neurons and correspondence by inhibitory and excitatory interactions between them.

Fig. 2 summarizes these of stereopsis. Input can contain varying amounts of feature information. A correlation mechanism compares the half–images globally without
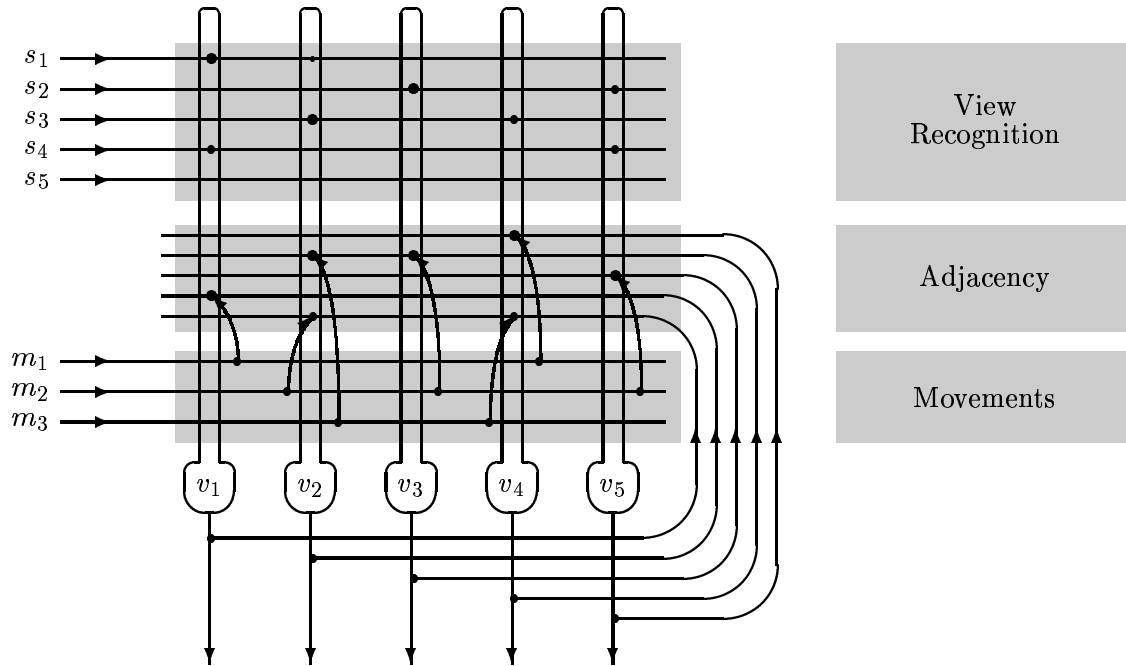
Figure 3: Simple associative network for learning a view–graph representation of spatial configuration. $(s_1, ..., s_5)$: local position information, e.g., view. $(m_1, ..., m_3)$: movement decisions; one and only one $m$–fiber is assumed to be active at all times. $(v_1, ..., v_5)$: view cells; the view cells are activated by sensory input $s$ (view recognition) and by "expectations" generated by the previously active cells and transmitted according to view–graph connectivity (adjacency). These expectations are modulated by the movement cells $m$. For details and simulations see Schölkopf and Mallot (1995).

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explicitly assigning disparities to feature pairs. It yields coarse results as are required for vergence control or overall distance estimates. A correspondence mechanism needs localized image features as its input. By solving the correspondence problem, it computes a depth estimate for every feature pair. Thus, it produces depth information at high resolution as is required for the perception of three–dimensional shape and depth–based image segmentation ("camouflage breaking", Julesz 1988).

In summary, the example of stereopsis shows two things:

- The interaction of psychophysics, computational theory, and neural network implementation in understanding the mechanisms and benefits of a perceptual competence.

- The notion of "evolutionary scaling" where simpler competences (e.g., distance estimates) can be understood as preadaptations for more complicated ones (e.g., camouflage breaking).

## 2.4    Learning and Memory: Spatial Relations

In neural network modelling, learning is often equated with weight dynamics. From a behavioral point of view, learning is change of behavior due to prior experience. The mechanisms of such changes of behavior are as complex as the mechanisms of behavior itself; they need not be restricted to synaptic plasticity.

