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## Attention and eye movement related activation of neurons in the dorsal prelunate gyrus (area DP)

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Neurons in area DP, the dorsomedial portion of the prelunate gyrus of awake monkeys (*Macaca mulatta* and *Macaca sylvana*), responded only little if at all to stationary or moving light stimuli. Circumscribed receptive fields could not be determined in the majority of cells. About 25% of the units became active at a certain gaze position, mostly ipsilateral to the recording site, and with a latency of 70–150 ms after the eye had attained this position with a saccade. About 70% of neurons were activated vigorously when the monkey looked attentively at an object, such as a face, a glove, a hand or simply towards the opening door, and explored it visually. These stimuli elicit attention as well as emotional responses. Photographed objects or faces flashed on a screen produced only little if any response. Our observations, therefore, suggest that the dorsomedial part of the prelunate gyrus may represent activities related to behavioral aspects of vision rather than to features of the visual image itself.

The prelunate gyrus of Old World monkeys contains several visual areas<sup>13,26–28</sup>. The lateral surface is occupied mainly by area V4, a coarsely visuotopically organized visual association area. Neurons in this area have large visual receptive fields between 2° and 10° diameter, and may be specifically responsive to the predominant orientation of a striped pattern, to moving stimuli, to colors or to stimuli rich in internal structure. They are distributed across this area in clusters each containing predominantly neurons responsive to the same type of visual stimulus<sup>8,23,25,29</sup>. In addition neurons were found that were specifically activated during or preceding eye movements, i.e. when the animal's attention was directed into a certain direction<sup>10–12</sup>, and neuronal responses have been described varying with the meaning of a stimulus within a task set<sup>14</sup> or depending on the general state of arousal or selective attention<sup>18,20</sup>.

The dorsal segment of the prelunate gyrus, the dorsal prelunate area or DP, was singled out as a

separate area, because it differs from the more lateral V4 region in its pattern of connections, its relation to callosal inputs and receptive field size<sup>1,9,27</sup>. Not much is known about the functional organization of this region. It borders dorsomedially on the lower visual field representation in V4<sup>17,25</sup>. Maguire and Baizer<sup>17</sup> noted that cells in this region are 'extremely unresponsive to the simple visual stimuli we have used, and we were unable to discover much about their visual field properties' (p. 1696). Andersen<sup>1</sup> mentions that neurons in this region are responsive to moving stimuli.

During our exploration of prelunate visual association area V4<sup>25</sup> we recorded also from this medialmost (dorsal) part of the prelunate gyrus. Cells in this region were indeed functionally very different from those in the more lateral parts of this gyrus. They were difficult to drive by simple or complex light stimuli, moving or flashing, which had been effective in exciting cells in the prelunate visual association cortex, and a receptive field could gen-

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erally not be determined. On the other hand, these neurons responded vigorously when the monkeys looked attentively at an object or a person. We were unable to design a formalized task by which these neurons could be specifically driven and therefore decided to analyze their activity during various stereotyped visuo-motor behaviors which could be controlled experimentally. It turned out that a large proportion of neurons in this dorsal prelunate region was specifically activated in relation to eye movements and during attentive visual exploration in certain behavioral conditions.

We report here on an extensive study in the right hemisphere of a male rhesus monkey (*Macaca mulatta*), and additional data came from one hemisphere of a Barbary ape (*Macaca sylvana*). Both animals were also used in preceding studies of the prelunate visual area and of area 17 (refs. 7, 25, see also for details of the methods). Animals were trained to fixate a small spot of light. By pressing a bar they could start a test cycle at random intervals. Within 0.3–9 s after bar pressing the fixation spot dimmed for 0.5 s and within that time the monkey had to release the bar in order to get a reward, some drops of juice delivered from a mouth piece. Monkeys completed between 5 and 10 cycles per minute and up to 1500–2000 cycles in one 3–4 h session. During the experiment, the monkey sat in a chair with his head fixed and the body and limbs free below the neck board. Movements of the ipsilateral eye were recorded with an infrared reflection system which monitored the horizontal and vertical eye movements separately<sup>2</sup>. During the experiment, the monkey sat in a 1.5 × 1.5 m experimental chamber. The wall in front of him was an opaque screen, the other walls were closed. On his right side was a door which opened towards the outside. The front frame of the door was at a visual angle of 30° from the monkey. Light stimuli or pictures could be projected and moved on the tangent screen (1 m in front of the eyes), on which the fixation point was projected. The fixation point could be moved by any desired function. However, we had to improvise most of the attention- and emotion-related tasks, because some of them involved active interaction between the monkey and the experimenter. The recording area was anatomically identified.

