PLENARY LECTURES

Wednesday, September 17th, 16.00
PLENARY LECTURE 1

The prefrontal cortex and the temporal organization of action
Fuster J.M.
UCLA, Los Angeles, USA

In evolution as in ontogeny, the cortex of association of the frontal lobe (prefrontal cortex) is one of the cortical regions to develop most and last. It constitutes nearly one-third of the totality of the neocortex in the human adult. The most extensive phylogenetic and ontogenetic development takes place in the cortex of lateral prefrontal areas. Neuropsychological studies demonstrate the importance of lateral prefrontal cortex for the execution of plans and goal-directed sequences of actions in behavior, speech, and reasoning. Functional studies provide strong evidence of the role of lateral prefrontal cortex in the formation of temporal structures of action in those three executive domains. This temporal integrative role is largely the result of the interplay of two time-bridging functions of prefrontal neuronal networks: working memory (retrospective) and preparatory set (prospective). Both these time-bridging functions engage prefrontal neurons in reciprocal cooperation with neurons of posterior (post-rolandic/post-sylvian) association cortex. This reciprocal cooperation, which is essential for the cognitive mediation of cross-temporal contingencies, constitutes the cortical component of the neural substrate of the perception-action cycle - i.e., the circular cybernetic flow of information between the organism and the environment in the process of executing an adaptive series of actions. In that process, the temporal integrative functions of the lateral prefrontal cortex are complemented by an inhibitory-control function of orbitomedial areas protecting the execution of actions from internal or external interference.

Thursday, September 18th, 09.00
PLENARY LECTURE 2

The hippocampus and declarative memory: cognitive mechanisms and neural representation
Eichenbaum H.
Center for Memory and Brain, Boston University, USA

It is widely accepted that the hippocampus and related brain areas mediate declarative memory, our capacity to recollect everyday facts and events. However, little is known about the fundamental cognitive mechanisms and neural representation that underlie the properties of declarative memory. Our working hypothesis is that the hippocampus, in concert with widespread areas of the cerebral cortex, mediates the recording of distinct experiences and links these representations within an organization that supports generalizations and inferences from memory. Evidence from observations on memory loss following damage to the hippocampus shows that the capacity to remember the flow of events in unique experiences depends on hippocampal function. In addition, the capacity to link related experiences and make inferences across memories depends on the hippocampus. Observations on the patterns of activity of neurons in the hippocampus shows that its networks encode episodic memories as sequences of events and the places where they occur. These networks also encode events and places that are common across related episodes, providing a mechanism for linking episodic representations into a larger organization of knowledge that is independent of the episodes in which it was acquired. This combination of coding properties suggests that the hippocampus contributes to declarative memory by mediating a network of linked memory representations. An attractive feature of this account of hippocampal function is that it offers a reconciliation of the current controversy between “spatial mapping” and declarative memory conceptions of hippocampal function, by providing a set of dimensions that could mediate the properties of both spatial and nonspatial memory.

Thursday, September 18th, 12.30
PLENARY LECTURE 3

Amygdala cortical network for goal directed behavior
Gallagher M.
Johns Hopkins University, Baltimore, USA

Certain goal-directed behaviors depend upon interactions between orbitofrontal cortex (OFC) and basolateral amygdala (ABL). This circuit is critical for integrating the incentive value of outcomes with predictive cues to guide action. Experiments in both rats and primates have shown that damage to OFC or ABL produces an inability to control behavior according to the motivational significance of cues or to modify behavior when the outcomes predicted by those cues change in value. Electrophysiological recording of neural encoding in each of these structures has provided complementary evidence for such functions. In recent research we recorded from OFC in intact and ABL-lesioned rats learning novel odor discrimination problems. As rats learned the significance of the odor cues, we found that lesioned rats exhibited marked changes in the information represented in OFC during the sampling of predictive cues. For example, a population of neurons that activate a representation of the predicted outcome during cue sampling in intact rats was virtually eliminated in rats with ABL lesions. In addition, the cue-activated encoding that remained in lesioned rats were less associative and more often bound to sensory features of the cue. Other behavioral studies indicate that the obligatory role of ABL in establishing certain encoding properties in OFC can be specific to establishing an associative representation that does not rely on the amygdala for its maintenance and utilization to guide action and decision making, functions that are invariably disturbed in patients with damage to this prefrontal region.

Friday, September 19th, 12.00
PLENARY LECTURE 4

After after-images
Weiskrantz L.
Oxford University, UK

As it is commonly assumed that visual negative after-images are caused simply by retinal adaptation, especially the bleaching of visual pigments, one may wonder what particular interest they could have for the study of brain and behaviour mechanisms. But the question is whether comparable adaptation changes can occur at later stages of the visual system independently of retinal inputs, i.e., that retinal changes may be sufficient but not necessary. Some historical and recent evidence that this may be possible in normal subjects will be discussed. Also, a study will be reviewed of a blindsight subject who has conscious after-images of visual inducing stimuli of which
he is unconscious. The contrast between these two states offers a unique opportunity to study brain activity of conscious versus unconscious vision. Some ERP evidence (in collaboration with A. Cowey, A. Rao, I. Hodinott-Hill, and K. Nobre) will be presented.

Saturday, September 20th, 12.00
PLENARY LECTURE 5
What, if anything, is the medial temporal lobe?
Murray E.A.
Laboratory of Neuropsychology, National Institute of Mental Health, NIH, USA
Fifty years ago a patient known as H.M. underwent a surgical procedure that rendered him densely amnesic. Initially, experts attributed his memory problems to removal of the hippocampus, but recent studies in nonhuman primates show otherwise. Anatomical, neurophysiological, and physiological findings indicate that the hippocampus is but one of several structures in the medial temporal lobe of primates, which collectively contribute to perception, memory and response selection, each in a specialized way.

Saturday, September 20th, 17.30
PLENARY LECTURE 6
Metric versus configurational framing of space
Paillard J.
CNRS-NBM, Marseille, France
The way in which space relationships are represented in the brain and intervene to organize our vision of a stable world in which we orient our motor behaviour has been the topic of enduring debates. In an earlier study we proposed to introduce a segregation between a “location space” (“un espace des lieux”) and a “shape space” (“un espace des formes”) (Paillard 1971). This distinction was, of course, consonant with the then emerging dissociation between “two visual systems” (Held 1970, Ingle 1967, Schneider 1969, Trevarthen 1970) and with a functional dissociation between “identification” and “location” processing of visual information. The model was derived from a study of the frog’s visuomotor behaviour by Ingle (1967) and of the hamster by Schneider (1969). These studies dissociated the role of collicular structures in orientation and localization from that of cortical visual areas in the perceptual discrimination and recognition of visual forms. More than ten years later was realized that both systems were corticalized in primates and man (Ungerleider and Mishkin 1982) thus leading to the present well known dichotomy between the “Where” and “What” processes with their distinctive parietal and temporal routes. This dissociation has since been confirmed by neuroanatomical, neurophysiological, and neuropsychological evidence. Emphasis was placed on the distinction between an “object channel” and a “space channel”, the first dealing with the analysis of the various features of the object (including its shape) and the second with spatial problems (more specifically, the extra-personal space where objects are located). The distinction initially proposed between a shape space and a location space drew attention to the fact that visual identification and location processes both had to solve spatial problems, but within two different reference frames: one in an object-centered co-ordinate system, the other in a body-centered one, the first being most involved in the perception an categorization of form, the second chiefly concerned with specification of places in a spatially oriented environment. We will give here a special emphasis on a motor-oriented approach. It assumes that the principal metric for coding spatial relationships is derived from the body’s own movements in space: that is, the spatial relationship between two locations can be coded in terms of the movement required to get from one to the other. This approach can account for the structuration of sensori-motor action-spaces based on a body-centered vectorial encoding of place in a location space (Paillard 1971) and to the elaboration of cognitive map at the representation level. The location space corresponds to the taxon systems (later described by O’Keefe and Nadell 1978). To what extent the object-centered configural encoding of gestalt in a shape space at the perceptual and representation level may also required some kind of scan path process (Norton and Stark 1971) still raises open questions, as well as how it may lead, through their centrally encoded image configuration, to shaping motor action in order to reproduce the spatial configuration like in drawing or more generally in expressing postural attitudes or spatio-temporal dynamic of movements configuration bearing some innate or acquired signification in social interchanges (by verbalisation, vocalisation or emotional expression). Thus we suggest to segregate topokinesis from morphokinesis as two modes of driving action, each requiring separated encoding process and neural networks. We shall demonstrated that the first are mainly dependent on innate or acquired feedforward schemas derived from self-induced proprioceptive reafferent information generated from body-centered goal oriented movements whereas the second depend on the extraction of invariant configurational properties from exteroceptive sensory information derived from object-centered exploratory and palpatory activities. Several aspects of this problem will be illustrated in the following experimental approaches: 1) the topokinetic properties of reaching vs. morphokinetik predispositions of the hand grip posture; 2) the palpatory activities of central vision through the head-free retino-centric small saccadic system vs. the egocentric saccadic eye/head foveal acquisition of the object (Frost and Pöppel 1976); 3) pointing to body place vs. matching the position of two body segments in position sense studies; 4) the double dissociation between body schema and body image in centrally and peripherally deafferent patients acknowledging the necessary distinction of these concepts in neurological studies. Phylogenetic and ontogenetic aspects of these problems will be considered together with their potential underlying neural mechanisms.
Continuous automated observations of mice behaviour in an enriched home cage
Kas M.J.H. (1) and Spruijt B.M. (2)
(1) Rudolf Magnus Institute of Neuroscience, University Medical Centre Utrecht, The Netherlands; (2) Veterinary Medicine, University of Utrecht, The Netherlands

