

Representations in natural and artificial systems

Groupreport, ZiF, 8.-12. March 1998

(Zeitschrift für Naturforschung, 1998, in press)

Peter König¹, Emilio Bizzi², Neil Burgess³, Nikolas Franceschini⁴, Mike Kilgard⁵, Mike Oram⁶, Gerhard Sagerer⁷, Christian Scheier⁸

¹Institute of Neuroinformatics, Zürich, Switzerland, ²Massachusetts Institute of Technology, Cambridge, USA, ³University College London, London, United Kingdom, ⁴CNRS/L.N.B., Marseille, France, ⁵UCSF, San Francisco, USA, ⁶NIMH/NIH, Bethesda, USA, ⁷Technische Fakultät, Universität Bielefeld, Deutschland, ⁸University Zürich, Zürich, Switzerland

1 Introduction and the agenda of the group discussions.

The concept of representation has proven useful in the study of nervous, computational and robotic systems. Examples of representation from neuroscience include descriptions of the visual system, where the activity of neurons reflect properties of the visual environment (e.g. Hubel and Wiesel 1968, Martin, 1994). Central brain areas contain representations: for example neurons in the hippocampus are influenced in a predictable fashion by the position of the animal (O'Keefe and Nadel 1978). In the motor system the activity of neurons relates to the activation of muscles and coordinate movement (e.g. Georgopoulos et al., 1982). The concept of a neural representation covers a wide range of phenomena, from the relation between sensory inputs and the environment through neural codes of an organisms location within the environment to the relationship between neural activity and motor actions allowing interaction with the environment. Issues of representation are also found in computational science and robotics. For example, computational models of information processing for categorization of inputs can be broadly divided into two classes: those that postulate a single “object-centred” representation of each category or object and those that postulate multiple units to represent each category or object (c.f. Bülthoff et al., 1995; Biederman and Kalocsai, 1997).

Questions about more abstract aspects of representations include the basis of the representation: Is a representation a holistic, “all knowing” entity or a “subjective” entity based on the experiences unique to the individual? Integral to the concept of representation are questions of how the representation was formed: How is a representation maintained? To what extent is a representation labile? What factors induce change in the representation?. In this group report we draw together current views of researchers from neuroscience, computational science and robotics regarding some of these issues. We take concrete examples based on the work of the participants and note areas of

agreement and disagreement. It should be noted at the outset that the level of agreement was high. Each member had made independently subtle shifts from the traditional views of their respective areas, leading to the resolution of previously disparate opinions between different disciplines. The consensus of opinion concerning representations suggests that rapid progress will be possible in the future.

To orient the reader, one of the major themes that quickly became clear during the discussions was that the use of representation in a passive sense was inconsistent with the available data. The interaction of a representation with the input and output structures of that representation were important and fit data in a more consistent manner than regarding representations as entities independent of the organism and its environment. These structures formed a closed loop: environment interacting with sensory representations, sensory representations interacting with representations of action and action interacting with the environment, which of course leads back to interaction with the sensory representations. The importance of this closed loop was determined by researchers of biological systems and researchers of artificial systems, so may be a general property of representations. Neil Burgess's examination of the representation of "Where am I?" in the place cells of the rat hippocampus provides an intuitive introduction to representations in biological systems. Studies of neural selectivity in primate temporal lobe (Mike Oram) suggest that representations of "What is that?" may be intimately tied to "What do I do with it?" Emillo Bizzi shows that representations of motor action allow for the learning of "How do I interact with it?" Evidence that interactions occur between different neural representations and that these interactions may be specifically related to behaviour is presented by Peter König. At this point we briefly take a diversion from examples of representations and consider, without resolution, the signal used by neural representations to solve the "binding problem". Studies of the fly (Nicolas Franceschini), complete with a robotic demonstration, indicate that a representation can be very transient based on the interaction of the agent (fly or robot) with its environment. Gerhard Sagerer examines representations in artificial systems and argues that appropriate representations meeting computational demands should be formed from "experience" and be situated in the present context, rather than from a complete set of rules placed within the system. Studies from robotics (Christian Scheier) show that the problem of object classification can be reduced and be transformed into a tractable form if the agent (robot) interacts with the environment. Finally Mike Kilgard describes work from the rat auditory cortex which demonstrates the impact that the environment and behaviourally relevant signals can have on representations and how representations can change in such a way as to allow the agent to meet new functional demands placed on the agent by the environment.

2 Natures of representations.

2.1 The representation of space in the rat hippocampus. (presented by Neil Burgess)

Place cells in the hippocampus of freely-moving rats tend to fire at a high rate only when the rat is in a particular portion of its environment and lesion of the rat's hippocampus impair its navigational ability (O'Keefe and Nadel, 1978). Place cell firing also shows interesting temporal aspects. The time of firing of spikes relative to the phase of the theta rhythm in the EEG appears to encode the location of the rat with greater precision than the firing rate alone (O'Keefe and Recce, 1993). Another clue to the neural basis of spatial representation comes from 'head-direction' cells which show the complementary pattern of spatial firing to place cells. These cells are found near to the hippocampus and code for the direction of the rat's head, irrespective of its location (Taube et al., 1990). However, it is still not clear what inputs drive the firing of these cells, or how their firing generates behaviour.

What is the nature of the interaction with structures upstream? In simple walled environments it seems likely that the rat uses the allocentric direction of each wall to distinguish it from the next, and that the distance from two or more of the walls determines the firing rate of each place cell (O'Keefe and Burgess, 1996). The role of distant visual cues may relate to the rat's internal sense of direction, and thus, indirectly to place cell firing. Local cues, distant visual cues and the rat's internal sense of orientation (possibly vestibular and proprioceptive in origin) all appear to contribute to the rat's internal sense of direction, and can each be systematically manipulated (Jeffery et al., 1997). The information relating to the distances probably also comes via a mixture of visual, olfactory, auditory, tactile and internal information, determined by what is available in a particular environment (e.g. Hill and Best, 1981).

What is the nature of the representation, what is its use, and how does it interact with structures downstream? The place cell representation of space is intriguing in the sense that it appears to reflect the rat's current location, independent of where it needs to go (Speakman and O'Keefe, 1990). How could this be useful? The simplest model (see Burgess et al., 1997) would postulate sets of cells downstream of the place cells that store the place cell representation at goal locations (e.g. by making strong synaptic connections from those place cells active at the goal location). This would allow the rat to return to a goal location by moving so as to maximise the similarity between the current place cell representation and the stored one. Such a simple 'snapshot' type

model has limitations, and more sophisticated models have been constructed by making use of the head direction cells and the temporal coding of information in place cell firing, and tested on a mobile robot (see Burgess et al., 1994; 1997).