Some general points concerning the relation of memory and learning will be dicussed later. As an example of behavior–oriented modelling of learning and memory, let us consider spatial memory and cognitive maps.

The two most basic mechanisms of spatial memory are (i) landmark or place recognition and (ii) path integration. Path integration is a working memory task in which the observer's position with respect to some starting point (i.e., the *home vector*) is constantly updated (see Maurer and Séguinot 1995 for review). This involves vector summation of the previous "home" vector and the current displacement vector, or, if both are represented in polar coordinates centered at the observer, trigonometric operations. Let us denote the distance of the home position to the observer and the angle towards home with respect to the observers heading as $(r, \varphi)$. If $v$ is its forward speed (in the direction of heading) and $\omega$ its turning velocity, we obtain the differential equations:

$$\dot{r} = -v \cos \varphi \tag{5}$$

$$\dot{\varphi} = \frac{v}{r} \sin \varphi + \omega, \tag{6}$$

where $\dot{r}$ and $\dot{\varphi}$ denote temporal derivatives. Note that there is no reference to an absolute (compass) direction in Eq. 6.

Neural network models of path integration have been suggested e.g. by Mittelstaedt and Mittelstaedt (1972/73) or Touretzky et al. (1993). Recently, McNaughton et al. (1996) have suggested a different mechanism based on frames of (hippocampal) place–cells representing the animal's environment. The current position is coded by activity in one of these cells. If the animal moves, the peak of acitivity proceeds to the appropriate cell representing the vector sum of the previous position plus the displacement. Clearly, this shift of activity has to be accomplished by appropriate connectivity among the place–cells. As in the trigonometric models, the current position is represented by activity, not by synaptic weights. The model of McNaughton et al. (1996) easily lends itself to integration with other modules of spatial learning, such as landmark recognition.

Sensory information related to the current position is the basis of the second major class of mechanisms in space memory, recognition of places and landmarks. While many models assume that the distance and direction of a set of identifiable landmarks can be directly perceived (e.g., Zipser 1985), a view–based approach based on the raw sensory input seems biologically more plausible. In this case, place recognition is equivalent to the recognition of views (or local position information from any other modality) and can be solved with a perceptron or radial basis function network. Recognition of places or views is not a goal in itself but is used to generate a movement decision appropriate at the recognized place. Views can be used as *guidances* if movements have been associated with them during learning (e.g., "go left at the big oak"). Alternatively, a

position matching some stored view or configuration of landmarks is sought in *visual piloting* (e.g., "go the the place where the oak is left and the pine is right").

Barto and Sutton (1981) describe a simple feed–forward network for associating local position information to movement decisions. After training, the network can be used to find a point defined by any specific combination of the position cues. A more elaborate scheme presented by Cartwright and Collett (1982) computes a movement direction from the comparison of the current view of the environment with a stored one. When performing the movements, the observer will approach the position from which the stored view (snapshot) was taken (visual piloting).

While chains of recognized places can be easily combined into routes, planning and choice between different routes requires more complex knowledge about the configuration of the known places. Schmajuk and Thieme (1992), for example, proposed a neural nework able to learn the connectivity of the places of a maze by exploration. This network, however, is not view–based, but rather relies on invariant identification of places from different viewpoints. A view–based approach to the learning of spatial configurations has been presented by Schölkopf and Mallot (1995), see Fig. 3. It is based on the notion of a view–graph composed of views (as nodes of the graph) and motion decisions (as links). Place recognition is not required, since the view–graph can be shown to be mathematically equivalent to the place–graph and can be used for planning, just like a graph of places. Kuipers and Buyn (1988) have used similar representations of spatial configurations, but with more complex movement behaviors as links between the decision points , for simulated robot navigation.

# 3    Elements of a Theory of Cognitive Behavior

The previous section presented examples of modelling approaches to cognitive behavior have been presented. This section attempts a more systematic account by collecting and discussing building blocks of a theory of cognitive behavior.

## 3.1    Biological Cybernetics and Control

Together with the information–processing paradigm discussed below, the notion of control is the most important paradigm of modelling behavior. Many simple behaviors serve control tasks, i.e. the maintenance of a steady state in a varying environment. The mathematical theory of control and feedback is well developed and has been successfully applied to a wide variety of behaviors, including flight stabilization in flies (see Egelhaaf et al. 1988) and eye movements in mammals (for review, see van Gisbergen and van Opstal, 1989), etc.