The genetic dissection of integrated behaviours requires refinement of behavioural phenotypes. The display and analysis of refined behavioural components have to be established by specific environmental stimuli that elicit ethological needs and by subsequent monitoring. At present, behavioural studies are conducted in short lasting dedicated tasks, thereby, ignoring behaviour normally displayed in the home cage. Furthermore, in these studies, behavioural analysis mostly reveals relatively simple parameters, such as frequencies, latencies, and duration. Therefore, we constructed an enriched home cage that includes the possibility to provide auditory and visual stimuli at a certain time or when the animal is at a certain place. Longitudinal continuous behavioural observations in this cage are based on the automated analysis of video images and permit differentiation between stimulus-induced specific behaviours, baseline levels, as well as behavioural rhythmicity. Moreover, it prevents the confounding influence of the effect of human interference, such as transport, on behavioural characteristics. So far, differences between inbred mice strains could be distinguished by analyzing features of their locomotor patterns. For example, C57bl6 mice display extensive exploration behaviour when compared to Sv129 mice, whereas, Sv129 mice prefer sheltered areas in the home cage when compared to C57bl6 mice. We also showed that these species-specific locomotor activity patterns were observed during novelty, but also in the days following placement in the cage. Thus, longitudinal automated behavioural observations in an enriched home cage allow dissociation of novelty- and baseline expression of locomotor activity patterns and exposure preferences in inbred or genetically modified mice strains.

Environmental background – implications for behavioural phenotyping
Wuerbel H.

Institute of Veterinary-Physiology, University of Giessen, Giessen, Germany

Behavioural phenotyping of mutant mice aims to elucidate the function of single gene products in terms of behaviour. The mice are normally reared under standard laboratory conditions to the age of testing when they will be exposed to a battery of behavioural tests. However, performance in these tests also depends on the test situation and on the animals' environmental background, i.e., their entire experiential history prior to testing. Experience-dependent plasticity of behaviour is substantial and can interact with genotype in non-adaptive ways. Thus, behavioural phenotypes of mutant mice may differ not only quantitatively, but qualitatively, depending on environmental background and they may be idiosyncratic to a single environmental background. Two aspects of current practice appear critical. First, the environmental background of laboratory mice is highly standardised from breeding to testing. As a result, external validity of behavioural phenotypes (i.e., their robustness across different environmental backgrounds) may be limited. Secondly, current standard housing conditions for mice interfere with normal brain and behavioural development, leading to impaired brain function and abnormal behaviours. Improving standard housing conditions and introducing environmental background as a variable in the design of phenotyping studies would not only improve the external validity of the results, but would also facilitate identification of promising gene-environment interactions that would otherwise go unnoticed.

Epigenetic factors influencing behavioural traits in rodents
Belzung C.

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Behavioural traits are influenced by a large number of factors, including proximal (testing conditions) and distal ones. Among these, one may mention genetic as well as epigenetic factors (from prenatal to early postnatal ones), which may interact in a complex way. We will present some data concerning the role of prenatal anxiety of the pregnant mother and the impact of the mothering style on the anxiety behaviour of BALB/c mice. The BALB/c mice are generally considered as a model of generalized anxiety disorder, as they display an elevated trait anxiety when compared to other inbred strains. It has repeatedly been proposed that this behavioural trait may be due to genetic factors. However, inbred strains of mice differ not only for their genetic background but also by many other factors, including intra-uterine environment, diet, mothering style. For example, an elevated stress hormone level during pregnancy may alter the intra-uterine development of the embryos and thus the behaviour of the offsprings when adults. To check for this, we reared BALB/c mice in enriched environments before and during pregnancy, so that they displayed a reduced trait anxiety; we then tested the anxiety behaviour of their offsprings when adults. Furthermore, in other experiment, we controlled the effect of mothering style on the anxiety behaviour of the offsprings and showed the huge effect of the poor maternal care displayed by BALB/c mothers on the offspring's adult behaviour. These two examples illustrate the impact of epigenetic factors on the behaviour of mice.

Behavioural phenotypes of common progenitor strains: implications for knockout research
Rodgers R.J.

Behav. Pharmacol. Lab., School of Psychology, University of Leeds, UK

Although the study of genetically-modified mice promises significant advances in our understanding of the molecular mechanisms of anxiety, it is remarkable that so many of the mutant lines thus far tested have been characterised as having an “anxiogenic-like” phenotype relative to their wild-type controls. While this bias may simply reflect the particular molecular targets studied to date, it may be telling us more about background genes (typically 129xC57) than any specific effect of the targeted mutation. In this context, recent data from our lab confirm that, relative to C57BL/6j mice, several 129 substrains do indeed appear to show higher levels of anxi-
The lateral prefrontal cortex in humans plays a major role in planning. Pharmacological challenge studies, designed to disentangle “high anxiety” vs. “low activity” interpretations, have revealed that 129S2/SvHsd mice are actually insensitive to the anxiolytic (but hypersensitive to the sedative) effects of chloridiazepoxide. Together, these data suggest that (1) exploration-based tests are inappropriate for the assessment of ALB in 129 subrains, (2) at least some 129 subrains have an abnormality in GABAA receptor function and, as such, (3) extreme caution should be exercised when interpreting both the behavioural and pharmacological phenotypes of 129-derived mutants.

**Wednesday, September 17th, 17.30**

**SYMPOSIUM 2**

**Human Anterior Prefrontal Contributions to Cognitive Control**

Pollmann S. (Organiser and Chair)
Day Clinic of Cognitive Neurology, University of Leipzig, Germany

**Introspectively oriented thought processes and the rostrolateral prefrontal cortex**

Christoff K.
MRC Cognition and Brain Sciences Unit, Cambridge, UK

The rostrolateral prefrontal cortex (RLPFC), or the lateral portion of the anterior prefrontal cortex, is known to be activated during complex tasks across a wide range of domains, including reasoning, episodic memory retrieval and working memory. Based on a review of the literature on reasoning and episodic memory retrieval, we have proposed that the critical process that underlies RLPFC function is the evaluation of self-generated information, or introspectively oriented thought. Recent empirical evidence provides direct support for this hypothesis; when evaluation of self-generated information was compared to the evaluation of externally generated information, we observed robust RLPFC activation, specific to this region alone. A finding that further supports this hypothesis is the observation that RLPFC becomes activated during rest, when compared to a simple visuomotor baseline. Such activation was strongly expected, given that rest encourages introspectively oriented thought processes while a continuously engaging visuomotor task discourages them. We propose that RLPFC is involved whenever attention is directed away from the environment, towards internal cognitive states or processes. RLPFC appears to interact with posterior prefrontal subregions (DLPFC and VLPFC) in a hierarchical fashion and may help implement subregional interactions within the lateral prefrontal cortex to form the basis of reflective mental processing, or introspectively oriented cognition.

**Functional organization of the lateral prefrontal cortex in human planning**

Koechlin E.
Inserm U483, Université Pierre et Marie Curie, Paris, France

The lateral prefrontal cortex in humans plays a major role in planning, i.e., in the human ability to organize behaviors or mental activities in sequences of goals or subgoals. In this talk, we present new brain imaging results showing that the lateral prefrontal cortex may be broken down into functionally segregated regions subserving distinct basic processes required in planning. We show that distinct regions, located along a posterior-anterior axis in the prefrontal cortex, are involved in selecting and maintaining goals based on either the present context, past events or combinations of both, while frontopolar regions are engaged when subjects process goal-tree sequences requiring to suspend temporarily the execution of a main goal to process secondary subgoals (nesting or branching processes). Altogether, our findings suggest that the collection of basic processes underlying planning provides an integrated theoretical framework to understand the functional topography of the lateral prefrontal cortex in humans.

**Dissociable mechanisms of attentional control of the set shifting behavior within the human prefrontal cortex**

Nagahama Y.
Department of Geriatric Neurology, Shiga Medical Center, Shiga, Japan

The Wisconsin Card Sorting Test (WCST) is a commonly used neuropsychological test that assesses abstract reasoning, particularly the ability to conceptualize abstract categories and to shift cognitive set. Although it has been clinically used for evaluating frontal lobe function, there is some controversy as to the specificity of the WCST of detecting frontal lobe damage, and it has been unclear whether different regions of the human prefrontal cortex carry out different subcomponent processes of the WCST. We investigated the detailed functional anatomy in the human brain related to the performance of the WCST. We used PET to explore the neurophysiological changes that accompany decreased WCST performance in aging, and demonstrated that the neural activity in the antero-dorsal prefrontal cortex (area 46) and postero-ventral prefrontal cortex (area 44) during the WCST was attenuated with advancing age in a different way. Moreover, we revealed in a recent functional MRI study that these two prefrontal subregions showed dissociable neural activations in the two different levels of response selection; that of “attentional set shift” and that of “reversal shift”. These facts suggest that the antero-dorsal prefrontal cortex and the postero-ventral prefrontal cortex have different neurophysiological roles in the process of shifting behavior in humans.