What is the relation to human hippocampal function? Selective damage to the human hippocampus appears to specifically impair the recall of events, often sparing the recognition of stimuli or pairs of stimuli (see e.g. Vargha-Khadem et al., 1997). How could this relate to the apparently spatial role of the hippocampus in rats? One suggestion is that recall of events is aided by memory for the context in which they occurred (e.g. Mayes et al., 1985). One way to reconcile the apparent roles of the hippocampus in rats and humans is to suppose that it stores the spatial context of events, and that this is an important recall cue in human episodic memory. More general arguments also suggest that allocentric (world-centred) representations might be more appropriate for the long term storage of object locations than egocentric representations (centred on the body, or a part of it), since the position of the body will tend to change over time. Alternatively, short term storage of the location of an object, between its perception and an immediate action upon it, might best use an egocentric representation since the location of the object relative to the effector will be needed for control of the action. The data indicating that the hippocampus supports allocentric representations (cf. egocentric representations in parietal cortex) can thus also be related to the data indicating hippocampal involvement in long-term episodic memory and parietal involvement in short term memory (see Burgess et al., this volume, for further discussion of this point).

2.2 Viewer centered representations in primate. (presented by Mike Oram)

Properties of the representation of objects in temporal lobe cortices indicate that, at the single cell level, processing of visual inputs occurs predominantly in a viewer-centred framework. Responses of temporal lobe neurons are in general dependent on the particular instance in which the object is seen. For example, neural responses of individual cells are contingent on the sight of the stationary head and body in a particular view (e.g. facing to the left of the viewer, Perrett et al., 1982; 1991, Desimone et al., 1984), orientation (upright) and size (Wachsmuth and Perrett, 1995; 1997). Other visual transformations (i.e. part occlusion and direction of ambient lighting, Wachsmuth et al., 1994, Hietanen et al., 1992) do not overall have such profound effects on the responses of neurons in the superior temporal sulcus (STS). Work from Tanaka, Logothetis and Miyashita suggests that the viewer-centred properties of temporal lobe neurons is not particular to neurons selective for the sight of heads and bodies, but reflect more general

aspects of representation in the temporal cortices (e.g. arbitrary wire shapes, fractal patterns, and other abstract visual stimuli, Tanaka et al., 1991; Logothetis et al., 1994; 1995; Miyashita and Chang, 1988; Miyashita et al., 1993). A second population of neurons in STS cortex respond only when the body or body parts are seen in motion (e.g. Perrett et al., 1989; Oram and Perrett, 1994; 1996). Again, these responses are mostly viewer-centered, in that a response is elicited only when a particular combination of view and direction of body motion is seen (e.g. left profile moving left, not left profile moving right nor right profile moving left).

What is the nature of the interaction with structures upstream and downstream? What is the use of the representation? It is suggested that viewer-centered visual processing is useful in enabling appropriate actions to occur, such as social interactions with others (e.g. talking with the person looking at you, not the person facing your left), and interactions between others (Perrett et al., 1995). Interactions with inanimate objects (picking up a knife by the handle, not the blade) may also require detailed representation of the object (Carey et al., 1997). Given the viewer-centered processing in "earlier" visual areas (e.g. the orientation selectivity in V1, V2, V4 and posterior inferotemporal cortices) the viewer centered nature of object representation in STS is not surprising.

The potential relationship between the type of representation of objects (e.g. viewer-centered) and how the organism may interact with those objects was further examined by reference to neurons in the STS which are selective for the sight of particular reaching actions (e.g. Perrett et al., 1989). In particular, examples of cells selectively responsive to moving towards a door from any direction and other cells responsive to the sight of another individual reaching towards and picking up an object were given (i.e. goal-centered). The selectivity of such cells shows that representations of visual stimuli within temporal cortex can be of actions. Rizzolatti and colleagues (Murata et al., 1997) have described cells in motor areas of frontal lobe which show similar visual response selectivities (e.g. picking action) as well as the responsiveness to the motor action when performed by the monkey. The projections from STS to frontal lobes suggest that such cells in motor areas may receive inputs from STS cells similar to those described. Such visual selectivities may be important in the learning of actions and social gestures (Carey et al., 1997). Finally, evidence exists from neuropsychological studies that representations of objects are necessary for interactions with those objects. Milner and Goodale (1993) studied a subject with brain damage resulting from carbon monoxide poisoning. The subject showed severe impairment of object recognition but maintained ability to interact with simple objects. While capable of performing simple object manipulation (e.g. posting a letter), DF was impaired when object manipulation became more complex (e.g. fitting a T shape into an appropriately shaped hole). This

again supports the proposal that the representation of objects in a viewer-centered frame of reference is an integral part of the ability to manipulate those objects appropriately.

2.3 Formation of internal models of motor tasks. (presented by Emilio Bizzi)

The hypothesis is that human subjects learn a new task as a result of repeated exposures to sensory signals coming from their moving limbs and their eyes while they interact with the environment. These repeated sensory signals are funneled to the motor areas of the central nervous system, where signals that activate the muscles are produced.

This iterative process would lead to the establishment of an internal model of the controlled dynamics – the body and its environment – through the gradual change of the synaptic strength of the neurons of cortical and subcortical motor areas. The internal model, according to this view, is embedded in the newly formed connectivity of a group of neurons. The activity of this group of neurons generates the neural impulses necessary for the execution of learned motor tasks. Motor learning and the control of dynamics are thus two facets of the same process.

What is the nature of the interaction with structures upstream? In general, in a visual-motor task, such as reaching with the arm toward a target, the first problem is one of transforming information regarding the target position, as presented in the visual domain, into a force to be applied by the muscles to the skeletal system in order to move the hand. Initially, the solution of this problem involves a set of coordinate transformations. The work of Andersen et al. (1985) suggests that the image of the target is transformed sequentially from retinocentric to a head-centered and finally a body-centered coordinate system.

To specify a limbs trajectory toward a target, the central nervous system must not only locate the position of an object with respect to the body, but also the initial position of the arm. The conventional wisdom is that proprioception provides information about arm configuration to be used in the programming of the arms trajectory.

The task of moving the hand to the target position is an ill-posed problem in the sense that an exact solution might either not be available or not be unique. For instance, if the goal is to move the hand from an initial position to a point in space, then, clearly there are a number of possible hand trajectories that could achieve this goal: the solution of this motor problem is not unique. Even after the central nervous system has chosen a particular path for the hand, its implementation can be achieved with multiple combinations

of joint movements at the shoulder, elbow and wrist – again the solution is not unique. Finally, because there are many muscles around each joint, the net force generated by their activation can be achieved by a variety of combinations of muscles. The situation is even more complex at the level of individual muscles: eventually the nervous system must specify the activation of each motor unit.

