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Research Report

The planning of a sequence of saccades in pro- and antisaccade tasks: Influence of visual integration time and concurrent motor processing

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ABSTRACT

Previous studies have shown that a saccade is coded in a specific reference frame according to its goal: to aim for a new object or to explore an object which has already been fixated. In a two saccade sequence, the second saccade aiming for a new object is programmed in a retinocentric reference frame in which the spatial location of the second object is stored in spatial memory before the first saccade and updated after its execution. The second saccade exploring the same object is coded in an oculocentric reference frame in which object size is directly transformed into a fixed motor vector, encoded in motor memory before the first saccade and simply applied after its execution. The integration of parafoveal visual information appears to be crucial in the selection of the appropriate reference frame. The two experiments presented here investigate how and when the saccadic system integrates visual information to plan a sequence of saccades. In separate blocks, subjects were asked to execute a sequence of prosaccades directed toward a single object or two short objects, or to execute a sequence of antisaccades in the opposite direction of the stimuli. The latency of the initial saccade was modulated by using the Gap-200, Gap-0 and Overlap-600 ms paradigms. The results show that the time available for segmenting the visual stimulation into discrete objects and application of a specific reference frame according to this segmentation is critical for saccadic planning.

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1. