Symp 6/4

ROLE OF PERIRHINAL CORTEX IN OBJECT INFORMATION PROCESSING AND OBJECT IDENTIFICATION

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The perirhinal cortex, a strip of cortex located in the ventromedial temporal lobe, plays a critical role in visual recognition memory. In addition, perirhinal cortex has been found to be important for relating together the different sensory features of objects, thereby facilitating object identification. Recent work suggests that perirhinal cortex contributes to both perception and memory. In "perception", it serves as the final stage in a ventral visual cortical processing stream, known as the "what" pathway, that is devoted to the perception and identification of environmental stimuli. Its special contribution to this type of processing is held to be in the representation of complex conjunctions of features. In "memory", perirhinal cortex participates in acquisition, retrieval, and long-term storage. Evidence from ablation and physiological studies suggests a critical role for the primate perirhinal cortex in the formation and retrieval of both intramodal and crossmodal stimulus-stimulus associations, associations that presumably endow objects with meaning. The perirhinal cortex, together with other cortical fields, also serves as a site of long-term storage of such knowledge. Its central role in many associative processes is likely due to its pivotal anatomical position linking representations stored in diverse sensory and motor areas, as opposed to any special computational function it might possess.

Symposium 7: From sensation to perception: Extra-retinal influences in parietal cortex
Organized by U. Ilg

Symp 7/1

NON-RETINOCENTRIC REPRESENTATION OF VISUAL INFORMATION IN MONKEY POSTERIOR PARIETAL CORTEX

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A fundamental problem in the control of visually guided movement consists in the different frames of reference in which sensory and motor signals do occur. The incoming sensory signals are organized in a retinotopic manner throughout several stages of the visual system whereas the outgoing motor commands are encoded with respect to singular muscles. Considering a typical interaction with an environment like reaching out for a target, obviously the problem arises in how to relate the incoming sensory signal with the required motor output. One hypothesis for solving this problem is a so-called coordinate transformation from retinocentric signals to signals encoded in a cranio-, ego- or even allocentric frame of reference. Several studies on awake monkeys have shown that activity of neurons in many cortical

areas (V3A, MT, MST, LIP, 7A, V6, and PMd) are affected by eye position. We thus consider the modulatory influence of eye position on neuronal discharges to be a common phenomenon in monkey cortex probably subserving an implicit representation of spatial information in a head-centered frame of reference. Cells explicitly coding in a head-centered frame of reference, as have been shown to exist also in area VIP, seem to be restricted to areas specifically involved in the control and sensory guidance of body parts other than the eyes.

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Symp 7/2

THE NATURE OF AUDITORY RESPONSES IN MACAQUE LATERAL INTRAPARIETAL AREA

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The lateral intraparietal area (LIP) of macaques has historically been considered unresponsive to auditory stimulation. Recent reports, however, indicate that neurons in this area respond to auditory stimuli in the context of an auditory-saccade task. To what extent are auditory responses in area LIP dependent on 1) training on auditory saccades and 2) the performance of an auditory-saccade task? To address these questions, two experiments were carried out. In the first experiment, LIP responses in two monkeys were recorded at two different times: before and after auditory-saccade training. Before auditory-saccade training, the animals had never been trained on any auditory task, but had been trained on visual tasks. Both before and after training, activity of LIP neurons was recorded while auditory and visual stimuli were presented and the animals were fixating. Before training 172 LIP neurons were recorded. Among these, the number of cells responding to auditory stimuli did not reach significance, while about half of the cells responded to visual stimuli. After training activity from 160 cells was recorded. These recordings showed that 12% of cells in area LIP responded to auditory stimuli, while the proportion of cells responding to visual stimuli remained about the same as before training. Auditory-saccade training therefore generated responsiveness to auditory stimuli de novo in LIP neurons. In the second experiment, recordings were made from 160 LIP neurons in two monkeys while the animals performed auditory and visual memory-saccade and fixation tasks. Responses to auditory stimuli were significantly stronger during the memory-saccade task than during the fixation task, while responses to visual stimuli were not. Moreover, neurons responsive to auditory stimuli tended also to be visually responsive, and to exhibit delay or saccade activity in the memory-saccade task. These results indicate that, in general, auditory responses in area LIP are modulated by behavioral context, are associated with visual responses, and are predictive of delay or saccade activity.Taken together, these results suggest that the context affects LIP responses. Within the pre-training context, in which auditory stimuli are meaningless, no auditory activity occurs in LIP. However, when auditory stimuli are meaningful as saccade targets due to training (whether or not saccades are actually executed), activity in LIP arises. Moreover, when the auditory