Cybernetic models are usually data flow models with a minimum of internal representation. It is therefore not clear how useful they are in the modelling of *cognitive* behavior. On the other hand, as has been convincingly demonstrated by Braitenberg (1984), seemingly complex behavior may in fact be produced by very simple mechanisms including feedback. The strong contribution that biological cybernetics can make to the study of cognitive behavior lies in the idea of finding *minimal* ("insect like") mechanisms for a given behavior, if at all possible. This does not mean that the existence

Abb. 98. Zentrenhierarchie des Hauptinstinkts Fortpflanzungsverhalten des Stichlingsmännchens. Erklärung im Text
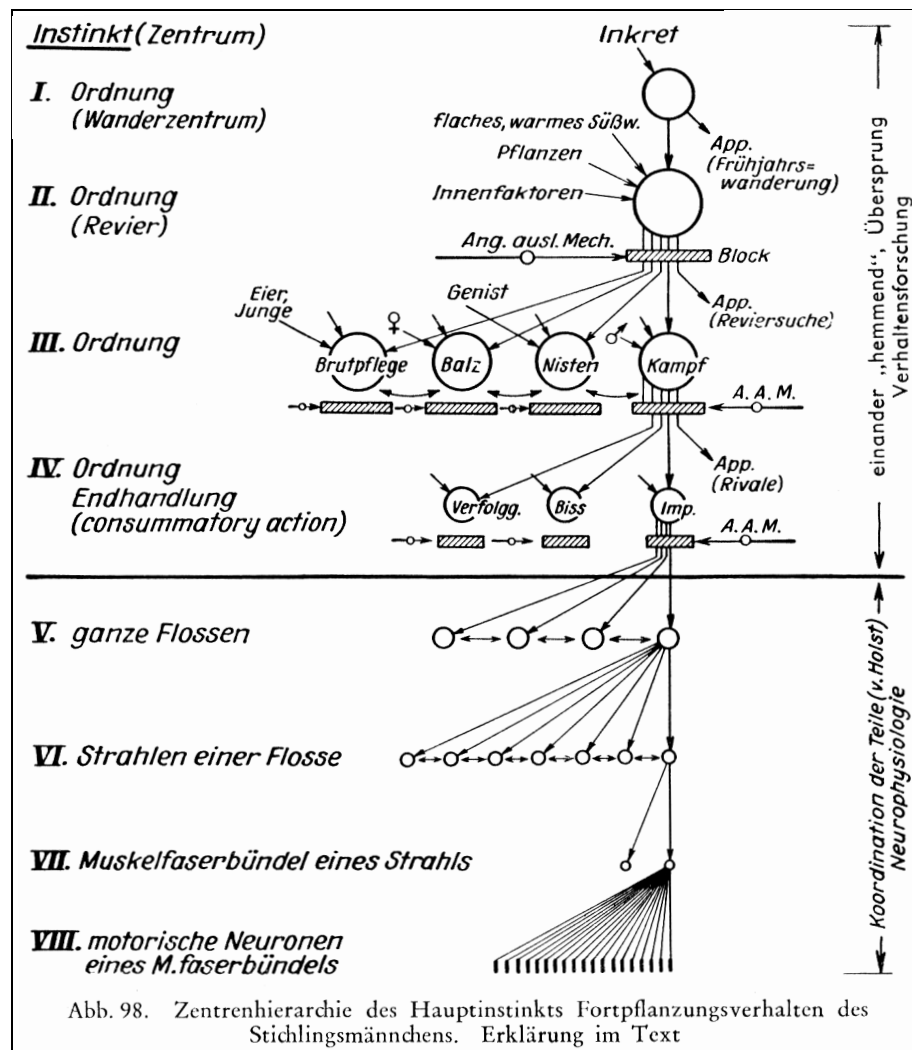
Figure 4: Modularization of mating behavior in a fish. From Tinbergen (1951). The version of the figure reproduced here is from the 1952 German translation by O. Koehler; it has been chosen since it is more elaborate than the original. The caption reads: *Hierarchy of centers of the main instinct reproductive behavior of the male stickleback. For explanations see text.*

of more complex mechanisms and representations should be denied; rather, the level of behavioral complexity at which they become inevitable should be determined.