**Distinct frontopolar and anterior frontomedian contributions to shifts of visual attention**

Pollmann S.
University of Leipzig, Day Clinic of Cognitive Neurology, Leipzig, Germany

In a series of event-related fMRI studies, we investigated which brain areas support the reallocation of attentional resources between visual dimensions, such as color or motion. Target detection in visual singleton search is slowed when consecutive targets are defined in different visual dimensions. Behavioral data provide evidence that attentional weight needs to be shifted between dimension-specific processing modules. Depending on the type of search, these attentional weight shifts can occur stimulus-driven or top-down controlled. We found a double dissociation in anterior prefrontal cortex: left frontopolar cortex was selectively involved in stimulus-driven dimension changes but not in top-down controlled dimension changes, whereas the reverse was observed in pregenual frontomedian cortex. Depending on whether targets were defined by
their color or motion direction, we found activation strength in visual areas V4 and hMT + to change accordingly. This indicated that target dimension changes were indeed accompanied by shifts of attention between visual dimensions. We carried out a patient study to investigate the functional significance of the dimension-change-related activation in frontopolar cortex. Patients with lateral frontopolar lesions showed significantly increased reaction times following stimulus-driven dimension changes. These increased dimension change costs were not observed with anterior prefrontal lesions excluding lateral frontopolar cortex. We conclude that anterior prefrontal cortex is actively involved in shifts of attention between visual dimensions, with lateral frontopolar cortex supporting stimulus-driven, and preprefrontal frontomedian cortex top-down-controlled shifts of attention, which result in attentional modulation of activation in dimension-specific occipital visual areas.

**Thursday, September 18th, 10.30**

**SYMPOSIUM 3**

**Basal Ganglia and Cognition**

Da Cunha C. (Organiser and Chair)
Universidade Federal do Parana, Curitiba, Brasil

**Multiple memory systems: the mnemonic functions of the neostriatum and their interaction with memory processing in other brain areas**

White N.M.
Dept. of Psychology, McGill University, Montreal, Quebec, Canada

Although the neostriatum appears to be homogeneous in conventional histological preparations it actually includes a complex array of structures which are differentiable on the basis of anatomical connections and neurochemistry. The striosomes (“patches”) receive diffuse input from cortical (predominantly frontal) areas and from hippocampus and amygdala. This structure is rich in opiate receptors. Surrounding the striosomes is the “matrix” which receives topographically organized input from all parts of the cortex and projects directly to high-level motor areas such as globus pallidus and substantia nigra. The matrix is rich in acetylcholine. Experiments utilizing this information suggest that: 1) the matrix may be the basis of stimulus-response (S-R, or “habit”) memory; 2) the striosomes may mediate a reinforcing function required for strengthening S-R memories in the matrix. The matrix is thought to process S-R memory independently of and in parallel with other brain areas that mediate different kinds of memory. The main evidence for this idea is the existence of memory tasks on which performance is impaired by lesions of the neostriatum, but improved by lesions of other structures, which are assumed to learn behaviours that interfere with those produced by the striatal memory system. Several examples of such interference will be examined for information about the contribution of the striatum to behaviour.

**The basal ganglia and cognition**

Robbins T.W.
Dept. of Experimental Psychology, University of Cambridge, Cambridge, UK

The basal ganglia must mediate several forms of cognitive function, given the heterogeneity of cortical inputs to the striatum. Supporting this principle are several examples of the ventral striatum being implicated in reward processing, and the dorsal striatum in stimulus-response (S-R) mapping. In the latter case, a task for rats requiring the continuous detection of brief visual targets, (the 5 choice serial reaction time task), utilises a neural system including the medial prefrontal cortex, striatum and subthalamic nucleus (STN). Bilateral, excitotoxic lesions of the lateral striatum essentially abolished task performance, despite largely intact simple associative, motor and motivational functions, suggesting the inconsistent retrieval of S-R task mappings. By contrast, whilst bilateral lesions of the nucleus accumbens core region had only minor effects, either excitotoxic lesions or dopamine depletion of the medial striatum, or excitotoxic lesions of the STN, produced substantial deficits in the accuracy of selection, and in response inhibitory functions. Crossed, asymmetrical lesions of the mPFC and either basal ganglia structure produced impairments as great as those produced by bilateral lesions to any of these regions, consistent with mediation of performance by an integrated cortico-basal ganglia system. Our parallel studies of the cognitive role of the basal ganglia in primates have focused on their mediation of the inhibitory processes required in repeated switching between tasks with consistent S-R mappings. Data will be reviewed of deficits in task-set switching in patients with Parkinson’s and Huntington’s diseases, complemented by findings from functional imaging studies in normal volunteers that implicate basal ganglia, as well as the prefrontal cortex, in some of the underlying response inhibitory mechanisms.
The substantia nigra pars compacta as an essential component of the striatal memory system

Da Cunha C.

Universidade Federal do Parana, Curitiba, Brasil

Intranigral administration of 1-methyl-4-phenyl-1,2,3,6-tetrahydropyridine (MPTP) or 6-hydroxidopamine (6-OHDA) to rats causes a partial lesion in the substantia nigra compact part (SNC) and a specific loss of dopamine and its metabolites in the striatum of rats. Three weeks after surgery these animals present learning and memory deficits but minor sensorimotor impairments. The cognitive deficits observed in these animals affect memory of a task proposed to model stimulus-response (S–R) learning – the cued version of the water maze task and the two-way active avoidance task, and working memory – a working memory version of the water maze, but spare long-term spatial memory – the spatial reference version of the Morris water maze. The lesion of the right or left SNC presented additive effects on the working memory impairment. Similar working memory impairment was also observed in rats with dopaminergic mesocortical lesion induced by the bilateral infusion of 6-OHDA into the prefrontal cortex. Furthermore, the microinfusion of lidocaine into the dorsal hippocampus, but not SNC lesion, impaired learning and memory in the spatial version of the water maze. An opposite situation was observed with the cued version. These results suggest that 1) the mesocortical pathway is an essential component of the working memory system; 2) the nigrostriatal pathway is an essential part of the memory system that processes S–R learning; and 3) it works independently of the hippocampal memory system that processes spatial/reational memories.

Thursday, September 18th, 10.30

SYMPOSIUM 4

Goals in Action

Prinz W. (Organiser)
Max-Planck Institute for Psychological Research, Munich, Germany

Elsner B. (Organiser and Chair)
University of Heidelberg, Heidelberg, Germany

Comparing stimulus-triggered reactions and goal-directed actions in behavioral and EEG-studies

(1) Laboratoire de Psychologie Experimentale, CNRS & Université René Descartes, Paris, France; (2) Max Planck Institute for Psychological Research, Munich, Germany; (3) Department of Psychology, The Pennsylvania State University, USA

How are voluntary actions different from externally triggered actions? We investigated participants’ actions in two settings that were identical with respect to the sequence and timing of stimuli and movements. In both conditions 35 visual stimuli appeared in a fixed temporal sequence (every 1,200 ms). Participants were asked to produce key presses to “bisect” the intervals between two subsequent stimuli. In the voluntary action condition, participants pressed one of two keys to determine the position of the next stimulus. By contrast, in the reaction condition participants pressed the key corresponding to the position of the preceding stimulus. Event-related cortical potentials differ in the two conditions. The reaction condition shows increased amplitudes of early sensory components reflecting the larger relevance of initial feature analysis in this condition. Moreover, a centro-parietal P3 and a fronto-central LRP presumably indicate stimulus-driven processes which take effect when movements are to be carried out in response to external stimuli. In the action condition, these components are reduced or absent. However, an early RP onset in this condition points out that the main preparatory effort takes place directly before movement execution.

How action effects are converted into action goals: evidence from behavioral and PET studies

Elsner B. (1), Hommel B. (2)
(1) Department of Psychology, University of Heidelberg, Germany; (2) Cognitive Psychology Unit, University of Leiden, The Netherlands

Actions are performed to attain desired goals, hence, to intentionally produce particular effects. Thus, knowledge about the typical consequences of a movement is important for voluntary action control. In behavioral and PET studies, we showed that acquired knowledge about action-effect relations indeed affects future actions. In the learning phase of our experiments, subjects perceived that movements (i.e., keypresses) were contingently followed by sensory events (i.e., tones of a certain pitch). In a following test phase, subjects had to respond to the former action-effect tones by pressing certain keys. Our results demonstrate that an action is primed whenever the associated action-effect is perceived, this leading to better performance. The neuronal basis of this behavioral effect was investigated with H215O-PET. Like in the behavioral studies, healthy subjects learned relations between keypresses (i.e., actions) and tones (i.e., action effects) prior to PET scanning. During PET scanning, subjects did not perform any movements, but only listened to learned action-effects or to a neutral tone that had not been associated with a movement. The functional activation of the anterior SMA-proper and the right hippocampus increased with the amount of action-effect tones presented. Thus, these brain regions seem to mediate learning and control of goal-directed actions by linking the representations of actions and their effects.