What are the implications for the formation of representations? A key feature of the task to which subjects were exposed involved a change in the mechanical environment with which their hand interacted. Because of this change, the internal model of the arm had to adapt to the new dynamics of the environment. In these experiments, subjects grasped the handle of a robot manipulandum – a two degree of freedom, lightweight, low-friction motor with a force-torque transducer mounted on the handles. Two torque motors were mounted on the basis of the robot. The manipulandum was programmed to produce forces upon the hand of the subject as the subject performed reaching movements. These forces were computed as a function of the velocity of the hand. When the manipulandum was producing a force field, there were forces that acted on the hand as it made a movement, effectively changing the dynamics of the arm. The force field initially caused a significant divergence from the trajectory that was normally observed for reaching movements (Shadmehr and Mussa-Ivaldi, 1994).

Through practice, the subjects hand trajectories converged to the trajectory observed before the application of the field. This convergence was gradual but monotonic in all subjects, consistent with an adaptive process whose goal was to compensate for the forces imposed by the field and to return the hands trajectory to that produced before the perturbation.

The subjects recovery of performance is due to learning. In order to investigate the neural changes underlying this type of motor learning, Shadmehr and Mussa-Ivaldi (1994) devised a simple but revealing experimental manipulation. After the training had been established, they removed unexpectedly the force field for the duration of a single hand movement. The resulting trajectories, named aftereffects, were approximately mirror images of those that were observed when the subjects were initially exposed to the force field. The magnitude of these aftereffects increased gradually with the practice period. The emergence of the aftereffects indicates that the central nervous system had composed an internal model of the external force field.

What are the implications for the maintenance of representations? Recently Brashers-Krug et al. (1996) investigated this question by exposing their subjects to perturbing force fields that interfered with the execution of reaching movements. After practicing reaching movements, these subjects were able to compensate for the imposed

forces and were able to guide the cursor accurately to the targets despite the disturbing forces. This group of subjects, which was tested 24 hours later with the same disturbing forces, demonstrated not only retention of the acquired motor skill, but also additional learning. Surprisingly, they performed at a significantly higher level on day 2 than they had on day 1.

A second group of subjects was trained on day one with one pattern of forces (say pattern B) immediately after learning a different pattern (A). Pattern B produced forces in a clockwise direction, but forces in the opposite direction were generated during exposure to pattern A. When this second group of subjects was tested for retention on day 2 on pattern A, Brashers-Krug et al. (1996) found that the subjects did not retain any of the skills that had been learned in A. This phenomenon is known as retrograde interference. Next, Brashers-Krug et al. (1996) investigated whether the susceptibility to retrograde interference decreased with time. They found that retrograde interference decreased monotonically with time as the interval between pattern A and B increased. When 4 hours passed before pattern B was learned, the skill learned during exposure to pattern A was retained – the initial learning had consolidated. What is remarkable in these results is that motor memory is transformed with the passage of time and in the absence of further practice, from an initial fragile state to a more solid state.

What is the nature of the interaction with structures downstream? Recently Bizzi et al. (1991, Giszter et al., 1993) investigated the circuitry of the cortico-spinal pathway and proposed that the spinal cord interneurons are organized in functional modules to produce muscle synergies. They could show that the spinal cord contains circuitry that, when activated, produces precisely balanced contractions in groups of muscles. These synergistic contractions generate forces that direct the limb toward an equilibrium point in space. Furthermore they could show that microstimulation of the lumbar gray resulted in a limited number of force patterns. A number of regions of the spinal cord gray from which the same force pattern was elicited were identified. The simultaneous stimulation of two sites, each generating a force field, results in a force field proportional to the vector sum of the two fields. Vector summation of force fields implies that the complex non-linearities that characterize the interactions both among neurons and between neurons and muscles are in some way eliminated. More importantly, this result has led to a novel hypothesis for explaining movement and posture based on combinations of a few basic elements. The limited force pattern may be viewed as representing an elementary alphabet from which, through superposition, a vast number of movements could be fashioned by impulses conveyed by supraspinal pathways.

Taken together the just described experiments indicate that: First, the internal

model of the disturbing force field develops and effectively cancels the external influence. Second, there is an enhancement of the internal model which does not depend upon practice, but only the mere passage of time. The process of consolidation of the internal model which takes four hours as a minimum and is not dependent upon practice. Third, the primary motor cortex may be viewed not as acting on individual muscles, but on using a limited set of basic force fields as basic building blocks to generate movements.

2.4 Interareal interactions in the visual system. (presented by Peter König)

The representation of visual stimuli by the primary visual cortex might be one of the best studied examples of a neuronal representation of the external environment. Nevertheless, the read out of this representation by neurons in other areas is poorly understood (König et al., 1996). To investigate the coupling between primary visual cortex and cortical areas considered to be downstream the interaction between area 17 (primary visual cortex) and parietal association cortex (area 7) was examined during a visuomotor GO/NO-GO task in the awake cat (Chiang et al., 1997; von Stein et al., 1997). Cats were trained to respond to target stimuli which emerged from a neutral mask, by either pressing a lever (GO) or by continuing to track the target visually (NO-GO). Local field potentials in both areas were recorded with bipolar electrodes, and synchronization within and between cortical columns of each area was assessed by cross-correlation analyses. Recordings during the prestimulus period, used as baseline, were dominated by power in the low frequencies. The mask stimulus elicited a strong evoked potential but only a moderate increase in synchronization between areas 17 and 7. In contrast, the subsequent target stimuli elicited a weak evoked potential but a much greater degree of synchronization both within area 7 and between area 17 and area 7. This increase was strongly dependent on the associated behaviour. Synchronization of both types was most prominent in the middle frequency range (5-20 Hz). While activity in this frequency range is usually associated with behavioural inactivity and lack of attention evidence was obtained that the increased coupling was specific for trials in which the cat was attentive and responded correctly. A surprising result was the effect of the presentation of new visual stimuli. Those surprising stimuli lead to a complete cessation of the coupling in the middle frequency range and to an increase of the synchronization in the gamma frequency band. In conclusion, our results provide direct physiological evidence, that the neuronal activity in primary and higher visual areas can synchronize. Furthermore, in a highly trained paradigm, the coupling is dependend on the behavioural relevance of the stimulus. And finally, the type of interaction as expressed

by the characteristic frequencies of the synchronized oscillatory activity is different for the readout of a overtrained behaviour and the presentation of new stimuli. Thus, the read-out of a cortical representation appears to be specific, reflecting the requirements of the task.