## 3.2 System Architecture and the Evolutionary Scaling of Modules

An important issue of a theory of behavior is the segmenting or decomposing the behavioral repertoire into modules. As Fodor (1983) pointed out, this can be done along two dimensions: One way is to start with modules for computation steps that can exchange their respective results and can be used in many different behavioral contexts,

whenever a certain computation is useful. This type of computation–oriented or "horizontal" modularization is economical in the sense that any piece of information, once retrieved, is then aviable to all subsystems that may want to use it (cf. "principle of least commitment", Marr 1982). The problem with this approach is that a complete behavior can only be implemented after all required computation modules are operating. Alternatively, modularization can be behavior–oriented. In this case, the system consists of a set of channels or vertical modules, each starting with a sensor and ending with some effector. The information processing is then instrinsic to each channel and exchange between the channels is not generally possible. The action–perception channels are reminiscent of the notion of instincts from behavioral biology (e.g., Tinbergen 1951).

In terms of evolution, behavior–oriented segmentation is much more likely to emerge than the computation–oriented type. Of course, this basic distinction is oversimplified. In reality, a behavior can often be decomposed into a hierarchy of sub–behaviors. At the lowest level, sub–behaviors such as muscle contraction or eye–movements may in fact be used by various, even conflicting large–scale behaviors, much as is stated in Marr's "principle of least commitment". At higher levels of animal behavior, the principle of least commitment does not hold. For example, visual information about the shape of an object can be present in one behavioral context, but not in another (e.g., Goodale et al. 1994). This is an example of a double dissociation, the technical term for violations of the principle of least commitment in neuropsychology.

Behavioral biology has worked out the hierarchical decomposition of behaviors in considerable detail (for an early example, see Tinbergen's 1951 book and Fig. 4). More recently, similar schemes have been invented and implemented in robots, such as the subsumption architecture, a special type of hierarchical breakdown of sub–behaviors (Brooks 1986).

A related aspect of module architecture is "evolutionary scaling". Behavioral competences, like any other trait in evolution, build on simpler predecessors that may have been used for less sophisticated versions of the same competence or in completely different contexts. The modularization of neural information–processing should thus reflect its evolutionary history. By this principle, certain architectures are more likely than others, and system analysis may be simplified by taking this into account. An example of evolutionary scaling in the case of stereovision has been discussed in Section 2.3. An attempt to apply this idea to autonomous robots has been presented by von Seelen et al. (1995).

## 3.3  Cognitive Competences as Adaptations

Behavioral ecology studies the fitness value of behaviors by balancing energy investments and reproductional success of a species as a function of such behaviors (Krebs and Davies 1993). It is not concerned with the mechanisms of behavior, but rather with their relevance in interaction with the environment.