stimuli become highly relevant as saccade targets, because the animals are instructed to perform auditory saccades, LIP activity is increased. This suggests that LIP activity to auditory stimuli reflects the oculomotor significance of auditory stimuli, that is the significance as potential saccade targets.
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Symp 7/3
ATTENTION AND MOTOR CONTROL IN THE NEGLECT SYNDROME
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In humans, lesions of the inferior parietal lobe (IPL) or inferior frontal lobe (IFL) lead to the syndrome of unilateral neglect. Neglect patients with right hemisphere lesions are unaware of or are impaired in responding to stimuli on their left. The results of many investigations suggest that visual neglect cannot be explained on the basis of a simple sensory deficit. Instead, it has been suggested that the syndrome is characterised by deficits in processes that require extraretinal information. Thus, it has been proposed that neglect is a disorder of representing space mapped with respect to the body, or that it results from a failure to direct attention, or alternatively that it results from an impairment of directing movements of the eyes or limbs into contralesional space. Furthermore, it has been suggested that whereas neglect patients with parietal lesions may suffer from a disorder of attention or of representing space, individuals with frontal neglect may have a disorder of 'intention' or of generating movements. The evidence for these proposals will be discussed. Experimental data will be presented supporting the view that parietal neglect is associated with an impairment in visuomotor control as well as of directing attention. It will be shown that patients with right IPL lesions have a disorder of initiating leftward movements and of selecting between potential motor plans. They also have an impairment in directing attention over time, as well as shifting it to the left.

Symp 7/4
REPRESENTATION OF GAZE-VELOCITY IN THE ACTIVITY OF NEURONS IN PRIMATE AREA MST
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The ability to estimate correctly the velocity of a moving objects is an essential prerequisite for successful goal-directed behavior. In order to determine the speed of an object, information from different sensory modalities has to be integrated. Exclusively in the case of a stationary eye of an observer, the velocity can be derived directly from the velocity of the image on the retina. As soon as the object is tracked by an eye or a head movement, the velocity of the eye and the head have to be added to

the velocity of the retinal image movement to reconstruct target velocity in space. The topic of this presentation will be the demonstration that the neuronal activity in the posterior parietal cortex of rhesus monkeys reflects this combination of retinal and extra-retinal signals to code for target velocity in space. Single-unit activity from area MST was measured while the monkeys performed two different paradigms. In a first experiment, the monkeys were trained to track an imaginary target defined by four parafoveal visual cues. In case of pursuit towards the imaginary target, no stimulation of the central visual field occurred. The pursuit-related activity was compared while the monkeys tracked a real and an imaginary target, respectively. For 87 single-units out of three animals, the activity was identical in these two tracking conditions. All neurons were located within area MST confined to the fundus and the anterior bank of the superior temporal sulcus. Control experiments ensured that the pursuit-related activity observed during tracking of an imaginary target was not caused by visual stimulation of peripheral receptive fields. To reveal the frame of reference in which this activity codes for the moving object trajectory, in a second experiment another monkey was trained to track a moving target either by an isolated eye or head movement, respectively. For technical limitations, this study was restricted to horizontal eye and head movements, and therefore only neurons which had a horizontal preferred direction were included here. Out of 57 neurons tested in this paradigm, 37 neurons displayed identical responses independent whether the monkey tracked the moving target by an eye or head movement. For 12 neurons it was possible to show that the pursuit-related activity had an extra-retinal component as shown above. Obviously, the activity of these neurons coded for gaze velocity instead of eye velocity. Taken together, these results suggest that the activity in area MST codes for the trajectory of a moving object in an extra-personal frame of reference independent of the actual executed motor action.
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Symp 7/5

ATTENTIONAL INFLUENCES ON VISUAL MOTION PROCESSING

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The processing of information in the visual system has traditionally been investigated as a 'bottom-up' process in which a series of subcortical and cortical areas extract information from the data stream supplied by the retinas. The neurons in these areas can be seen as filters tuned for various visual aspects, such as color, form, motion etc. that are designed to allow a faithful representation of the visual environment. This has been a very successful approach that yielded a wealth of knowledge about the functioning of the visual system. But it has become increasingly obvious, that even early steps in cortical visual information processing of sensory information are influenced by factors, other than the information supplied by the retinas. Such influences include occulomotor aspects (eye position and eye movement information), and selective attention. While the former are addressed by other talks in this symposium the latter is the focus of the work presented here. Attentional effects can strongly modulate neuronal signals that have been previously considered purely sensory, i.e. determined solely by the