Why don’t we imitate all the time? Neuropsychological and neuroimaging data on the inhibition of imitative responses

Brass M., Derrfuss J., von Cramon D.Y.
Dept. of Neurology, Max Planck Institute of Cognitive Neuroscience, Leipzig, Germany

There is converging evidence from different fields of neuroscience that the mere observation of an action leads to a tendency to imitate that action. It was assumed that such tendencies are based on a direct matching of the observed action onto an internal motor representation. If this assumption holds true, one has to postulate a mechanism which allows us to overcome imitative response tendencies and to avoid confusion between internally generated and externally triggered action goals. We investigated this hypothesis in two neuroimaging studies and a patient study. Our results suggest that the inhibition of imitative response tendencies requires cortical regions which are involved in distinguishing self-generated and externally triggered motor representations. These findings help to understand neuropsychological and psychiatric symptoms like “imitation behavior” and “echopraxia” in which patients confuse intentionally generated and externally triggered action goals.
Recognition of one’s own actions in normal subjects and schizophrenic patients
Franck N.
Institut des Sciences Cognitives, Bron, France

Positive symptoms of schizophrenia seem to be relevant to a dysfunction of the awareness of one’s own action. One possible explanation for this difficulty would arise from an impaired self-monitoring (Frith 1992). Patients would fail to attribute self-produced thoughts or actions to their real origin. The consequence of this failure would be an impaired self-monitoring (Frith 1992), which would make them unable to disentangle intensions that arise from external stimuli from those self-generated. First-rank symptoms such as verbal hallucinations, thought insertion, delusions of influence could derive from this impairment. Another hypothesis (Georgieff and Jeannerod 1998) proposed that understanding actions performed by others could be based on internal simulation of those actions. This theory is supported by the fact that different modalities of action representation share a subliminal activation of the motor system (Fadiga et al. 1995) and that functional imaging studies show largely overlapping patterns of activation related to cerebral activity during imagination, preparation, and observation of a given action (Grezes and Decety 2001). The results of studies that distorted the feedback of subjects’ actions, to evaluate their capacity in detecting the distortion, showed that patients with schizophrenia present impaired abilities to recognize their own movements and to correctly refer the origin of an action. Patients with first-rank symptoms were significantly more impaired than other patients in such tasks (Franck et al. 2001, Frith 1992, Johns and McGuire 1999). Regional cerebral blood flow (rCBF) were recorded during a task of action attribution in 8 normal subjects and 8 schizophrenic patients experiencing frequent first-rank symptoms (but not during the PET data acquisition). In normal subjects, two main brain areas presented a modulation of their activity as a function of the degree of discrepancy between the movement executed and the movement seen on the screen: the right inferior parietal lobule (angular gyrus) and the insular cortex (Ferrer et al. 2003). In schizophrenics, we did not find any co-variation between the degree of distortion and rCBF in either right inferior parietal cortex nor in insula (Ferrer et al., in review). The absence of a modulation of brain activity across the 4 experimental conditions and the finding of a difference in activation between the two extremes conditions show that patients with first-rank symptoms, outwards the manifestation of these symptoms, differ from controls for subtle modulation of brain activity. These results could be related to pathological experiences of patients.

Thursday, September 18th, 15.00

SYMPOSIUM 5

Pheromones - from Genes to Behaviour
Keverne E.B. (Organiser and Chair)
University of Cambridge, UK

Metabotropic receptors and olfactory recognition memory
Kendrick K.M.
Department of Neurobiology, The Babraham Institute, Cambridge, UK

Olfactory cues are used extensively by animals for social recognition and provide useful models for studying brain mechanisms of learning and memory. We have used olfactory memory paradigms for offspring recognition in sheep, and social recognition and social transmission of food preferences in mice, to investigate neural substrate involvement and neurotransmitter signalling systems involved in memory formation as well as its maintenance in both the short and the long-term. These studies have revealed a critical role for the olfactory bulb and piriform cortex in both memory formation and recall. Glutamatergic activation of NMDA and AMPA receptors, and subsequent release of nitric oxide acting via soluble guanylate cyclase, is important for enhancing glutamatergic and GABAergic transmission in response to learned odours. NMDA and AMPA receptors also appear to be critical for maintaining memory recall in the short-term. However, neither of these ionotropic receptors, nor nitric oxide signalling, play a role in memory recall after consolidation. At this time, within the olfactory bulb, enhanced glutamatergic and GABAergic transmission is instead maintained by up-regulation of class 1 metabotropic glutamate receptors. Blockade of mGLuR1a receptors, but not mGLuR5, in the olfactory bulb interferes with memory recall post-post consolidation (8-10 h after memory formation) but has no effect on memory formation or recall at earlier time-points. These results reveal dynamic changes in receptor signalling pathways involved in forming and maintaining short as opposed to long-term olfactory recognition memories.

Oxytocin and social recognition in mice
Young L.J.
Center for Behav. Neurosci. and Dept. of Psychiatry, Emory University, Atlanta GA, USA

Oxytocin (OT) is a nanopeptide produced in the hypothalamus and released from the posterior pituitary into the bloodstream where it is most often associated with regulating the milk ejection reflex and uterine contractions. In addition, OT released centrally modulates parental care, social bonding and sexual behavior. More recently, pharmacological and knockout mouse studies have indicated that OT plays an important role in individual recognition. Male OT knockout mice display an inability to recognize individuals even after repeated exposure, despite normal spatial learning and non-social olfactory habituation. This deficit is completely ameliorated by a single injection of OT prior to, but not after, the initial exposure. Using Fos immunoreactivity as a marker of neural activity during a social exposure, we have determined that while several olfactory processing structures show normal activation upon olfactory investigation, OT knockouts fail to display activation in the OT receptor rich medial amygdala. Infusion of a low dose of OT into the medial amygdala, but not into the main olfactory bulb, reinstates individual recognition. These results suggest that OT neurotransmission in the medial amygdala is required for the proper processing of social olfactory signatures in order to establish social memories. Together with other studies on the behavioral effects of this peptide, these findings support the notion that OT plays a prominent role in regulating the processing of social stimuli as well as complex social behaviors in mammals.

Vomeronasal mechanisms underlying mate recognition in mice
Brennan P.A.
Department of Zoology, University of Cambridge, UK

Female mice learn to recognise the urinary pheromones of the mating male during a sensitive period of a few hours following mating. This pheromonal memory is vital for their reproductive success, as it prevents the oestrous-inducing effects of the mating male’s phero-
mones from aborting his own offspring. The individuality of the pregnancy blocking signal is influenced by MHC type and is conveyed by the vomeronasal system. Learning is dependent on noradrenergic transmission in the accessory olfactory bulb (AOB) and is associated with a long-lasting increase in the inhibitory control of mitral/tufted cell projection neurons in the AOB. These neural changes are consistent with a simple hypothesis for mate recognition in which the pheromonal signal from the mating male is selectively disrupted at the level of the AOB. Electrophysiological recordings of the local field potential (LFP) from the AOB of freely behaving female mice have revealed prominent oscillations in the low theta frequency range. The peak frequency of these oscillations increased following exposure to male urine. Before mating, there was no difference in the LFP response to urine from males of different inbred strains. Following mating, a dramatic increase in the power of the LFP oscillations was observed across frequency ranges. Furthermore, there was now a differential response to urinary pheromones from the mating compared to non-mating male. These results suggest that pheromonal learning might involve long-lasting changes in the synchronization of neural activity in the AOB.

The dichotomy between the main and vomeronasal (or accessory) olfactory systems is further reflected at the level of the molecules that serve as receptors, or putative receptors, for their respective sensory stimuli. In the main olfactory system, odorant receptor (OR) genes encode seven-transmembrane proteins and are members of a multigene family that may comprise as many as 1,000 genes in mouse and human. In the accessory olfactory system, two families of genes encoding seven-transmembrane proteins have been proposed to encode pheromone receptors. The first family of vomeronasal receptor (VR) genes is expressed selectively in neurons of the apical zone of the epithelium of the VNO. The second family of VR genes is expressed in neurons of the basal layer. There are no conserved motifs between the two families of VRs, and VRs have no sequence homology with ORs. These chemosensory receptors are encoded by some of the most complex gene repertoires in the mammalian genome. Mining the Celera and public databases, we composed a first near-complete draft of the mouse V1R repertoire, cataloguing 137 intact genes in 12 distinct families. Our exploration of the human V1R repertoire resulted in the discovery of the five human V1R genes with an intact open reading frame. Axons of neurons expressing a given V1R or V2R converge onto numerous glomeruli in the accessory olfactory bulb. Interestingly, dendrites of second-order neurons (mitral cells) frequently project to glomeruli of the same type. Thus, the initial divergent pattern of projections is rendered convergent in the accessory olfactory bulb.

**Thursday, September 18th, 15.00**

**SYMPOSIUM 6**

**Anatomical Correlates of Conscious Perception**

Karnath H.-O. (Organiser)
University of Tuebingen, Tuebingen, Germany

De Gelder B. (Chair)
Tilburg, The Netherlands

**Why visual attention and awareness are different**

Lamme V.A.F. (1.2)
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Visual awareness is often equated to what is in the focus of attention, notwithstanding that there are a number of reasons from the psychological or theoretical perspective to distinguish between the two. Perhaps the clearest argument to separate attention from awareness can be made from the neural perspective. In neural terms, definitions of visual attention and awareness can be formulated that clearly distinguish between the two, yet explain why attention and awareness are so intricately related. Attention can be defined as the convolution of sensory processing with long- and short-term memory. Awareness, on the other hand, depends critically on recurrent processing, mediated by horizontal and feedback connections. By combining the two, we understand why we seem only capable of conscious reports about what is in the focus of attention. At the same time, we must conclude, however, that we also have phenomenal experience of what is outside that focus.