As long as only one species with a homogeneous gene pool is concerned, mathematical models can be based on the notion of a fitness landscape (e.g., Weinberger and Stadler 1993), i.e., a function assigning a fitness value to each possible genome. If such a potential function exists, adaptation can be modelled as hill–climbing on the
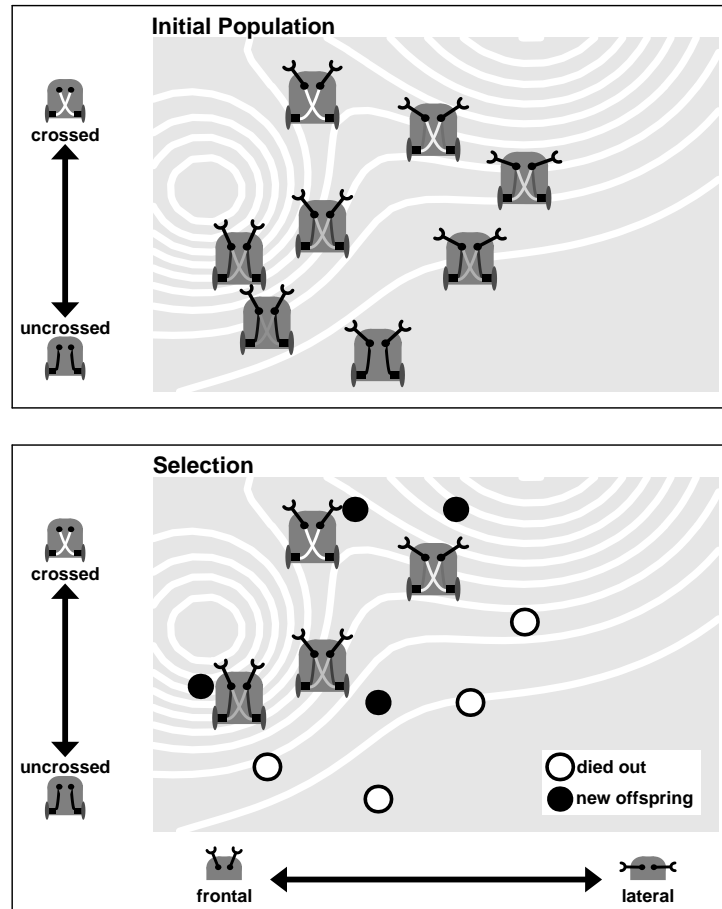
Figure 5: Simple example of simulated evolution for the joint optimization of two traits (sensorimotor coupling: crossed or uncrossed; sensor direction: frontal or lateral). The corresponding hypothetical fitness landscape is visualized by its contour lines. At each iteration, a population of individuals with some variance is simulated and fitness values are determined. In the selection phase, the individuals with lower fitness are removed while the others reproduce with some new variation or recombination. As a result, the whole population moves upward in the fitness landscape.

potential implemented as combinatorial optimization. Genetic algorithms (e.g., Forrest 1993) provide one powerful means to do this (see Fig. 5). The specification of the fitness function in terms of the genome requires extensive assumptions on coding or gene expression. This can be partially avoided by choosing higher–level parametrizations of the possible phenotypes and consequently optimizing these continuous parameters. This technique is known as evolutionary optimization. Another special choice of coding is used in genetic programming, i.e., the combinatorial optimization of the performance of computer programs written in some formal programming language (for an application to animal behavior, see Koza et al. 1992).

Most traits are not evolved as an adaptation to an unchanging environment, but

in a process of co–evolution with a variety of other species or populations evolving simultaneously. In this situation, no fitness surfaces exist. Adaptation then becomes a local, or micro–evolutionary concept, which still drives evolution but can no longer be used to predict long–term trends. Mathematical techniques pf modelling co–evolution include game–theory, genetic algorithms, and cellular automata.

A comprehensive review of simulated evolution is beyond the scope of this paper. What is important in the present context is that genetic algorithms provide a powerful strategy for the self–organization of complex systems. They may thus prove to be a useful tool in studying system architecture and evolutionary scaling (see also Section 4.1 below).

## 3.4   Learning and Memory

In recent years, much progress has been made in the neuropsychology of memory (see, for example, Squire 1987 and the reviews in Gazzaniga 1995). Here, I will briefly discuss the distinction between working, procedural, and declarative memory and try to relate it to the behavior–oriented view of cognition. This distinction is also one of the best examples of the modularization of cognition.

Excepting possibly reflexes, all behavior involves memory of some kind. In the simplest case, i.e. working memory, information required for the continuity of an ongoing action is stored; presumably, this is done in the sustained activity of some neuron or circuit. A well–studied example is the delayed release of saccadic eye–movement after some visual cue. In the time gap between cue presentation and the go–signal for the saccade, the position of the cue is stored in the ongoing activity of a neuron specific to this position (Fuster 1995). No special learning mechanism is required for this since information is simply maintained for a while, without separate mechanisms for storage and recall. Another example of working memory studied in animal navigation is path integration (cf. Section 2.4), which enables animals to return straight to a starting point even after highly curved excursions. Working memory is a "buffer" in which the current position relative to the starting point is stored and continuously updated.