Recordings were from the dorsalmost 8 mm of the

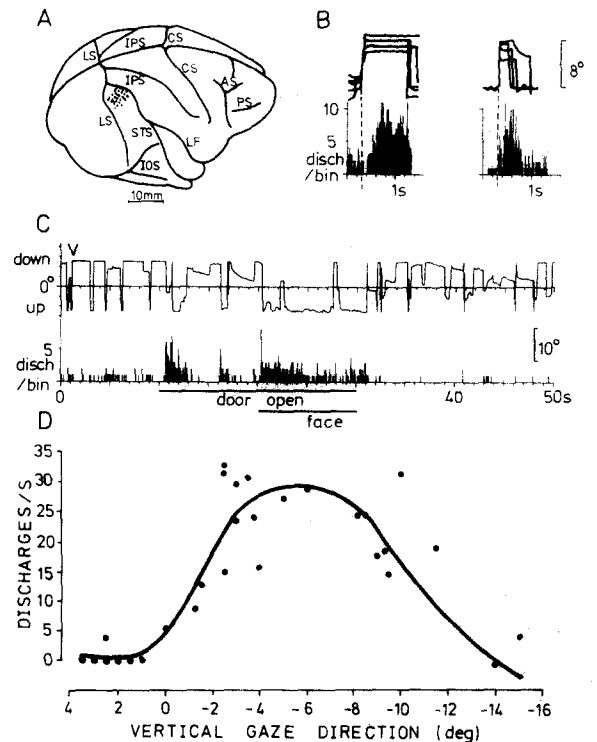


Fig. 1. Eye-position-dependent activations of neurons recorded in area DP. A: lateral view of the right hemisphere of a macaque monkey. The dots indicate the location of penetrations. LS, lunate sulcus; STS, superior temporal sulcus; IPS, intraparietal sulcus; LF, lateral fissure; CS, central sulcus; AS, arcuate sulcus; PS, principal sulcus; IOS, inferior occipital sulcus. B: eye-position dependent activities of DP neurons are visual responses. 4–5 saccades were superimposed with the respective discharge activity of two different neurons. Activation begins between 50 and 100 ms after the beginning of the saccade and continues while the gaze stays in the new position. During and preceding the saccade, activity may be sometimes decreased. Binwidth: 10 ms. C: this unit always discharged when the monkey looked upwards during visual exploration of the open door or of the face of a person appearing in the open door (see lines below record). The upper trace records vertical eye movements. 0° represents the center of the visual axis with the head fixed. The lower trace is the discharge rate of a single unit counted at a binwidth of 50 ms. D: discharge rate (ordinate) of another neuron plotted against vertical gaze direction (0°-straight ahead direction). Each point represents the discharge rate during fixation of the fixation point which was moved up and down. Eye movements were saccades into the new direction, and not pursuit movements.

prelunate gyrus (Fig. 1A), usually from the superficial cortex (300–2000  $\mu\text{m}$ ), and a few from the infolded cortex (2000–4000  $\mu\text{m}$ ). The responsiveness of neurons in this part of the prelunate cortex differed significantly from that of neurons in the intermediate and lateroventral part of the prelunate

gyrus<sup>25</sup> and from that found in the striate cortex<sup>7</sup>. It was in many respects more similar to that of neurons in the parietal cortex as described by others (for review see refs. 1, 16, 19) although some differences were obvious as will be documented below. Out of 127 units, 108 have been studied systematically. Most units were activated in one way or another when the monkey directed his gaze into a certain direction or towards an object or while exploring it. In the majority of these units (70%) attentional and emotional factors played an important role. Stationary flashes of light including photographs of objects, of animals or human and animal faces elicited little or no response. Circumscribed receptive fields could not be clearly delineated in the majority of cells. In the few cells in which a receptive field could be determined, it was in the lower contralateral visual quadrant, 5°–15° from the fovea and the diameters were between 15° and 25°. We could distinguish different response types although many neurons shared both eye position and attention-related activation.