**Understanding space awareness as a function of structure in the primate cortex**

Clavagnier S., Falchier A., Kennedy H.
INSERM U371, Bron, France

The increased sensitivity of anatomical tracers has revealed increasing numbers of connections between cortical areas in the monkey. The increased complexity of the system has been inversely proportional to faith in finding a relationship between the structure and function. To do just that we have developed two new parameters to describe cortico-cortical connectivity. Firstly, the SLN indicates: (i) direction of information flow (if a given connection is feedforward or feedback); (ii) hierarchical distance between areas, (permitting creation of determinate models). Secondly, the FLN determines the relative contribution of connections of a given area to a particular target area (for instance allowing the comparison of feedback to feedforward or dorsal versus ventral influences on a target area). To test the analytical power of these parameters, we examined the influence of eccentricity on connectivity in the visual system. Results show two distinct systems related to the central and peripheral part of area V1. The central part of V1 is more connected with the ventral pathway and the peripheral with the dorsal and the auditory system. Because psycho-physical function changes with eccentricity in the visual field, these results show that they are constrained by changes in cortical connectivity. We speculate that a similar quantitative analysis of the input to areas of the superior temporal lobe will give insight in the contribution of individual areas to awareness of space.
Anatomo-functional models of unawareness: spatial neglect and extinction

(1) Dept. of Cognitive Neurology, Univ. of Tuebingen, Tuebingen, Germany; (2) School of Psychology, Univ. of Nottingham, Nottingham, UK

Spatial neglect has been classically associated with damage to the right hemisphere’s inferior parietal lobule and temporoparietal junction (TPJ). We have suggested that these classical findings might have been biased by the inclusion of patients who suffer from visual field defects (VFDs) as well as neglect. In support of this idea, we have demonstrated that when patients with VFDs are excluded, the region most commonly associated with neglect is the right superior temporal gyrus (STG) and planum temporale (PT). However, it could be argued that excluding patients with VFDs will inadvertently create a selection bias: favoring patients with more anterior damage. In response, we have conducted a new study based on an unselected 7-year sample of consecutively admitted patients with right hemisphere lesions and spatial neglect (with or without visual field defects). The results demonstrate that the right STG and PT are the cortical structures most frequently damaged in neglect patients. A second study revealed that the TPJ is actually the neural substrate of visual extinction. Therefore, dissociated neural substrates are observed for spatial neglect and for visual extinction. The TPJ thus seems to play a crucial role for conscious detection of distinct stimuli or changes in the environment. In contrast, spatial neglect is associated to the STG and PT, areas that underlie the spontaneous exploration of the environment.

Functional imaging of conscious vs. unconscious processing of visual information

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Institute of Cognitive Neuroscience and Institute of Neurology, University College London, 17 Queen Square, London WC1N 3AR, UK

Opening our eyes on waking from a dreamless sleep, the immediacy and directness of conscious experience belies the complexity of the underlying neural mechanisms, which remain incompletely understood. Not only are the mechanisms underlying consciousness of fundamental scientific interest, but disordered conscious experience is a common and disabling feature of many neurological and psychiatric disorders. I will review some examples of our functional magnetic resonance imaging studies in normal subjects and patients with focal cortical lesions, which provide new insights into the mechanisms involved. These data complement behavioral, neuropathological and electrophysiological findings by suggesting that activity in functionally specialized areas of ventral visual cortex is necessary for visual awareness. However, our recent work suggests that activity in ventral occipital and temporal cortex is not sufficient to support conscious vision without a contribution from parietal and prefrontal areas. Such a contribution may reflect processes such as selective attention and working memory. Reciprocal interactions between parietal and ventral visual cortex may thus serve to selectively integrate internal representations of visual events in the broader behavioral context in which they occur, leading to the richness of our conscious experience and providing a fundamental neural substrate for conscious visual experience.

Thursday, September 18th, 17.30

SYMPOSIUM 7

Advances in Understanding Hippocampal Contributions to Memory Formation

Stewart M. (Organiser)
Milton Keynes, UK

Riedel G. (Organiser)
Aberdeen, UK

Sandi C. (Chair)
UNED, Madrid, Spain

Temporary hippocampal inactivation dissociates two forms of memory processes in a radial-maze discrimination task in mice

Marighetto A.
NRS for Cognitive Neuroscience, Bordeaux, France

Contrasted effects of aging as well as hippocampal lesions were previously observed in a radial maze discrimination paradigm depending on the way the arms (three positive and three negative) were presented to the mouse. While lesioned or aged mice normally acquired the go – no go version of the task (i.e., arms presented one at a time), they next failed to choose the positive arm within pairs (i.e., in two-choice discriminations), but displayed normal preference for the positive arms when all these arms were opened simultaneously, i.e., in six-choice discriminations. Our interpretation is that two-choice comparisons constrains the use of relational representations of past experiences whereas six-choice discrimination could be solved on the basis of adapted response to each arm (procedural memory) as acquired in the go – no go phase. Among a set of indirect evidence supporting the hypothesis that such a selective deficit for the two-choice situation might stem from insufficient relational processing of incoming information during go – no go acquisition we will report on the effects of intrahippocampal lidocaine injections. Indeed, we observed that inactivation of the hippocampus prior to each session of go – no go acquisition was sufficient to produce, in the subsequent test phase, the same selective impairment for the two-choice situation as the one seen in aged or hippocampus-lesioned mice. Thus, normal hippocampal processing during acquisition appears to be critical for one form of memory expression assessed in situations requiring comparisons between two arms which were experienced separately. Long-term retention data also suggest that this supposedly relational/declarative form of memory sustaining such two-choice discriminations might be more vulnerable to the passage of time than the procedural form which is spared by hippocampal inactivation.

Subregional analyses of hippocampal mediation of pattern separation, pattern association, and pattern completion in the rat

Kesner R.P.
Department of Psychology, University of Utah, Utah, USA

A series of experiments will be presented aimed at testing the hypothesis derived in part from the description provided by computational models of the hippocampus that different subregions of the dorsal hippocampus subserve different intrinsic processes including pattern separation, pattern association, pattern completion, short- and intermediate-memory. Based on the use of specific behavioral
paradigms and specific neurotoxic lesions of the dentate gyrus (DG), CA3, and CA1 subregions of the dorsal hippocampus, the general findings are that a) the DG, but not CA1 or CA3, subregion supports spatial pattern separation, b) the CA3, but not CA1 or DG, subregion supports object-place, odor-place pattern associations, spatial pattern completion, and spatial short-term memory c) the CA1, but not DG, subregion supports temporal pattern separation, object-trace-place, object-trace-odor pattern associations, and d) the CA1, but not the CA3, subregion supports intermediate spatial memory. The set of double dissociations among subregions suggest that for temporal and spatial information different subregions subserve different functions. Furthermore, the data provide support for some computational models of the hippocampus.

The role of mossy fibre-CA3 projection in spatial learning in mice
Riedel G.
Dept. of Biomed. Sci., Univ. of Aberdeen, Scotland
The hippocampus is a primary structure involved in spatial learning and memory formation, and it is widely believed that the mossy fibre (MF)-CA3 connection constituting part of the tri-synaptic circuitry has a distinguished role in mnemonic processes. A cognitive profile of selective hippocampal manipulations in mice is presented to characterise the functional role of the MF-CA3 in the circuitry. We evaluated the role of the dentate gyrus (DG), from where MFs originate, in spatial reference and working/short-term memory in an open-field water maze using selective neurotoxic lesions. Based on our results, we affirm that DG is essential for acquisition of spatial reference memory and supports spatial working/short-term memory. MFs synapse onto CA3 pyramidal cells, and within the presynaptic neurones is zinc which is coreleased with glutamate. To test the hypothesis that translocation is zinc is necessary for the formation of spatial memory, we selectively applied a transient zinc-chelating agent. The results confirm that spatial learning relies on the release of zinc by MF, but enhancement of glutamate receptor activation can circumvent the zinc blockade deficit. Coadministration of the zinc chelating agent and a mGluR allosteric modulator do transiently ameliorate spatial learning which is otherwise impared by zinc chelation. These data suggest that an intact and fully functional MF-CA3 connection is necessary for spatial learning in mice, and propose that acquisition of spatial knowledge rely critically on computations performed by DG and CA3.

Morphological correlates of learning in mammalian hippocampus
Stewart M.G.
Departmentof Biological Sciences, The Open University, Walton Hall, Milton Keynes, United Kingdom
Based upon the Hebbian principle, memory formation following learning is believed to result from alterations in neural circuitry due to changed synaptic efficacy. Long term, this is most likely to involve structural changes and the hippocampus has been identified as a crucial site in the process of memory formation. However, there is no consensus as to the precise nature of morphological changes in synapses and neurons, perhaps because of the differing nature and time scales involved in the various models studied, coupled with different methodological approaches to measuring morphometric parameters. Even with a carefully defined paradigm such as long term potentiation (LTP) of the perforant path in the hippocampus, which may provide a model for memory formation (Abraham et al. 2002) J Neurosci 22: 9626), data on synaptic morphological changes can vary from laboratory to laboratory. Agreement on the nature of synaptic changes in hippocampus resulting from learning is similarly lacking. Here 2 main paradigms were used to study morphological plasticity in rat hippocampus: (i) LTP induced in vivo via perforant path stimulation and (ii) spatial learning in a Morris water maze. Unbiased stereology and 3-dimensional reconstruction techniques were applied to ultrathin serial sections of hippocampal tissue viewed at high magnification in an electron microscope. Several comparisons can be made: 1) LTP and spatial learning can cause major alterations in spine and synaptic morphology as little as 6 hours after initial potentiation, though these changes may be transient; 2) not all morphological changes are due to LTP per se, stimulation alone or stress can produce morphological changes; 3) the effects of stress on synaptic morphology can be rapidly reversed by spatial training.

Supported by BBSRC.