Procedural memory is a form of long–term memory closely related to behavior itself. Basically, it concerns the tuning of behaviors or motor sequences and the build–up of skills. The resulting behavior is still rather stereotyped, the learned changes lying more in the "parameters" of the behavior than in its basic plan. It is this type of learning that most neural network techniques apply to. Hebbian learning allows the association of one neural activity pattern to another. For example, a fixed relationship between a sensory input and a motor output can be learned in this way. Longer sequences of actions are often learned by reinforcement. Consider two chains of actions serving different tasks; examples are two partially coinciding routes in a maze leading to different goals or climbing a tree first to gain a wide view and again to harvest fruit. If one of these sequences is mastered, it would be useful to transfer the common part to the other action sequence. This, however, it not possible in reinforcement learning, since no reinforcement was generated for task B when learning task A. A general limitation of procedural learning seems to lie in this lack of knowledge transfer between behaviors serving different goals.

Flexibility of behavior, that is planning and active choice between alternatives, re-

Table 1: Memory and learning in a behavioral perspective

| Memory | working (short–term) | procedural ("online") | declarative ("offline") |
|---|---|---|---|
| Behavior | all non–reflexive behavior | adaptation of stereotyped behaviors, skills | flexibility, planning and active decision making |
| Learning | retain activity pattern (sensory input etc.) | associate two activity patterns (e.g., sensor to motor) by Hebbian or reinforcement learning | recognize sensory situations and/or learn what to expect from possible actions in current situation; latent learning; instrumental learning |

quires a different form of memory called *declarative.* It contains items that are so to speak "offline" from the production of behavior, such as expectations about what will happen as a consequence of various possible actions (instrumental learning), or recollections of previous experiences (episodic memory). This set–aside storage of declarations (if–then expectations, recollections of events or places, rules, names etc.) can be used as a planning stage for the selection of behaviors. Thus, declarative memory does not in itself produce or modify behavior, as do procedural and working memory, but is used by some third module to make selections amongst possible behaviors.

Table 1 attempts to summarize this comparison of types of behaviors, memory required, and learning mechanisms used.

**Recognition.**    Memory and perception meet in the competence of recognition. This is may be the reason why researchers with a background in machine vision tend to consider recognition the key issue of learning. In fact, theories of machine learning often deal exclusively with the training of pattern classifiers and the statistics of data sets in some feature space. Neural network models of recognition (perceptrons, radial basis function networks) normaly rely on supervised learning, for which biological justifications are hard to find. The behavioral relevance of recognition lies in the selection between different behaviors, e.g., in the case of key–stimuli triggering stereotyped behavioral responses. Psychophysical experiments on recognition normally employ naming tasks, i.e., the behavioral task is to utter the name of the recognized object or person. In experiments involving various behavioral contexts, such as naming and grasping objects, dissociations between the different tasks have been found (Goodale et al. 1994).

## 3.5   Information

The notion of information is central to most modelling approaches in cognitive neurobiology. This is in spite of the fact that, at least in this context, a satisfactory definition of the term is not available. As was mentioned before, the idea is that information is what travels along the arrows in the diagram of the action–perception loop (Fig. 1). We can distinguish three major aspects:

**Quantity.** Measures of the amount of information travelling along a channel or being stored in some memory can be based on mathematical statistics (Shannon 1948, Brillouin 1951; for a modern account see Cover and Thomas 1991). This notion of information is relevant for accessing the effort of transmission or the storage capacity of neural networks (e.g., Palm 1992). It is, however, of little use when studying the relevance of some piece of information for its bearer.

The "informational coupling" between two finite–state systems can be described by mutual information (Marko 1966, Cover and Thomas 1991). Mutual information measures the amount by which the uncertainty about the next state of one system is reduced when the state of the other system is known. When applying this to two communicating animals (e.g., Mayer 1970), treating the communicative behaviors as the states, mutual information can be used to quantify concepts such as the intensity of communication (strength of informational coupling). Related assymmetrical measures, such as conditional entropy, may be used to determine the direction of information flow, i.e., which one of two speakers dominates.

An important issue dealt with in the statistical theory of information is coding, i.e. the rules by which information is represented in neural activity patterns. As an extension of the classic idea of labelled line coding (see Section 2.2), a theory of population coding has been developed that seems well suited to describe the representation of information in neural systems. For review see Snippe (1996).