(a) *Activation by eye position.* About 25% of the neurons showed a strong activation when the monkey looked in a certain direction. In the examples of Fig. 1C, the door at the *right side* of the animal chair was opened, the monkey directed his gaze towards the door looking up and down, and when the experimenter's face appeared in the door, the monkey fixated it for some time. The unit was activated during fixation periods in the upward gaze direction. Such eye position-related neuronal activations had always a definite latency after the eye had reached its position within the gaze field. In Fig. 1B we summed the activity during saccades into the respective gaze fields of two different neurons. The activation started between 50 and 140 ms after the eye was in the new resting position. This latency of activation after termination of a saccade is in the same range as visual latencies of neurons in other parts of the prelunate visual association area<sup>25</sup>, and of the few neurons in DP, which could be activated reliably by light flashes.

The mean discharge rate of such neurons depended roughly on the final eye position. In Fig. 1D we plotted the discharge rate of such a neuron against vertical eye position during vertical saccades in a fixation task. The fixation point was moved up

and down to various positions above and below the straight-ahead position, and the monkey looked at it for periods of various length. The mean discharge rate increased with gaze deviations below the O-position with a large variation, but decreased again during saccades of larger amplitude.

Eye position neurons in DP are thus activated only when the monkey looked in a certain direction, which we may call the *gaze field*. If a target is fixated outside that gaze field, no activation is seen. By moving the fixation point regularly forth and back through the gaze field, the activity of neurons usually did not change gradually with the changing eye position, but became more active at a certain position and remained at this elevated level as long as the stimulus and the gaze were in that direction. A precise determination of the gaze field is difficult because the eye position as such is only one factor affecting the activity of such neurons and, other factors such as visual attention may play a role as well (see below). A rough estimate of the magnitude of the gaze field of eye position-activated neurons gives an order of 10°–20° in most neurons. Units were usually not activated by eye position when the monkey just moved his gaze aimlessly through the room while the fixation point was turned off or while, towards the end of a session, the monkey did not work at his task any longer.

(b) *Attention related activation.* The discharge rates of the majority of cells in DP (70%) were specifically affected, mostly excited, sometimes inhibited, when the monkey looked attentively at something. Attention within the context of our experimental setup is defined as a behavior, in which the monkey visually explores an object or a new visual situation. Often expectation was involved as well. Such attention-related activations could be also dependent on eye position or could go hand in hand with gaze position-related responses.

Fig. 2 shows two examples from neurons with such attention-related activations. The unit in Fig. 2A was transiently slightly activated when the door to the right side of the monkey (ipsilateral to the recording site) was opened, but did not continue although the monkey still looked in the same direction. When a face appeared in the direction of the monkey's gaze, the unit became vigorously active. This activation was not modulated in phase with the single saccadic

eye movements, when the monkey looked steadily up and down exploring the entering person and his face. Similarly, when a leather glove, which was used for handling the animal, was shown after door opening, the unit was strongly activated (not shown). The other unit (Fig. 2B) was even slightly inhibited when the open door attracted the monkey's attention and gaze, but was strongly activated when a face appeared. There was some modulation of this activation with the explorative eye movements, but this could not be related to a well-defined eye position. There was a slight suppression of activity when the person disappeared and closed the door, although eye position was about the same as before