What is the nature of the representation and the relevant variables? In these experiments the activity of cortical neurons has been measured by recording the local field potentials with bipolar electrodes. Do these accurately reflect the unit activity and are they assumed to be causally effective? The origin of the local field potential as measured by intracortical electrodes has not been settled yet. However, experimental as well as theoretical work indicates that it reflects the currents in the apical dendritic trees of pyramidal neurons. Thus, as the bulk of synaptic connectivity is local, it is reasonable to assume that the local field potential reflects unit activity (Gray and Singer, 1989). This, however does not imply causal effects of field potentials on the dynamics of the system. In the present experiments the local field potential is used as an indirect measure of the neuronal activity.

The coupling of neuronal activity in different areas of the visual system occurs predominantly with zero phase lag (König et al., 1995; König and Engel, 1995; Roelfsema et al., 1997). There is presently no evidence of information coded by the relative phase of neuronal activity, but only of tagging parts of a distributed representation for common processing.

What is the nature of the interaction with structures upstream and downstream? The brain is a recurrent system, where any stage can not be viewed in isolation. The interaction between the different levels however, appears to be asymmetric. The higher areas do not change the level of activity in the primary one, but differentially coupling into the representation depending on the requirements of the task (see also König and Luksch, 1998).

What are the implications for the formation and maintenance of representations. The observation of coupling between the two areas in different frequency bands for trained and new stimuli suggests the existence of two different modes of operation. One may be for the read out of established representations, another possibly for the formation of new representations. However, these results are preliminary and the underlying mechanisms not yet understood.

2.5 Space, time, and the binding problem. (An interlude)

The hypothesis of binding by synchronization of neuronal activity has been introduced for several reasons (Peter König). The most important aspect is the flexibility it allows in tagging distributed representations for joint processing. In a highly repetitive task, it seems natural to create specialized circuitry for fast and effective performance (also see 2.4 above). Flexibility in a situation where the cross talk created by the presence of other objects can not be ignored, however, the specific synchronization of neuronal activity pertaining to one object appears to be a valid solution. The existence of double selective neurons, e.g. color and orientation, orientation and velocity, ... does not make the task of detection continuity in a distributed representation trivial, but can actually be used to facilitate synchronization (Roelfsema et al., 1996) and allow the differential readout by other neurons. Thus, in order to investigate the relevance of the precise timing of neuronal activity paradigms employing flexible tasks have to be used.

The proposition that the 'binding problem' may be solved by neurons coding for specific combinations of sensory attributes from a particular stimulus (Oram and Perrett 1994; see also this volume) is a reasonable one (Neil Burgess). It may be attacked on the grounds that coding for all possible combinations of attributes of objects would require a number of neurons even greater than present in the brain. However it is interesting to note that, for physical objects, the binding problem could be solved by neurons responding to pairs of sensory attributes and object locations. All of those neurons that code for a particular location that are currently active then represent all of the sensory attributes of the object at that location. In this sense spatial location may have a specific importance beyond attributes such as color or shape. Neurons coding for all possible combinations of attributes would not be necessary. However, it should be noted that in other modalities (e.g. audition) spatial location might not be a reliable segmentation cue (Mike Kilgard).

In the situation of the "binding" of form and motion (Oram and Perrett, 1996), STS neurons responsive to particular body views moving in particular directions show response sensitivity to Johansson type figures (lights attached to the joints, then all other visual information removed). This shows that "motion cues" alone can have information about the body form. This conjunction greatly simplifies the binding problem (Mike Oram).

Looking at the integrative properties of neurons, each receiving input from thousands of other neurons, the binding - i.e. the integration of information - is actually the default of the system operation (Peter König). Thus to integrate the complete information in a reduced environment should not pose special difficulty. However, the problem arising in environments of reasonable complexity is to keep unrelated sources

apart. Here, interacting stimuli give rise to cross-talk between different processing channels, and using the temporal domain to avoid this cross-talk might be one solution among others.

The example of cell responses being able to use motion to extract form indicates that the apparent separation of channels need not be complete (Mike Oram). In striate cortex, the sensitivity to objects outside the classic receptive field indicates this again. Further, cells of V1 are rarely (if ever) only sensitive to one stimulus attribute, but rather show tuning to many (e.g. orientation, spatial frequency, colour etc). It is this conjoint selectivity that makes the notion of "red" detectors and "triangle" detectors meaningless.

This is a very good point, and the other side of the coin is that the interaction between channels previously thought to be separated, e.g. the magno and parvocellular system (Sawatari and Callaway, 1996) is the origin of the cross-talk in realistic environments (Peter König). It is not clear whether this "cross-talk" is noise (i.e. unwanted) or "by design" to integrate these two channels (Mike Oram).

From a technical point of view the distribution of information seems to be possible in quite an easy way (Gerhard Sagerer). Assume, that faces are coded and represented by a number of different features. An instance of a certain feature gives a hint to one or more individual faces, which are "active". Here active means that out of all stored faces a number of individuals are preselected by the context. The collection of features gives estimates on individuals but only on those which are preselected. The most probable one will be chosen. Compared to computer architectures, a small subset of a great number of registers is selected as working memory by an offset address. Switching the context means changing the offset. All the addresses of registers are interpreted according to this offset. The "world" outside this subset is not activated in the given situation. For the re-cognition of individuals, establishing a context guarantees good estimates for the task. The problem of near misses and therefore the need for very detailed features and their available number of features can be reduced, if there exists a good selection mechanism for contexts

Another problem to be addressed by any description of the visual system is the amazing speed of its performance (Mike Oram). The properties described above are present in less than 100ms from stimulus onset. Given the structure of the visual system and a total mean delay of 5ms by each synaptic step, this does not leave any room for iterative processing, but the activity seems to rush through the system and establish the stimulus specificity on the very first go. How this can fit into a scheme depending on the synchronization of neuronal activity is unclear.

The rapid processing of new stimuli is also a problem of schemes using very sparse representations for the representation of visual stimuli (Eilon Vaadia). Are we born with those neurons or do they develop their specificity on the fly? Is this compatible with the performance of primates?

2.6 On the representation of space by means of visual motion. (presented by Nicolas Franceschini)

Humans and many animals including insects can make use of visual motion detection to navigate at high speed in most complex environments. Inspired by recent electrophysiological studies on flies a robot was constructed whose visual system exclusively computes motion. Nevertheless, it has been demonstrated to cope with complex, unpredictable environments, and navigate without 'bumping into things'. By attempting to extract the essence of visually-guided locomotion from the cartoon-like visual system of the fly and reproducing it on a physical artefact, this approach has underlined the two-way interaction that exists between vision and locomotion, whereby locomotion proper is just as necessary to the visual system as a visual system may be necessary for locomotion.