**Quality and Meaning.** The amount of information can be quantified without referring to the meaning or content of the data or to their relevance in a behavioral context. When studying content and relevance, the specifics of the behavior and the environment, that is to say the "informational needs" of an animal have to be considered. This is the subject of sensory ecology in the sense of Dusenbery (1992) and computational theory of competence (Marr 1982).

**Information processing.** That the brain processes information does not imply that this is done by symbol manipulation. In particular, neural activities are not *arbitrary* representations of sensed stimuli or intended actions. Rather, similar stimuli are usually represented by similar patterns of activity, leading to an "isomorphic" representation, as discussed by von Seelen and Mallot (1988). Clearly, the brain does not run programs in a computer science sense and there is no simple notion of variable binding. This isomorphism between the representation and the represented is also reflected in population coding, as mentioned above. It results in robustness against errors and graceful degradation.

Analogous or isomorphic mechanisms of information processing in the brain are the subject of the whole field of neural networks research. It is beyond the scope of the present paper to review this work. Instead, I would like to mention some elementary neural operations on which information processing in the brain may be based. On the level of the biophysics of single cells (see Koch and Poggio 1987), these include spatio–temporal summation in dendritic trees, detection of coincident incoming activity, thresholding and nonlinear interactions between various inputs, as well as various forms of plasticity, most notably long–term potentiation. On the network level, spatio–temporal filtering in continuous stimulus representations or topographic maps

(e.g., lateral inhibition, motion energy filters) is one of the most powerful operations. Nonlinear dynamics including correlation, winner–take–all mechanisms or propagating activity volleys play also an important role in information processing.

# 4    Experimental Methods

While this paper is mostly concerned with models, I would like to briefly discuss two recently developed methods that allow novel experiments on the complete action–perception circle.

## 4.1    Bio–Robots

An autonomous robot in a real environment is a powerful model of a behaving organism. Braitenberg (1984) has stressed the usefulness of robotics as a synthetic approach to behavior. Models of behavior that have been postulated to account for experimental data can be tested very rigourously by implementing them in a real–world robot and observing the resulting behavior in a natural environment; for an instructive example, see Webb (1995). The advantages of the hardware implementation over a pure simulation are:

1. Real–world robots operate in closed loop. In simulations, it is virtually impossible to foresee and model the stimulus combinations arising in natural complex environments.

2. The robustness of the hypothesized mechanisms is assessed simultaneously.

3. In simulations, it is tempting to take certain pieces or steps of the computation for granted, using their result without caring how the system could acquire this information. In a hardware implementation, such shortcuts are much more obvious and easier to avoid.

   Recent work on biomorphic robots focusses on the four topics mentioned below. It appears that, at the time being, the flow of information is directed mainly from biology to engineering. However, with the development of technical systems implementing biological principles, more rigorous testing and simulations of these principles becomes possible. This will also lead to a deeper understanding of the biological mechanisms.

**Active vision.**    Vision is in many respects an active process (Bajcsy 1988, Ballard 1991, Blake and Yuille 1992). Most notably, movements of eye and head simplify a number of otherwise complicated problems in the computational theory of vision. Visually tracking a moving object, for example, simplifies recognition of that object since it is now at rest on the image plane. At the same time, it allows a division of labor between different parts of the retina, since expected image motion will be small in the center and larger in the periphery. Among the large number of active camera heads (see Murray et al., 1992, for review), the work of Ahuja and Abbott (1993) and Krotkov and Bajcsy (1993) has addressed the interaction of focus, vergence, and disparity cues.

**Architecture and evolutionary scaling.** Biomorphic robots start from simple tasks to be performed in a complex world, rather than from complex tasks in specialized environments (Brooks 1986). Therefore, their behavioral competences are built "vertically", i.e., from sensors to effectors with the least possible number of computation steps in between. This strategy results in special purpose solutions such as 360° vision for optic flow analysis (Chahl and Srinivasan, 1996) or inverse perspective mapping for obstacle avoidance (Mallot et al. 1989, von Seelen et al. 1996, Košecka et al. 1995). Building on these special solutions to implement more sophisticated competences, an evolutionary architecture of mechanisms and competences is created. Of course, in order for this architecture to work, the sequence in which the different competences are built has to be carefully selected.