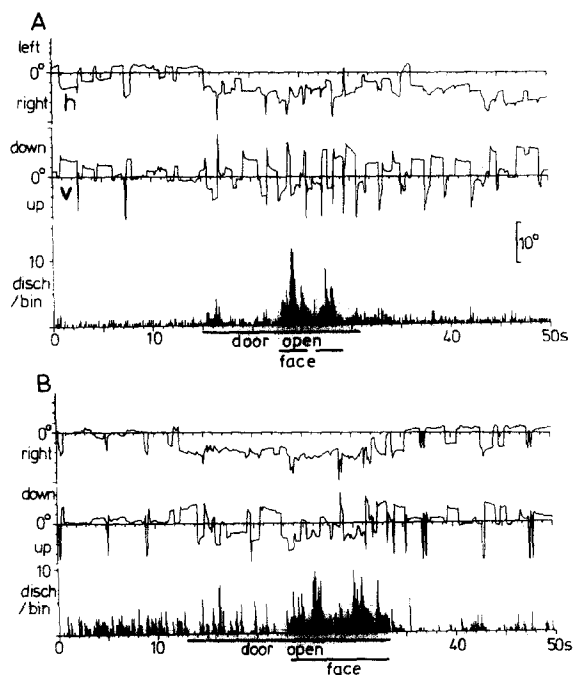


Fig. 2. Activation of neurons in DP during attentive visual exploration of objects or new visual situations. Upper traces in A and B: horizontal and vertical eye movements, lower traces: discharge rates of single units, counted at 50 ms binwidth: A: this unit was slightly and transiently activated when the monkey looked towards the door when it was opened, but a strong activation appeared when somebody showed his face in the open door. Note, that the predominant eye position did not change significantly and that the activation peaks are not clearly related to a definite eye position. B: the activity of this unit was even slightly suppressed when the door was opened, but was strongly activated when a face appeared in the door. Also here, the eye position did not significantly change, and individual discharge peaks are not related to major eye movements. The door was at the right side of the monkey and ipsilateral to the recording site.

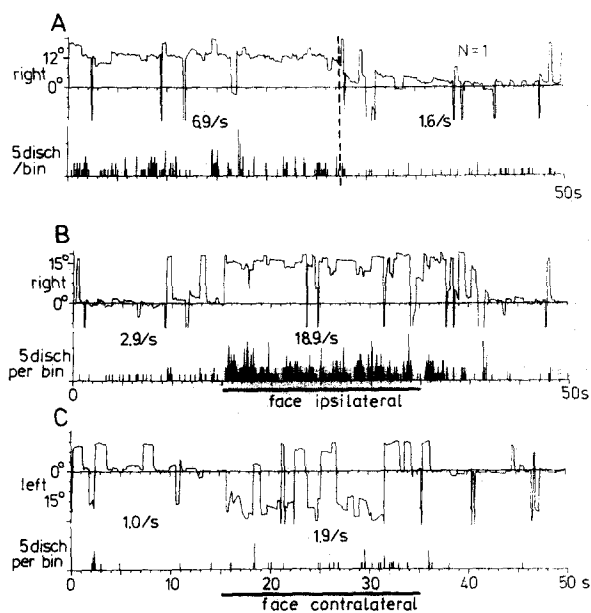


Fig. 3. Eye position-related activation is enhanced during attentive looking. A: this unit was slightly more active when the monkey looked at the fixation point moved 12° to the right (left half of recording) from the straight ahead axis (right half). B: a strong activation appeared during eye position towards the right, when the monkey looked at a face on its right side. C: no significant activation was seen while the monkey looked at the same face on the left side. Mean discharge rates per second during the various situations indicated on top of the records.

the door opening manoeuvre, where the activity was clearly higher.

Also, purely eye position-related activations could be enhanced by attention as documented in the example of Fig. 3. This unit showed a slightly increased discharge rate, when the fixation point was moved to the right (Fig. 3A), but none during upward or downward movement (not shown). When a face appeared at a position about 15° to the right from the monkey, the unit was activated much more strongly (Fig. 3B) than when the monkey just looked at the fixation point in that direction. When the face appeared on the left side, the unit was not or only insignificantly activated, while the monkey was looking at it (Fig. 3C).

The attentive visual exploration of a behaviorally significant situation or object thus appears to be the major variable in many cells recorded in the dorsal prelunate gyrus. Complete independence of the attention-related activation from the gaze direction was found only in one neuron, however. This neuron

became active whenever an object was explored, wherever it was in the visual environment and independent of its behavioral significance.

**Conclusions.** Neurons in the dorsomedial prelunate gyrus (area DP) thus differ from those in the more lateral prelunate association area V4, in that they respond only poorly or not at all to moving or stationary visual stimuli, which were effective in lateral prelunate neurons<sup>25</sup>. In some respects, the eye position neurons in the dorsal prelunate gyrus were similar to fixation neurons in the parietal association cortex (area 7) as described by Hyvärinen<sup>16</sup> and Mountcastle and his colleagues<sup>1,19</sup>. They were similar in as much as a gaze field could be defined in some neurons at least roughly<sup>22</sup> and as they could become active when the animal visually explored an object relevant to him<sup>21</sup>. Yet, the activations of these neurons were clearly visual in that they had a definite latency of 50–150 ms after a saccadic jump towards the new target. Pure oculomotor neurons as defined by Motter and Mountcastle<sup>19</sup> were not found in DP, but the change of discharge rate dependent on the location of the fixation point and thus the direction of gaze without any changes in the visual environment suggests an oculomotor contribution to the activation of these neurons.