First, the process of motion detection was analysed in the housefly. As the retinal mosaic is readily accessible, elementary motion stimuli were induced by using a specially-built 'microscope-telescope'. Two neighbouring photoreceptor cells with a diameter of 1 micron each were stimulated in sequence, thereby simulating a micromovement in the visual field. Simultaneously the response of an identified neurone in the lobula plate was recorded with a microelectrode (Franceschini et al., 1989). This technique allowed to establish a functional diagram of a typical fly 'local motion detecting neuron' and to characterize its various dynamics and nonlinearities.

Second, the signal processing associated with a fly local motion detecting neuron was transcribed into analog electronics, opening the way to the realisation of a complete creature equipped with a compound eye. This compound eye is panoramic (in the azimuthal plane only) and comprises 118 visual detectors. Each pair of facets gives input to a local motion detector. The system is installed onboard of the creature, and is responsible for guiding the movement of the robot (Franceschini et al., 1992).

This visually-guided robot demonstrator shares the many properties with its biological forerunner: (1) a zig/zag locomotor strategy, whereby pure translations alternate with pure rotations - as observed in flying flies; (2) analog processing in each local motion detecting neuron and throughout the visuomotor system; (3) parallel processing

in the local motion detecting neuron array, giving rise to retinotopic circuitry; (4) asynchronous processing in the local motion detecting neurons, each one carrying out its computation regardless of its neighbour; (5) panoramic visual field and nonuniform sampling of visual space by the facet mosaic; (6) exoskeleton construction (no backbone).

What is the nature of the representation? Obstacles are represented in a retinocentric frame of reference (which is refreshed after each saccade) by the azimuthal location of those local motion detecting neurons which detected contrasts with a retinal slip speed larger than a threshold value. Each one of these ‘dangerous’ contrasts generates a forbidden sector for the next step and all the forbidden sectors are fused, leaving permitted sectors within which the robot chooses its next direction. In response to the detected obstacles, the robot makes body and eye saccades, during which vision is disabled (c.f. corollary discharge). The novel direction adopted for the next step is the closest to that of the target within the permitted sectors. Thus there is no symbolic representation of the obstacles, and the robot needs hardly any memory, not only because it sees its whole environment at any given time, but also because it does not have to carry out any path planning. Most importantly, vision exclusively takes place during the pure translation phases of locomotion. The robot must actually move in order to see and thereby creates a representation of space. Thus the nature of the representation can be fully appreciated only in the behaving artefact.

This exercise in “visually-guided navigation based on motion detection” showed that a decent representation of space can be achieved by detecting relative motion and that this representation is sufficient for a creature to take proper actions and steer safely and rapidly (50 cm/s) in a contrasted, unpredictable environment. This is done by the 12 kg fully autonomous creature, as all its all-analog computation is carried out onboard. Further studies have shown that the same principle can be used not only for steering but also for controlling the cruising speed of a vehicle so that it automatically adjusts to the cluttering of the environment (Martin and Franceschini, 1994).

Building a complete biologically-derived creature and keeping close to nature in terms of locomotory principles, signal processing and architectures guarantees a rich feedback to biology. It raised new problems, which led to the design of novel experiments with the animal that might not have been thought of otherwise. From the outcome of these experiments a novel robot was built, which incorporates new features. Switching to and fro from neurobiology to robotics appears to be one way to foster both sciences at one and the same time.

2.7 Hybrid Representation in Artificial Systems. (presented by Gerhard Sagerer)

Artificial systems which act in a real environment must have knowledge about possible objects, events or processes. At a first glance, objects and their features can be viewed as data, processes in the external world and behaviours of the system as programs, and events can be viewed as special transitions between states of the external world. In the AI and Pattern Recognition community a lot of work is still dealing with the problem of representation of objects and processes from that point of view (c.f. Sagerer and Niemann, 1997). According to the perception action cycle, the matching of perceived stimuli to some internal prototypes or categories is one major basis. Various types of neural network (c.f. Ritter et al., 1994) or statistical (c.f. Schuermann, 1996) approaches are proposed for this problem. Common to these paradigms is that a classification of a stimulus as an entire object or event is performed. In contrast, most explicit knowledge representation techniques collect information of parts or on certain features to classify an object or event according to the underlying hierarchy. Therefore, the part-whole relationship also offers a procedural semantic how to evaluate the data in a sequential manner. Combination of symbolic representation and analogue representation by weights can be combined to form hybrid schemes as proposed in Kummert et al. (1993). Additionally, several hierarchies in the sense of a stratified model can be distinguished. From the bottom to the top in this model the binding by sensory input decreases and the amount of a priori information used for the interpretation increases. The control flow depends on the certainty of actual estimations on the reliability. Levels e.g. may be edges, templates, colors, shape, objects. Classification and interpretation of perceived signals help to built a representation of the state of an agent. It must be enriched by information about internal features. Because not all information about the external world is observable and not all observable information can be represented in a certain state, probabilistic modeling is necessary. Following (Ballard, 1997) Markov-Models and Markov-Decision-Processes can describe behaviours and programs of natural and artificial systems in an adequate way. Again hierarchies of such models concerning both the representation of states and the transitions and actions can be constructed. Two further hierarchies must be taken into account: the precision of results and the time needed to get some results. The importance of iterative processing as well as the different time scales is pointed out in (Ballard, 1997). Iterative algorithms allows an incremental processing which can guarantee a fast availability of guesses and longer processing time improves these estimations. The coordination of processing units with a large variation of processing time is still an open problem. Up to now only first steps are made in order to construct situated robots (Poole et al., 1998) for suitable complex environments and

tasks. But on the other hand the cooperation of different disciplines for this goal resulted already in large improvements.

2.8 The embodiment and the formation of representations. (presented by Christian Scheier)

Categorization involves a mapping of regions of input space belonging to one object onto an invariant output. Category learning consists in the acquisition of this mapping. There are two main problems involved in learning category representations of real world objects. First, the sensory stimulation from one and the same object can vary greatly depending on distance, viewing angle, lighting conditions etc. This is also called the object constancy problem. Second, objects belonging to different categories can result in very similar sensory stimulation. The surprising point about these problems is that they are (subjectively) easily solved by biological agents, but very hard for artificial recognition systems (e.g. Ullman, 1996). In a recent study Moses et al. (1994), for example, have compared face images from different individuals, views (5 per individual), and illumination conditions (4 per individual). The comparison of these images by means of several similarity measures indicated that the differences induced in the changes in viewing conditions were large compared with the difference between the different individuals. Humans, however, that had to recognize the same images had a very high (97%) recognition rate when trained with a single image of each one of the individuals and tested on all other images.