**Social behavior and cooperation.** What is the global behavior of a group resulting from various individual behaviors? For rather simple behaviors, this question has long been investigated using the methods of statistics and game theory (see Stickland et al. 1995 for an instructive example). In artificial life, simulated agents are used to study the relation of individual and group behavior, e.g. in swarm building (Reynolds 1993). Actual robots that cooperate in more complex tasks such as collecting items have been studied, e.g., by Kube and Zhang (1994). Again, the advantage of such hardware simulations lies in the occurrence of unforeseen problems and solutions.

**Self–organization.** Genetic and evolutionary algorithms (see Forrest 1993) are a powerful method for self–organizing robot control structures; see Section 3.3 for a brief explanation. Cliff et al. (1993) have adapted an artificial neural network controlling the movements of a Khepera robot to simple vision tasks such as wall–following and homing. Huber et al. (1996) have studied an opto–kinetic response behavior evolved by a robot with two visual motion detectors navigating in a textured corridor.

## 4.2 Virtual Reality

The second methodological development relevant to the study of cognitive behavior is virtual reality or interactive computer graphics as a tool for behavioral experiments (Fig. 6). In standard psychophysical experiments (marked PP in Fig. 6), behavior is usually very simple, such as hitting a button, etc. At the same time, the stimuli used are rather unrealistic, normally being selected for theoretical reasons rather than for their importance or salience in natural environments. Using more elaborate computer graphics (CG), more realistic stimuli can be generated, combining multiple visual cues with the high controllability required for experimenting. The action–perception loop can be closed by interactive computer graphics and, adding other sensory modalities, by virtual reality (VR). Thus, virtual reality technology allows us to carry out open and closed loop experiments with human subjects. Until now, similar experiments have been possible only with much smaller animals. Experiments in the real world (RW) are, of course, still necessary as controls. Comparisons between VR experiments and real world controls have been presented ,e.g., by May et al. (1995). VR experiments on spatial learning have been carried out, e.g., by Aginsky et al. (1996) and Gillner and Mallot (1997).
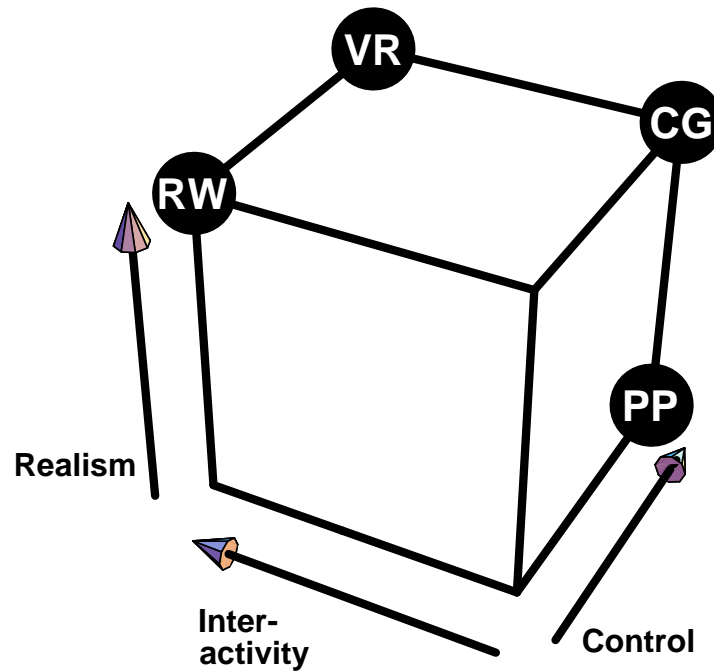
Figure 6: Characterization of experimental methods for the study of visual perception and action in terms of stimulus controllability, realism, and the subject's possibility to interact. PP: classical psychophysics using simple stimuli. CG: computer graphics psychophysics. VR: virtual reality or interactive computer graphics. RM: real world experiments.

## 5   Conclusion

Theoretical models of complex behavior are still in their infancy. At this time, neither a general theory nor a satisfactory catalogue of methods for experiments and modeling can be provided. In this paper, I tried to collect a number of useful ideas and instructive examples on which future research can built. In my view, the key issues are:

- Architecture and evolutionary scaling of modules,

- The nature of informational coupling in the action–perception cycle,

- Bio–robotics and virtual reality as new experimental techniques.

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