The most striking functional property of dorsal prelunate neurons is their strong visual activation during attentive fixation and visual exploration. The fact that this activation is not dependent on the exact eye position and may not be modulated by explorative saccades indicates that it is not due to visual fixation as such. But it is usually only seen, when an object is explored in a more or less restricted gaze direction. We may consider the activation of such units a visual excitation in *conjunction* with attentional behavior. The dorsal prelunate neurons thus make up a spectrum from predominantly gaze direction-activated neurons to neurons that are predominantly or exclusively activated by turning visual attention and thus the gaze to an object.

Attention-related changes of neuronal responses are usually investigated in formalized tests and consist of changes of receptive field properties, of feature selectivity or of response amplitude to a physically identical but attended or not attended stimulus or set of stimuli<sup>8,11,20</sup>. The aim in these

studies is to keep the visual environment or the stimulus stable and only change the state or direction of attention. This approach is methodologically clean, but it only represents that aspect of attention which is defined by the task, namely directed expectation or general responsiveness. Visual attention in the strict sense cannot be separated from foveation including accommodation and binocular fusion. The discharge behavior in the dorsomedial prelunate cortex as investigated in this report is directly related to visual attention so defined. Neither in area 17 nor in the lateral prelunate association cortex V4 which we have investigated under the same experimental conditions, did we see such striking visual attention-related activations<sup>7,25</sup>. Some V4 neurons may show increased responsiveness to stimuli rich in internal structure, or if such a stimulus is moved or turned irregularly<sup>25</sup>, they may show significant response differences to rewarded or non-rewarded stimuli<sup>14</sup>, receptive field properties and responsiveness may change when a stimulus is attended or not<sup>20,24</sup> and the activation of some V4 neurons may be clearly related to eye movements under exclusion of a direct visual contribution<sup>10</sup>. Yet, in a behavioral setting such as the one reported here, we have never seen such closely attentional behavior-related activity patterns in lateral V4. Only in the ventrolateral part of the prelunate gyrus, on the posterior bank of the supratemporal sulcus and lateral from the movement sensitive area MT similar response dependence on attention was observed<sup>25</sup>. It could therefore be that the upper and lower visual field periphery of V4 on its ventral and dorsal surface are surrounded by a cortex which is more specifically related to visual attention than V4 itself.

When considering mechanisms for the visual attention and eye position-related activations of dorsal and ventral prelunate neurons, one has to take into account both the conjunctive dependence on eye movements and the purely visual responsiveness, i.e. activation after the eye has been moved by a saccade into a new position, or after the gaze has been directed for further detailed visual-foveal exploration into a new field of visual attention. This activation is not due to moving the receptive field of a given neuron into a position where it is exposed to an excitatory aspect of the visual environment, since visual receptive fields were

either large and thus affected by essentially the same visual environment as during altered gaze direction (e.g. during the fixation task with the fixation point moving over a neutral background) or no visual responses could be elicited at all with meaningless test stimuli that did not attract attention (and gaze). We therefore conclude that the conjunction between the oculomotor command with the visual stimulus excites these neurons or, in other words, the oculomotor command which determines the direction of visual attention opens a gate which makes these units responsive to the stimuli of the visual environment. Since most units did not respond in relation to eye movements when the monkey was not in a task situation and when his gaze moved around in irregular saccades, the oculomotor gating mechanism must be under control of a *voluntary* eye movement control mechanism. Whether this reaches these neurons via association fibers from the frontal eye field or the parietal association cortex, or from the superior colliculi via the pulvinar, must be left open at this point. It can only be speculated, as to

what extent these eye movement-gated visual responses have a function in the cognitive representation of the visual environment or whether they have command function for other aspects of visual attention such as accommodation or pupillary constriction. In this context it is indeed interesting that in a visual area within the lateral suprasylvian cortex of the cat which may be considered roughly homologous to the primates dorsal prelunate cortex<sup>4</sup> neurons are found, the activity of which is related to lens accommodation or pupillary constriction<sup>3</sup>. One should, of course, realize in such considerations that activations of neurons by sensory stimuli can be interpreted in both ways, as representing specific cognitive aspects and as command signals for behavioral responses<sup>5,6</sup>. Lesions of a cortical region in which visual attention and visual representation are linked in such a way should lead to cognitive deficits such as described in monkeys after total ablation of the prelunate gyrus<sup>15</sup> or as found in human visual agnosias.

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