Thursday, September 18th, 17:30

SYMPOSIUM 8

Cross-modal Organization and Plasticity of Brain and Behaviour in the Blind
Rauschecker J.P. (Organiser and Chair)
Georgetown University, Washington, DC, USA

Cross-modal interactions and reorganization in animals
King A.J.
University Laboratory of Physiology, Oxford, UK
The registration of sensory maps in the superior colliculus (SC) is critical to the role of this midbrain nucleus in the control of orienting movements. During development, vision is used to calibrate the spatial tuning of auditory neurons in the deeper layers of the SC. Our experiments suggest that topographically-organized visual signals, originating from the superficial layers of the SC, provide a template that guides the refinement of auditory inputs. This cross-modal plasticity allows the multisensory signals from a common source to be linked during the growth period when the relative geometry of the different sense organs is changing. Given this dominant role of vision, it might be expected that auditory spatial abilities would be impaired in blind individuals. However, in keeping with other studies, we found that ferrets that were visually-deprived in infancy by binocular eyelid suture could localize sound as accurately as normal animals and actually appeared to exhibit improved azimuthal acuity. The accuracy with which these animals could localize visual and auditory cues was then measured after opening the eyelids. In contrast to adult ferrets that had been raised normally, these animals failed to localize spatially-congruent multisensory targets any more accurately than the auditory stimuli presented alone. Thus, although adaptive changes may take place that enhance the processing capabilities of the remaining senses, early loss of vision seems to impair the ability of the brain to coordinate and integrate information across the senses.
Cross-modal interactions and reorganization in human subjects

Kujala T.
Helsinki Collegium for Advanced Studies and Cognitive Brain Research Unit, Department of Psychology, University of Helsinki, Finland

Recent development of brain research techniques has made it possible to study the interaction of different modalities and plastic changes across them in human subjects. It was found, for example, that the occipital cortex of early-blinded humans is activated by auditory and somatosensory stimulation. This was originally demonstrated with electroencephalography (EEG), but later confirmed with spatially more accurate methods such as magnetoencephalography (MEG), positron-emission tomography (PET), and functional magnetic resonance imaging (fMRI). Subsequent studies showed that the occipital cortex of the early-blinded has a functional role in the processing of sensory information. Transcranial magnetic stimulation, with which it is possible to transiently interfere with neural processing, caused braille-letter distortions or omissions in blind subjects during Braille reading when this stimulation was applied to the occipital cortex. Unlike previously proposed, recent evidence indicates that cross-modal changes might take place even after the childhood. Posterior brain areas were activated by attended sound changes and during Braille reading in subjects who had lost their sight after the childhood. Recent studies have investigated which occipital areas in early- and late-onset blindness are activated by non-visual tasks. A critical time period has been proposed if during which the individual goes blind, both striate and extra-striate areas are recruited by non-visual modalities. After this period, presumably only the extra-striate areas become cross-modally reorganized.

Cross-modal plasticity of spatial functions in the blind

Röder B.
Experimental and Biological Psychology, Philipps-University, Marburg, Germany

Since the visual system has the highest spatial resolution it has been argued that vision is important for the development of spatial representations of the remaining senses as well. Therefore, a lack of visual input should result in impaired spatial skills. In one study, two sub-tests of German intelligence tests, the Figure-Selection-Test of the IST2000 and the Mirror-Image-Test of the Wilde Intelligence Test were transformed into an enlarged tactile version. In addition, a short test for verbal intelligence was put into Braille. The sighted and blind groups did neither differ in there general (verbal) intelligence nor in their results for the spatial tests. Moreover, the significant correlation between the visual and tactile version of the Figure-Selection-Test in the sighted suggests that the latter can be used to assess spatial skills (in the blind). In an image scanning experiment participants haptically acquired a spatial layout consisting of five landmarks. They were instructed to mentally image a light plastic coin flying from one landmark to a second landmark. Reaction times increased as a function of the distance between the start and designation point in both groups. Similarly, both sighted and blind participants showed increasing reaction times with an increasing mental rotation load. Moreover, during spatial imagery both sighted and blind groups displayed an activation over parietal cortex which has been associated with spatial operations. These findings contradict arguments that although blind people may be able to solve spatial tasks they use verbal instead of analogous strategies.

The role of visual cortex in tactile processing: a metamodal organization of the brain

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Laboratory for Magnetic Brain Stimulation, Behavioral Neurology Unit, Beth Israel Deaconess Medical Center, Harvard Medical School, 330 Brookline Avenue, Boston, MA, USA

On functional brain imaging (PET or fMRI) early blind subjects show activation of their visual cortex, both striate and extrastriate, when reading Braille. Disruption of the visual cortex in early blind subjects with TMS significantly impairs their ability to perform a tactile spatial discrimination task. Such effects are not found in sighted controls or late blind subjects. Pairing the presentation of a Braille stimulus to a finger pad with TMS to the somatosensory or visual cortex at specific interstimulus intervals allows to study the timing of the contribution of the visual cortex to tactile information processing. Results to date reveal a specific role of the visual cortex in perception, rather than detection, of the tactile stimuli in the blind subjects at a time of around 60 ms after the application of the tactile stimulus. In sighted subjects undergoing 5 days of complete visual deprivation and tactile immersion training we also find activation of the occipital cortex on fMRI by tactile stimulation of the fingers. Transient blocking of the visual cortex with TMS at the end of the five days, but not at baseline or following removal of the visual deprivation, disrupts tactile Braille symbol discrimination establishing the functional role of the “visual cortex” in haptic processing. Similar recruitment of the visual cortex for processing of auditory information can also be demonstrated. None of these changes are seen in not-blindfolded control subjects. This extremely rapid cross-modal plasticity suggests the existence of tactile and auditory inputs into visual cortex in normal human subjects that can be unmasked by visual deprivation. These results suggest that the visually deprived visual cortex seems capable of being devoted to processing of other, tactile or auditory, inputs. This might represent cross-modal plasticity. However, these results also raise the possibility of a metamodal organization of cortical areas in which for example the “visual cortex” decodes spatial information regardless of input modality. While visual information might be best suited for this kind of computation, in the absence of visual input, other sensory signals can be employed. Work in sighted subjects performing appropriate tasks supports such a notion. Asked to judge the roughness of an array of raised dots, subjects engage the somatosensory cortex, as predicted by work in primates. However, the occipital, visual cortex plays a critical role when subjects have to judge the spacing between dots using the same arrays. These findings are consistent with results of TMS and functional imaging studies of other, similar tasks. It might be argued that visual imagery accounts for the role of visual cortex in some tasks in the sighted. However, if congenitally blind and sighted employ the same cortical brain region for the same task, we might be better served thinking of metamodal processing, rather than arguing that the same brain activation patterns are generated by fundamentally different mechanisms.

Supported by the National Eye Institute, National Institute of Mental Health, and the Harvard-Thorndike General Clinical Research Center.
Coding in the Brain: Integrative Hypotheses Revisited

Wróble A. (Organiser)
Nencki Institute of Experimental Biology, Warsaw, Poland;
Eckhorn R. (Organiser)
Dept. of Physics, University of Marburg, Germany

Beta activity and attentional mode of the visual system

Wróble A.
Nencki Institute of Experimental Biology, Warsaw, Poland

In agreement with the old hypothesis that the descending feedback projections in the visual system might be activated during attention processes we have shown that in the cat: (1) cortico-geniculate feedback has a build-in potentiation mechanism acting at the beta frequency. By means of this mechanism the thalamic cells may be activated and consequently lower the threshold for transmission of visual information; (2) the enhanced beta activity, as shown by chronic local field potential recordings, is propagated along the feedback pathway solely during attentive visual behavior; (3) this attention-related activity consists of 100-350 ms long bursts which appear simultaneously in cortical and thalamic sites that are involved in central vision and both also correlate in time with gamma oscillatory events; (4) such bursting activity spreads to all investigated visual centers, including the lateral posterior-pulvinar complex and higher cortical areas; (5) the idle beta oscillatory rhythm observed in number of visual structures during non-visual stimulation changes towards a specific pattern of synchronization during attentive seeing. Similar data are obtained during visual behavior in humans. We suggest that the observed pattern of beta activity represents temporary activated mosaic of functional connections needed for current visual scan. For example, it may produce the background activation for gamma synchronization and perception. Our hypothesis for the role of the cortico-thalamic pathways in attentive perception may be easily applied for all stages of visual and possibly other sensory processing.

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Dynamic cortical cooperation related to visual perception

Eckhorn R., Gail A., Bruns A., Gabriel A., Al-Shaikhli B.
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We have continued testing the hypothesis of visual feature-binding by synchronization in monkey visual cortex. Current support for this hypothesis comes from recent results demonstrating local synchrony among rhythmic or stochastic gamma-activities (30-90 Hz) – including their perceptual modulation – and decoupling of gamma-activity among neural groups representing figure and background. However, gamma-synchrony in primary visual cortex is restricted to few millimeters, which challenges the binding-by-synchronization hypothesis for larger cortical distances. But we found that this restriction is due to extensive traveling gamma-waves, randomly altering their directions. Thus, across intermediate distances, phase continuity of these waves may still support coding of object continuity. Finally, across large distances we observed cortico-cortical interactions among low-frequency signals and the envelopes of amplitude-modulated gamma-signals. We discuss potential mechanisms of near-, medium- and far-range cooperativity on the basis of spike-coding model networks. In conclusion, we propose that the binding-by-synchronization hypothesis, initially restricted to synchrony of oscillatory gamma-signals, be extended to more general forms of signal coupling, including near-range phase synchrony (coherence) between gamma-activities, medium-range phase continuity of gamma-waves, and far-range coupling involving low-frequency signals and envelopes of gamma-signals.

Organization and function of cortical states: the role of on-going and evoked cortical dynamics in sensory processing

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Ongoing cortical activity (activity in the absence of intentional sensory input), must play an important role in sensory perception, since it modulates stimulus-evoked activity, and is related to behavior. However, the relation between ongoing activity and internal representations of the external world is unknown. We have recently found that ongoing activity in the cat visual cortex is composed of dynamically switching intrinsic cortical states many of which closely correspond to the orientation columns. Namely, functional maps that were thought to occur only when evoked, were observed to arise instantaneously and completely spontaneously. In my talk I will show the spatio-temporal organization of this activity, its interactions with stimulus-evoked activity, and the way it affects the actual behavior of the monkey. We, therefore, suggest that the ongoing activity could represent the brain’s internal context, influencing perception and behaviour. I accomplished this goal in anesthetized and awake behaving animals by continuously observing the space-time dynamics, without signal averaging, of cortical population activity (Dye Imaging, Electroencephalogram and Local-Field-Potential) together with recording from a single neuron (intracellular or single-unit) and then calculating the relationship between them.