What are the implications for the formation of representations? Traditionally, the formation of category representations has been thought of as a problem of learning a function that maps a sensory input onto an explicit, internal category representation (e.g. category nodes in connectionist models). The main problem with this approach is that due to the problems mentioned earlier, such a function might not exist, at least not in the raw sensory data. Nolfi (1996), for example, has shown that a backpropagation network (i.e. a powerful function approximator) performs very poorly in the seemingly simple problem of learning the distinction between a small cylinder and walls. Put differently, the relevant structures are "hidden" or are only "marginal", so that an uninformed learning algorithm is unable to detect them. Such input spaces are also said to be of type 2 (Clark and Thornton, 1997). Type 2 data sets have to be transformed into type 1 spaces in order for the regularities to come to the fore. Recent research in embodied cognitive science suggests that this transformation can be achieved by means of specific interactions of an agent with the objects to be learned (c.f. see Pfeifer and Scheier, 1998). In other words, instead of transforming the data internally (e.g., by various

recoding strategies, see Clark and Thornton, 1997), an agent can generate the regularities by appropriate interactions with the object. This in turn simplifies the category learning (representation formation) process. Or, in other words, their movements transformed the former type 2 problem into a type 1 problem. Similar conclusions were obtained in a recent study where agents had to learn to distinguish between 3 types of objects (small and large cylinders, and walls) by interacting with the objects in appropriate ways (Scheier and Pfeifer, 1998). The regularities needed to learn to represent the three categories were not contained in the raw data and thus could not be learned as such, but rather had to be generated by the agents through specific interactions such as circling around objects. This suggests that embodiment might play an important role in the formation of representations in that it enables an agent to transform its sensory stimuli such that it can learn the appropriate input-output mapping. This in turn significantly reduces the amount of processing necessary to form representations.

2.9 Interactions and an educated guess. (presented by Mike Kilgard)

The mammalian brain is a highly sophisticated self-organizing system, which continually adapts its responses to best match the environment an individual occupies. Exactly what is meant by the best match is unclear, however. There is no objective way to define what an optimal representation of sensory or motor information would look like. There are certain qualities of neural representations which they should have if they are to be of adaptive value to the organism.

What is the nature of representations? Information should be of a form that is readily useful for modulating behaviour. For example although visual information arrives in retinotopic coordinates, guiding grasping movements would be easier if the location of objects could be determined in body-centered coordinates. Sensory information which is parsed into behaviourally important features, such as color and motion, also appears to facilitate behavioural responses and associations which depend on these features. Representational strategies which facilitate appropriate categorization and generalization functions also improve behavioural performance. Because the brain has finite storage capacity and computational power, efficient use of these resources is important. The stability of representations is also a significant factor to consider.

What are the implications for the formation of representations? Although it is possible, in principle, to learn about the world via simple trial and error, such a strategy is not particularly efficient and risks getting the organism killed in the process. For example, organisms which determined what plants were poisonous by eating each new

species encountered and waiting to see if it got sick are unlikely to survive long. Organisms which randomly change their representational strategy hoping to stumble into improved performance are likewise doomed. Fortunately by virtue of their evolutionary history biological organisms are able to combine interaction with the world with another important strategy: guessing. Animals come preequipped with guesses about how to handle many situations. Having good guesses about how to handle particular novel situations or how to represent novel stimuli would obviously impart an evolutionary advantage. Human infants, for example, do a great deal of exploration of the world with their mouths, but fortunately this exploration is combined with innate knowledge that certain tastes (particularly bitter ones) are to be avoided. Thus many items can be expelled without determining whether they actually cause sickness. Behavioural research is replete with examples of animals making good behavioural choices even in completely novel situations. When an animal does not know what to do it guesses and often these guesses are shaped by simple rules which are genetically encoded (i.e. rats hate cats and babies are afraid of stimuli which indicate high energy sources, such as loud sounds and bright lights). It appears that simple rules also guide the brain in changing its representations of sensory information.

Without good guesses even apparently simple problems like extracting basic features from sensory information can be intractable, because the sensory input could be transformed in an infinite number of ways. It is rarely obvious from the sensory stream what the behaviourally relevant features might be. Although the problem is made easier when the organism is fortunate enough to have receptors which only encode information which is directly relevant (i.e. frog retina, is there a robot analogy? Also see 2.5 above), in most higher organisms data is not so heavily pre-processed and the problem remains underconstrained.

The auditory cortex provides concrete examples of several of the rules cortex uses to guide its own plasticity. Although it is intuitive that improving the representation of stimuli which are consistently associated with behaviourally arousing situations (probably signalled by ascending neuromodulatory systems) would be a useful strategy, it is not clear what an improved representation would be like. Merzenich and colleagues (1990) have shown that there is an expansion of the region of the auditory cortex map representing the frequency range heavily exercised during extensive behavioural training. Thus it appears that one way to improve the representation of sensory stimuli is to increase the number of cortical neurons which respond to them.

Alterations of receptive field size have also been observed following behavioural training. Interestingly, the direction of the change was dependent on the nature of the

task. Receptive field sizes were increased following temporal tasks (discrimination of amplitude modulation rate), and decreased when fine frequency discrimination was required (Recanzone et al., 1992; 1993). This same differential plasticity was generated independently of any behavioural task by pairing different classes of stimuli with electrical stimulation of the cholinergic nucleus basalis (Kilgard and Merzenich, 1998). In this paradigm temporally modulated tones resulted in larger receptive fields, while pairing two different tone frequencies with nucleus basalis stimulation resulted in smaller receptive fields. One advantage of this paradigm is that it allows for the mechanisms of plasticity to be observed independently of behavioural engagement with the stimuli. These results demonstrate that the cortex can use the input itself to determine how to alter its internal representations.

Thus it is the combination of built-in rules and real-world interactions which allows the brain the flexibility to generate appropriate compensation for damage to sensory systems, functional recovery from central nervous system damage, maintenance of precise sensory representations, and improvements in behavioural skills (Merzenich et al., 1990).

3. Discussion

The evidence presented in the above examples represents some of the great progress that has been made in understanding the representation of spatial, visual, auditory and motor information in both natural and artificial systems. A number of principles of representation were common to all of these examples. The importance of the interaction of organisms with their environments was observed in each of the systems studied. The spatially specific firing of hippocampal place cells depends upon the autonomous movement of the rat around its environment, and is not present when the rat is immobilised. In the primate temporal lobe, representation of objects is predominantly in a viewer-centred reference frame which, unlike an object-centred representation, allows for appropriate interaction with objects. The learning of representation of motor action within a force field provides the most direct example of the importance of interaction with the world in learning. The coupling of local field potentials in striate and parietal cortices is also dependent upon the interaction of the cat with its environment. The fly guides its movement using a representation of the world derived from the optic flow generated by its own motion. Recent work on artificial systems focuses on classification and knowledge representation based on events experienced *in situ*, rather than on the traditional complete world model (collection of all features, objects, physical laws etc). Motion of a robot within its environment can greatly simplify the problem of forming a behaviourally

useful representation by providing additional (e.g. temporal) structure to sensory input. Experiments conducted in auditory cortex suggest that the nature of plasticity is dependent on the exact nature of the sensory input, with the relationship between different stimulus attributes and behavioural importance causing appropriate changes in the representation of the stimuli in auditory cortex. Experiments conducted in auditory cortex demonstrate that cortical representations adapt, using clues provided in the structure of the behaviourally relevant sensory inputs. These examples demonstrate the importance of an organism finding appropriate representations for generating behaviour. In turn, the interaction with the environment plays an essential role in this process. Thus, the nature of a representation has to be considered in the context of the behaving organism or artefact. Taking these insights seriously will lead to increasing demands on the complexity of experiments and the theoretical analysis. However, facing the task to understand neuronal representations, this is not completely surprising.

