Saccadic Reaction Times and Activation of the Prelunate Cortex: Parallel Observations in Trained Rhesus Monkeys*

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Summary. Rhesus monkeys were trained to fixate a small spot and saccade to a second stimulus in the near periphery if the fixation spot went off. In different tests the target stimulus could occur at various delay times before or after the offset of the fixation spot. During periods of single unit recording from the prelunate cortex neural events were measured together with saccadic reaction times (SRT). If the stimulus was visible for a period of time (1 or 0.5 s) before the fixation spot disappeared (positive "delayed saccade" task) the SRT reached values of more than 300 ms. The SRTs were shorter when the target stimulus occurred simultaneously with the offset of the fixation spot ("saccade" task). SRT were shortest (~ 150 ms) if the target stimulus appeared 100-250 ms after the offset of the fixation spot (negative "delayed saccade" task). Moreover, they decreased with the time of daily training.

The different behavioural conditions resulted in different types of cortical activity with different latencies: In "saccade" and negative "delayed saccade" tasks the neurons on-responses could be enhanced in comparison to the passive visual on-responses during stationary fixation. The latencies of the on-response and the enhanced on-response were equal with approximately 80 ms. In striking contrast the latencies of the presaccadic activation (PSA) in the positive "delayed saccade" tasks were more than twice as long with about 200 ms. Daily training influences both the SRTs and the PSA: The SRTs become shorter by more than 150 ms in positive "delayed saccade" tasks (delay: 300-500 ms) and the percentage of PSA-neurons decrease from more than 70% to less than ~ 20% after 3 weeks of daily training and recording. The temporal aspects of events preceding visually guided eye movements are important to understand the serial and parallel processing in cortical and subcortical structures that are involved in the learning, initiation, and execution of goal directed movements.

Key words: Vision – Eye movements – Association cortex – Saccadic reaction time – Monkey

Introduction

In recent years it has been established very clearly that different neural structures receiving sensory input from retinotopically defined parts of the visual field also have access to extra retinal signals that modulate the passive sensory response properties of single cells. Among these are the superior colliculus (Goldberg and Wurtz 1972), the frontal eye fields (Wurtz and Mohler 1976), and the posterior parietal cortex (Bushnell et al. 1981), as reviewed by Wurtz et al. (1980). Recently, we have demonstrated that the responses of neurons in the visual association cortex at the prelunate gyrus can also be modulated by extra retinal events (Fischer and Boch 1981b). In particular, cells in all of these structures display an enhanced response to the onset of a light stimulus if this stimulus is simultaneously selected as a target of a saccadic eye movement. The enhancement effect is specifically related to eye movements in the frontal eye fields (Goldberg and Bushnell 1981) and in the superior colliculus (Wurtz and Albano 1980) and the response modulation seems to be related to directed visual attention without goal directed movements in the parietal cortex (Robinson et al. 1978; Mountcastle et al. 1981). In the prelunate cortex we do not have positive direct evidence for attentional effects but an influence of attention cannot as yet be
excluded. It is clear, though, that many prelunate cells discharge before visually guided saccades to continuously visible targets (Fischer and Boch 1981a), i.e. these neurons discharge just like those in the frontal eye fields (Bushnell and Goldberg 1979) — at a time when there is no change of stimulation in the receptive field. This activation will be called presaccadic activation (PSA).

The relation and interaction between sensory and non-sensory neural events in different visual structures and their functional implications for the initiation of visually guided eye movements must be based upon a certain timing of events within the period of time between the onset of a new stimulus, the physical command to move the eye to that stimulus and the beginning of that movement, i.e. within the saccadic reaction time (SRT).

The present study attempts a step towards an understanding of the temporal interrelationship between physical, neural, and oculomotor events. The paper presents new data on latencies of neural activation and saccadic reaction times under various visual and behavioural conditions in particular during prolonged periods of training, and shows in which way neural discharges in the prelunate cortex support the initiation of eye movements that an animal has to learn in a laboratory task.

Material and Methods

Training

Five monkeys (*Macaca mulatta*) first learned to fixate a small red fixation spot (0.05° in diameter) which was presented on a large hemispheric screen (radius 90 cm) in front of the animals, sitting in a primate chair at a distance of 57 cm. Upon onset of the spot the animal had to pull a lever and to hold it for randomly varying periods of time between 1 and 9 s. Then the fixation spot dimmed and the animal had to detect the dimming and release the lever for water reward. During the execution of this “fixation” task the monkey should ignore other visual stimuli which eventually appeared in his visual field.

After the monkeys had learned the “fixation” task the head was fixed by a permanently implanted metal bar and training was continued using an additional second task: after 2 s of stationary fixation a visual stimulus occurred in the periphery. Simultaneously the fixation spot disappeared and the animal had to saccade to the new stimulus. This was achieved by dimming the intensity of stimulus if the fixation spot happened to be off after the random period was over. This second task is called the “saccade” task. Three animals had to learn this task before collection of data began and in one monkey (“Bilbo”) we recorded single unit activity and eye movements while he learned this task.

Finally, we also varied the time between stimulus onset and fixation spot offset: for negative delay times the spot went off between -30 and -300 ms before the new stimulus appeared. For positive delays the stimulus came on before the spot was extinguished. This task is called the “delayed saccade” task. Three animals were exposed to the “delayed saccade” task but not before the first day of recording, and one animal was not used for this task at all. In one monkey (“Omi”) daily recording did not begin before she had been trained in all tasks for some weeks.

Figure 1 shows schematically the sequence of events in trials where eye movements were required. Cases 1 and 3 in Fig. 1 display, for instance, large positive and negative delay times. Case 2 in Fig. 1 corresponds to the “saccade” task at zero delay time where the stimulus onset and the fixation spot offset are simultaneous. In a given trial only one task was used and trials were repeated 10–30 times with intertrial intervals in the order of 1.5 s. After the beginning of a trial the fixation spot was usually present for 2000 ms. The positive delay times for the stimulus onset varied between +30 and +1500 ms. In the negative “delayed saccade” tasks the stimulus appeared 2000 ms after the trial started while the fixation spot disappeared between -30 and -300 ms before stimulus onset, such that the time of stationary fixation before the execution of an eye movement was kept constant.

Recording

Finally, the skull over one hemisphere was opened by a 20 mm diameter craniotomy and a metal cylinder was implanted for daily mounting of a microelectrode drive. Transdural single unit recordings began on the following day using glass isolated Pt-Ir electrodes. Daily recording continued for up to 3–5 weeks in each hemisphere. Intervals of a few weeks between recording periods were used for additional observations of saccadic reaction time. Penetrations were placed at the posterior lateral part of the superior temporal sulcus and in the anterior part of the prelunate gyrus above the tip of the inferior occipital sulcus (see Fig. 2). Eye position was recorded by an infrared sensitive device (Bach et al. 1982) with a precision of 0.1°.

Other details of training, visual stimulation, anatomical reconstructions, recording single unit activity and eye movements have been described earlier (Fischer et al. 1981; Poggio and Fischer 1977).