Precise synchronization dynamics in cortical networks – feasibility and constraints

Neurobiology and Biophysics, Inst. of Biology III, Albert-Ludwigs-University, Freiburg, Germany

Studies of cortical network function on the basis of multiple single-neuron recordings have revealed neuronal interactions which depend on stimulus and behavioral context. These interactions exhibit dynamics on several different time scales, with time constants down to the millisecond range. Mechanisms underlying such dynamic network organization are investigated by experimental and theoretical approaches. Our current research focuses on two interrelated aspects: precision and variability of cortical network activity. Starting from previous model work in which we investigated conditions for the occurrence of precise joint-spiking events in cortical network activity, I will present recent findings from ongoing experimental and theoretical work in our laboratory, undertaken to test and expand the model predictions. Specifically, I will discuss new findings regarding the feasibility and constraints of precise synchronization dynamics in cortical networks, resulting from a critical
An animal model of intrusive emotional memories

Diamond D.
University of South Florida, Tampa, USA

Abstract not received
rons of the mesopontine tegmentum: the Ch5 neurons of the pedunculopontine tegmental nucleus (PPTg) make monosynaptic excitatory input mainly to substantia nigra pars compacta while the Ch6 neurons of the laterodorsal tegmental nucleus (LDTg) make similar projections into the ventral tegmental area. This laboratory has adopted a strategy involving the use of excito-toxic lesions and drug administration in an attempt to analyze the functions of mesopontine cholinergic innervation of midbrain DA neurons in regard to reinforcement. Experiments involving natural reinforcers (analysis of consummatory behaviour and operant responding for food) and experiments involving artificial rewards (drug sensitization studies and intravenous self-administration of drugs) all indicate that mesopontine cholinergic neurons provide information about reinforcement to midbrain DA neurons.

**Synaptic plasticity in substantia nigra and forebrain dopamine release**

Blaha C.D.

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In *vitro* electrophysiological studies have shown that tetanising electrical stimulation (TES) of nearby glutamatergic (Glu) afferents can induce long-term depression (LTD) of dopamine (DA) cell activity in the substantia nigra (SN). LTD can also be blocked by bath-applied amphetamine (AMP), but not by NMDA (APV) or metabotropic (MCPG) Glu receptor antagonists. These data suggest that AMP subverts this form of synaptic plasticity and therefore may be involved in the early developmental stages of drug addiction. However, in *vitro* studies cannot identify the sources for this reduction in synaptic efficacy or whether it has functional consequences in terms of changes in forebrain DA release. Here we show for the first time in anaesthetized rats that electrical stimulation of prefrontal cortex (PFC) Glu cells projecting to SN evokes a transient increase in striatal DA release recorded in real-time (sub-ms) with fixed potential amperometry. TES of the PFC attenuated PFC-evoked striatal DA release by >50%. Consistent with *in vitro* data, intra-SN infusions of AMP blocked TES-induced attenuations in PFC-evoked responses, whereas APV and MCPG were without effect. These data suggest that LTD is an important compensatory mechanism of excitatory control of midbrain DA systems that can be compromised by psychostimulants. Future studies will examine sensory control of midbrain DA cells mediated via the superior colliculus and pedunculopontine nucleus and functional consequences of synaptic plasticity within these projection systems on forebrain DA transmission.

**The tectonigral projection: a source of short latency sensory input to midbrain dopamine neurons?**

Redgrave P.

Dept. of Psychology, University of Sheffield, UK

Midbrain dopamine (DA) neurones are particularly sensitive to unexpected, biologically salient events, to which they exhibit a stereotyped short latency (<100 ms), short duration (~100 ms) population response. The functional significance of this response is unclear, however, its latency suggests, in most cases, it derives from pre-attentive perceptual processing. The ability of DA neurones to signal different classes of sensory event will therefore depend on the discriminative properties of afferent sensory circuitry. Surprisingly, very little is known about the origin of relevant sensory inputs to midbrain DA neurones. Recently, we have discovered a direct pathway from a primary sensory structure, the midbrain superior colliculus, to substantia nigra pars compacta and ventral tegmental area. Anterograde tracing data show the tectonigral projection has a medial-lateral topography and makes contacts with both DA and non-DA neurones in pars compacta. Synapses characteristic of both excitatory and inhibitory input were also found. Tectonigral cells of origin are located primarily in the intermediate and deep layers of the superior colliculus. Parallel electrophysiological experiments have shown that the superior colliculus is a critical relay for the transmission of short latency visual input to substantia nigra pars compacta. These experiments suggest that the tectonigral projection could be a source of rapid, relatively unprocessed sensory input to DA containing regions of the ventral midbrain.

**Saturday, September 20th, 09.30**

**SYMPOSIUM 12**

**Genes, Brain and Behavior**

Roubertoux P.I. (Organiser and Chair)

Institut de Neurosciences Physiologiques et Cognitives, INPC-CNRS Marseille, France

**Genetic effects on human cognition: lessons from the study of mental retardation syndromes**

Flint J.

Wellcome Trust Center for Human Genetics, Oxford University, UK

The molecular basis of human cognition is still poorly understood, but recent advances in finding genetic mutations that result in cognitive impairment may provide insights into the neurobiology of cognitive function. I review progress that has been made so far and assess what has been learnt from this work on the relationship between genes and cognitive processes. I review evidence that the pathway from genetic lesion to cognitive impairment can be dissected, that some genetic effects on cognition are relatively direct. I argue that the study of mental retardation syndromes is giving us new clues about the biological bases of cognition.

**Genes and cognition: the meaning of the links**

Roubertoux P.I.

Institut de Neurosciences Physiologiques et Cognitives, CNRS Marseille, France

In rodents and in humans, different approaches conclude that genes are linked with behavioral variation and particularly with cognitive processes. Roughly, we can estimate that the number of genes linked to behaviors in mice is more than several thousands. The results of genome sequencing programs should challenge the hypotheses of a linear relationships between genes and phenotypes. The number of genes that are present in our genome or in mouse genome does not exceed 30,000. Assuming that less than 20% of these genes are expressed in the brain, no more than 6,000 genes may be implicated in brain functioning and its behavioral outputs. Considering that about half of these genes codes for sensorial functions, the number of remaining genes is lower than the number of genes that were previously identified for their implication in brain or behavioral processes. To solve this paradox, we must consider the polyvalence of the gene as a central concept for understanding the genotype-phenotype relationships. We examine the different mechanisms resulting in polyvalence. The consequences for understanding the relationships between brain and behavior and for the general taxonomy of behaviors will be discussed.
Neuro-behavioral disorders in Down syndrome
Dierssen M.

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Down syndrome (DS) phenotype results from overdosage of a cluster of proteins encoded by several human chromosome 21 (HSA21) genes. We have generated murine models with different levels of expression of selected some of the candidate genes on human chromosome 21, aiming to isolate just those genes that are responsible for the specific features of the DS phenotype. Transgenic and knockout mice, with mutations in genes expressed in the brain, provide powerful new tools for understanding the genetic substrates of behavior. Using a wide variety of relevant behavioral paradigms, our laboratory developed a strategy for cognitive/behavioral phenotyping by which several fascinating new transgenics and knockouts are presently being phenotyped. The objective of the project is to identify the physiological role of gene products and the role of their overexpression in the complex pathophysiology of the disease, the developmental consequences of the trisomy and the impact on behavior and the learning and memory processes during development and in the adult. The first phase of this project identifies cellular and molecular substrates that regulate the emergence of different forms of learning and memory. The second phase determines how the interaction between these gene products and the environment contribute to the expression of learned behaviors. Findings from these studies have provide new insights into some of the underlying neurobiological dysfunctions associated with human disorders resulting in impaired learning and memory such as mental retardation, and specifically DS.

Genetic analysis of associative performances in drosophila and bees
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In Drosophila melanogaster food search behaviour, groups of flies swarm around and aggregate on patches of food. We wondered whether flies explore their environment in a cooperative way as interactions between individual flies within a population might influence the flies’ ability to locate food sources. We have shown that the food search behavior in the fruit fly Drosophila is a two-step process. Firstly, “primer” flies search the environment and randomly land on different food patches. Secondly, the remaining group of flies moves to the most favorable food source and aggregate there. We call this a “search-aggregation” cycle and show that flies explore the environment as collective group with social interactions. We show that exploratory skills imply associative performances and some drosophila mutants do consistently behavioral mistakes. Although this behavior don’t present the sophistication of bees in which social tasks are strictly defined, molecular tools and genetic methodologies allow us to investigate and compare the role of genes involved in exploratory phenomenon in the two models.

Saturday, September 20th, 15.00

SYMPOSIUM 13

Cerebellum: Cognition and Emotion

Strata P. (Organiser and Chair)
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Role of the cerebellum in learning and memory
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Evidence is now conclusive that the cerebellum and its associated circuitry is essential for both learning and retention of the classically conditioned eyeblink response and other behavioral responses, to the extent tested. Evidence will be reviewed concerning the relative roles of the cerebellar cortex and interpositus nucleus in this form of learning.