4. References

- Andersen R., Essik G. and Siegel R. (1985), The encoding of spatial location by posterior parietal neurons. *Science* 230, 456-458.
- Ballard D.H. (1997) An Introduction to Natural Computation, MIT Press.
- Biederman I. and Kalocsai P. (1997), Neurocomputational bases of object and face recognition. *Philos. Trans. R. Soc. Lond. B* 352, 1203-1219.
- Bizzi E., Mussa-Ivaldi F. and Giszter S. (1991), Computations underlying the execution of movement: A biological perspective. *Science* 253, 287-291.
- Brashers-Krug T., Shadmehr R. and Bizzi E. (1996), Consolidation in human motor memory. *Nature* 382, 252-255.
- Bulthoff H.H., Edelman S.Y. and Tarr M.J. (1995) How are three-dimensional objects represented in the brain? *Cereb. Cortex* 5, 247-260.
- Burgess N., Donnett J.G., Jeffery K. and O'Keefe J. (1997), Robotic and neuronal simulation of the hippocampus and rat navigation, *Phil. Trans. Roy. Soc., London B* 352, 1535-1543.
- Burgess N., Recce M. and O'Keefe J. (1994), A model of hippocampal function. *Neural Networks* 7, 1063-1081.
- Carey D.P., Perrett D.I. and Oram M.W. (1997), Recognizing, understanding and reproducing action. In (Eds Boller, F and Grafman, J) *Handbook of Neuropsychology* 11, 111-129.
- Clark A. and Thornton C. (1997), Trading spaces: computation, representation, and the limits of uninformed learning. *Behavioral and Brain Sciences* 20, 57-90.
- Chiang C., von Stein A. and König P. (1997), Interareal coupling in the awake behaving cat is dependent on the behavioural context. *Soc.Neurosci.Abstr.* 23, 405.5.
- Desimone R., Albright T.D., Gross C.G. and Bruce C (1984), Stimulus selective properties

of inferior temporal neurons in the macaque. *J. Neurosci.* 8, 2051-2062.

Franceschini N., Riehle A. and Le Nestour A. (1989), Directionally selective motion detection by insect neurons. In: 'Facets of Vision'; Stavenga D.G and Hardie R.C., Springer, Berlin.

Franceschini N., Pichon J.M. and Blanes C. (1992), From insect vision to robot vision. *Phil. Trans. Roy. Soc. London, B* 337, 283-294.

Georgopoulos A.P., Kalaska J.F., Caminiti R. and Massey J.T. (1982), On the relations between the direction of two-dimensional arm movements and cell discharge in primate motor cortex. *J. Neurosci.* 2, 1527-1537.

Giszter S, Mussa-Ivaldi F and Bizzi E (1993), Convergent force fields organized in the frog's spinal cord. *J. Neurosci.* 13, 467-491.

Gray C.M. and Singer W. (1989), Stimulus-specific neuronal oscillations in orientation columns of cat visual cortex. *Proc. Natl. Acad. Sci. U S A* 86, 1698-1702.

Hientanen J.K., Perrett D.I., Oram M.W., Benson P.J. and Dittrich W.H. (1992), The effects of lighting conditions on responses of cells selective for face views in the temporal cortex. *Exp Brain Res.* 75, 417-429.

Hill A.J. and Best P.J. (1981), Effects of deafness and blindness on the spatial correlates of hippocampal unit-activity in the rat. *Exp. Neurology* 74, 204-217.

Hubel D.H. and Wiesel T.N. (1968), Receptive fields and functional architecture of monkey striate cortex. *J. Physiol. (Lond.)* 195, 215-243.

Jeffery K., Donnett J.G., Burgess N. and O'Keefe J. (1997), Directional control of hippocampal place fields. *Exp. Brain Res.* 117, 131-142.

Kilgard M.P. and Merzenich M.M. (1998), Cortical map reorganization enabled by nucleus basalis activity. *Science*, 279, 1714-1718.

König P. and Engel A.K. (1995), Correlated firing in sensori motor systems. *Current Opinion in Neurobiology* 5, 511-519.

König P., Engel A.K., Roelfsema P.R. and Singer W. (1995), How precise is neuronal synchronization. *Neural Comp.* 7, 469-485.

König P., Engel A.K., Roelfsema P.R. and Singer W. (1996), Coincidence detection or temporal integration. The role of the cortical neuron revisited. *TINS* 19, 130-137.

König P. and Luksch H. (1998), Active sensing - closing multiple loops. *Z. Naturforschung* (this volume).

Kummert F., Littmann E., Meyering A., Posch S., Ritter H., Sagerer G. (1993) A hybrid approach to signal interpretation using neural and semantic networks. In *Mustererkennung*, Springer Verlag, pp 245-252.

Logothetis N.K., Pauls J., Bültholff H.H. and Poggio T. (1994), View-dependent object recognition by monkeys. *Current Biol.* 4, 401-414.

Logothetis N.K., Vetter T., Hurlbert A. and Poggio T. (1995), Shape representation in the inferior temporal cortex of monkeys. *Current Biol.* 5, 552-563.

Martin K.A.C. (1994), A brief history of the "feature detector". *Cereb. Cortex*, 4, 1-7.

Martin, N., Franceschini, N. (1994), Obstacle avoidance and speed control in a mobile vehicle equipped with a compound eye. In: 'Intelligent Vehicles', I. Masaki (ed.),

M.I.T. Press, Cambridge U.S.A. pp. 381-386.

Mayes A.R., Meudell P.R. and Pickering A. (1985), Is organic amnesia caused by a selective deficit in remembering contextual information? *Cortex* 21, 167-202.

Merzenich M.M., Recanzone G.H., Jenkins W.M. and Grajski K.A. (1990), Adaptive mechanisms in cortical networks underlying cortical contributions to learning and nondeclarative memory. *Cold Spring Harb. Symp. Quant. Biol.* 55, 873-887.

Miyashita Y. and Chang H.S. (1988), Neuronal correlate of pictorial short-term memory in the primate temporal cortex. *Nature* 331, 68-70.

Miyashita Y., Date A. and Okuno H. (1993), Configurational encoding of complex visual forms by single neurons of monkey temporal cortex. *Neuropsychologia* 31, 1119-1131.

Milner A.D. and Goodale M.A. (1993), Visual pathways to perception and action. *Prog. Brain Res.* 95, 317-337.

Moses Y., Adini Y. and Ullman, S. (1994), Face recognition: the problem of compensating for illumination changes. *Proceedings of the European Conference on Computer Vision*, p. 2986-296.

Nolfi S. (1996), Adaptation as a more powerful tool than decomposition and integration. Technical Report 96-03, Department of Neural Systems and Artificial Life, Institute of Psychology, C.N.R., Rome, Italy.

O'Keefe J. and Burgess N. (1996), Geometric determinants of the place fields of hippocampal neurones. *Nature* 381, 425-428.

O'Keefe J. and Nadel L. (1978), *The Hippocampus as a Cognitive Map*. UK: Oxford University Press.

O'Keefe J. and Recce M. (1993), Phase relationship between hippocampal place units and the EEG theta rhythm. *Hippocampus* 3, 317-330.

Oram M.W. and Perrett D.I. (1994), Responses of anterior superior temporal polysensory (STPA) neurons to biological motion stimuli. *J. Cog. Neurosci.* 6, 99-116.

Oram M.W. and Perrett D.I. (1994), Modeling visual recognition from neurobiological constraints. *Neural Networks* 7, 945-972.

Oram M.W. and Perrett D.I. (1996), Integration of form and motion in the anterior superior temporal polysensory area (STPA) of the macaque monkey. *J. Neurophysiol.* 76, 109-129.

Perrett D.I., Rolles E.T. and Caan W. (1982), Visual neurons responsive to faces in the monkey temporal cortex. *Exp. Brain Res.* 47, 329-342.

Perrett D.I., Harries M.H., Bevan R., Thomas S., Benson P.J., Mistlin A.J., Chitty A.J. Hietanen J.K. and Ortega J.E. (1989), Frameworks of analysis for the neural representation of animate objects and actions. *J. Exp. Biol.* 146, 87-114.

Perrett D.I., Oram M.W., Harries M.H., Bevan R., Hietanen J.K., Benson P.J. and Thomas S. (1991), Viewer-centred and object-centered coding of heads in the macaque temporal cortex. *Exp. Brain Res.* 86, 159-173.

Perrett D.I., Oram M.W., Wachsmuth E. and Emery N.J. (1995), Understanding the behaviour and 'minds' of others from their facial and body signals: Studies of visual processing within temporal cortex. In (Eds Nakajima T. and Ono T.) *Emotion, memory and behaviour: Studies on Human and non-human primates*, Japan Scientific

Societies Press, 155-167.

Pfeifer R. and Scheier C. (1998), Understanding Intelligence. Cambridge, Mass.: MIT Press.

Poole D., Mackworth A. and Goebel R. (1998) Computational Intelligence, Oxford University Press

Murata A., Fadiga L., Fogassi L., Gallese V., Raos V. and Rizzolatti G. (1997), Object representation in the ventral premotor cortex (area F5) of the monkey. *J. Neurophysiol.* 78, 2226-2230 .

Recanzone G.H., Merzenich M.M. and Schreiner C.E. (1992), Changes in the distributed temporal response properties of SI cortical neurons reflect improvements in performance on a temporally based tactile discrimination task. *J. Neurophysiol.* 67, 1071-1091.

Recanzone G.H., Schreiner C.E. and Merzenich M.M. (1993), Plasticity in the frequency representation of primary auditory cortex following discrimination training in adult owl monkeys. *J. Neurosci.* 13, 87-103.

Ritter H., Martinez T. and Schulten K. (1994), Neural Networks. Addison Wesley.

Roelfsema P.R., König P., Engel A.K. and Singer W. (1996), The role of neuronal synchronization in response selection: A biologically plausible theory of structured representation in the visual cortex. *J. Cog.Neurosci.* 8, 603-625.

Roelfsema P.R., Engel A.K., König P. and Singer W. (1997), Synchronization between areas of the visual, parietal and motor cortex of the awake behaving cat. *Nature* 385, 157-161.

Sagerer G. and Niemann H. (1997), Semantic Networks for Understanding Scenes. Plenum Press

Sawatari A. and Callaway E.M. (1996), Convergence of magno- and parvocellular pathways in layer 4B of macaque primary visual cortex. *Nature* 380, 442-446.

Scheier C. and Pfeifer R. (1998). Category learning through self-generated structure. *Proceedings of Simulation of Adaptive Behavior Conference* (in press), Cambridge, Mass.: MIT Press.

Schuermann, J. (1996), Pattern Classification. John Wiley & Sons, New York.

Shadmehr R. and Mussa-Ivaldi F.A. (1994), Adaptive representation of dynamics during learning of a motor task. *J. Neurosci.* 14, 3208-3224.

Speakman A.S. and O'Keefe J. (1990), Hippocampal complex spike cells do not change their place fields if the goal is moved within a cue controlled environment. *Eur. J. Neurosci.* 2, 544-55.

Tanka K., Saito H., Fukada Y. and Moriya M. (1991), Coding visual images of objects in the inferotemporal cortex of the macaque monkey. *J. Neurophysiol.* 66, 170-189.

Taube J.S., Muller R.U. and Ranck J.B. (1990), Head-direction cells recorded from the postsubiculum in freely moving rats. I. Description and quantitative analysis. *J. Neurosci.* 10, 420-435.

Ullman, S. (1996). High-level vision. Cambridge, Mass.: MIT Press.

von Stein A., Chiang C. and König P. (1997), The effect of experience and behaviour on interareal interactions. *Soc.Neurosci.Abst.* 23, 405.

Wachsmuth E., Oram M.W. and Perrett D.I. (1994), Recognition of objects and their component parts: Responses of single units in the temporal cortex of the macaque. *Cerebral Cortex* 4, 509-522.

Wachsmuth E. and Perrett D.I. (1995), Generalising across object orientations and size. In (Eds Walsh, V and Butler, S) *Perceptual constancies*. OUP, Oxford.

Wachsmuth E. and Perrett D.I. (1997), The physiology of shape generalisation (size and orientation). In (Eds Walsh, V and Kulikowski, J) *Perceptual constancies: Why things look as they do*. CUP, Cambridge

Vargha-Khadem F., Gadian D.G., Watkins K.E., Connelly A., Van Paesschen W. and Mishkin M. (1997), Differential effects of early hippocampal pathology on episodic and semantic memory. *Science* 277, 376-380.