Neural circuits of fear memories
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Fear conditioning is a model of emotional learning in which an unconditioned stimulus (US), e.g., electrical footshocks, becomes associated not only with an appropriate conditioned stimulus (CS) but also with the environment in which the punishment is administered, i.e., the training context. Although it is well known that the cerebellum plays an important role in the nictitating membrane reflex, there are no reports on its involvement in the learning process of fear responses. By reversible tetrodotoxin inactivation technique, we show that cerebellar involvement in fear conditioning consolidation is quite long-lasting (from not less than 96 up to 192 hours) and that there are functional differences between the interpositus nucleus (IN) and the vermis (VE). IN appears to be necessary only to consolidate memory of fear of the acoustic CS, while VE is necessary for both acoustic CS and context memory consolidation. The involvement duration of cerebellar sites is longer than those previously obtained for basolateral amygdala and the dorsal hippocampus. In addition, by means of electrophysiological (patch-clamp) recordings, in vermal slices following fear conditioning there is a long-lasting potentiation of the synaptic transmission between parallel fibers and Purkinje cells (PC). The long-term change is synaptic specific, since the climbing fiber to PC synapse is not modified. These results provide evidence that the cerebellum is crucially involved in the consolidation.

Cognitive and emotional processes in human
Molinari M. (1,2) and Leggio M.G. (1,3)

(1) IRCCS Santa Lucia Foundation; (2) Catholic University, Institute of Neurology; (3) University of Rome “La Sapienza”, Dept. of Psychology, Rome, Italy

Different lines of evidence are focussing the cerebellar role in the pathophysiology of behavioural disturbances such as autism, dyslexia and schizophrenia and it has been proposed a role of the cerebellum in affect and psychosis. Early experimental observations linked the cerebellum with arousal, autonomic phenomena as well as stereotyped aspects of affective functions. Electrical cerebellar stimulations performed in the attempt to control epilepsy often have been reported associated with emotional effects. Recently neuroimaging data are providing further support to the notion of a cerebellar role in affection and behaviour. Morphological differences in cerebella of patients with depression have been reported in different studies. Cerebellar activation has been reported after pain stimuli or even for simple expectation of pain, after recollection of emotionally relevant personal life episodes. We have recently suggested that implicit learning deficits in cerebellar damaged subjects may depend from impairment in the processing of sensory inputs. Similar impairment in implicit learning and in sensory processing has been observed in two of the cerebellar re-
lated behavioural disturbances namely, dyslexia and obsessive compulsive disorder. Furthermore, clinical and cerebral blood flow data are also supporting the existence of emotional related disturbances in subjects with cerebellar lesions.

Cognitive learning in cerebellar subjects
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There is strong evidence both in the animal and human literature that the cerebellum is involved in motor learning. The paradigm most often examined is classical conditioning of the eyelink reflex. More recent studies suggest an additional role of the human cerebellum in other forms of associative learning, e.g., visuomotor associative learning and fear-related associative learning. Data of our own group showed that: (i) cerebellar subjects were impaired in learning the association between a number and a color (Drepper et al. (1999), Brain 122: 87-97) or two colors (Timmann et al. (2002) Neuropsychologia 40: 788-800). Deficits could not be related to motor performance deficits or increased attentional demands during performance of the motor part of the task (i.e., to press a button); (ii) cerebellar patients were impaired in fear-conditioning paradigms (Maschke et al. (2000) J Neurol Neurosurg Psychiatry 68: 358-364 and 72: 116-118). Likewise, cerebellar activation was seen during fear-conditioning using functional brain imaging techniques (PET and fMRI) in healthy human subjects (Frings et al. (2002) Neuroreport 13: 1275-1278). Given the homogenous microscopic structure of the cerebellum, the underlying role of the cerebellum in the different forms of associative learning may be the same. It may involve timing, building the association between different stimuli and/or building the association between a stimulus and a motor response. Evidence for the latter will be discussed based on more recent findings in the literature.

Saturday, September 20th, 15.00
SYMPOSIUM 14
Widespread Cortical Contributions to Visual Attention
Roelfsema P.R. (Organiser and Chair)
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Attentive contour grouping revealed by activity in the primary visual cortex
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Visual scenes that are encountered in everyday life are crowded with information. Attention is employed to isolate a subset of this information, and to segregate it from irrelevant items. It is essential that visual attention can be directed to a single object, even when it is large and overlaps with other image components. We studied the physiological and psychophysical correlates of “object-based” attention by using a “curve-tracing” task in which subjects have to group contours into elongated curves. There are two curves in this task. The subject has to group together all contours that belong to a target curve, while another, distracting curve has to be ignored. This task was used in electrophysiological experiments in awake monkeys, and also in psychophysical experiments with humans. In the monkeys, contour grouping is reflected by a modulation of neuronal activity in the primary visual cortex (area V1). Neuronal responses to the contours that have to be grouped together are stronger. This indicates that contours, which are bound into a coherent representation, are labelled with an enhanced neuronal response. The response enhancement does not yet occur during the initial neuronal responses evoked by the appearance of the stimulus, and that are determined by bottom-up connections from the LGN. The response enhancement rather occurs after a delay of approximately 150 ms, and is presumably determined by feedback connections and lateral connections within area V1. The delayed response modulation reflects the monkey’s interpretation, since it is changed if the monkey makes an error in the contour grouping task. We also recorded from the frontal eye fields (FEF) during the same task. In our task, the monkeys respond by making an eye movement to a circle at the end of one of the curves. The temporal profile of responses in area FEF resembles that in area V1. Also in this area, initial responses are driven by bottom-up connections, and do not yet distinguish between relevant and non-relevant contours. After a delay of about 150 ms, however, the responses to the relevant contours are enhanced, just as in area V1. This suggests that the representation of relevant contours simultaneously “lights up” across many areas of the visual cortex. We studied the same task in human observers. Psychophysically, attention is directed to the contours that have to be grouped together. Attention appears to spread across all segments of the target curve, presumably because these segments are collinear and connected to each other. Moreover, the spatial profile of visual attention during this task resembles the spatial profile of the response enhancement in the visual cortex. Taken together, the results indicate that spatially separate segments of an elongated curve are tentatively bound into a coherent representation, by simultaneously labelling neurons in various cortical areas with an enhanced firing rate.

Attentional modulation of motion processing
Treue S.
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Visual motion processing has long been thought to be a purely bottom-up process not influenced by the behavioral relevance of the stimuli. Recording from the parietal pathway of the visual cortex of macaque monkeys trained to perform visual tasks under different attentional conditions we have instead demonstrated that the representation of moving stimuli is systematically modulated by attention already early in the hierarchy of cortical processing. This modulation is multiplicative, i.e., it causes enhanced responses to attended and reduced responses to unattended stimuli independent of their position along the neuron’s tuning curve, preserving the selectivity of the neurons, but increasing the influence of attended and reducing the influence of unattended stimuli. We have further shown that attentional modulation can be based on the attended location as well as the attended stimulus features. On average these two effects are of about equal strength and can be combined approximately linearly. A comparison of attentional effects to the modulation evoked by stimulus contrast show a high degree of similarity that suggests common mechanisms and is consistent with a change in apparent contrast by attention. These results demonstrate widespread and powerful influences of attention on sensory information processing and are consistent with a feature-similarity gain model of attention in which the strength of attentional modulation reflects the similarity between a cell’s sensory preferences and the currently attended set of stimulus parameters.
Selective attention to the component features of multidimensional visual objects: the role of primate area V4
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Visual selective attention has been shown to modulate activity in primate area V4 under a variety of contexts. For example, attention to spatial locations and to target objects can enhance responses to attended compared to ignored visual input. In a recent series of experiments we investigated whether activity of area V4 neurons can also be modulated by selective attention to the component features of a multidimensional visual object. Animals were trained to discriminate either the color or the orientation of a colored bar stimulus, and we measured responses of single V4 neurons to stimuli presented inside their receptive field (RF) when one vs. the other feature of the stimulus was task-relevant. The simple prediction was that selectivity of V4 neurons for a given stimulus feature might be enhanced when that feature was to be discriminated vs. when the other feature was to be discriminated. Contrary to this prediction, only a minority of V4 cells changed their pattern of selectivity as a function of the required discrimination. Activity shortly after onset of the RF stimulus reflected whichever feature was capable of driving the neuron’s response, regardless of the required discrimination. However, for about one third of the cells, activity in a later phase of the trial developed to encode which of two alternative behavioral responses was required by the relevant stimulus feature. Thus, it appears that feature-selective attention can modulate neural activity in area V4 by translating the attended feature of a visual object into a task-relevant category, i.e., by explicitly representing only the information that is relevant to guide behavior. These results will be discussed in the broader context of how visual selective attention is implemented across cortical areas and behavioral demands.

Visual attention in frontal cortex
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Models of visual attention and saccade target selection propose that within the brain there is a topographic map of visual salience that selects, through a winner-take-all mechanism, locations for further processing. Evidence from a series of experiments in monkeys performing visual search tasks suggests that the frontal eye field (FEF) functions as a visual salience map. The FEF is located in the prefrontal cortex and is usually regarded as a motor structure that is involved in producing eye movements because it sends eye movement commands to the superior colliculus and the neural circuit in the brainstem that generates saccades. The FEF is also reciprocally connected with many extrastriate visual areas and recent studies have shown that it is involved in visual processing. Visually responsive neurons in FEF combine bottom-up and top down influences to identify conspicuous objects in a search array regardless of the feature that renders conspicuousness. Furthermore, visual selection in FEF is not dependent on saccade production. Thus, in addition to specifying the goal for eye movements, the selective activity in FEF may serve as a generalized visual spatial attention signal that can influence the activity of neurons in extrastriate visual cortex.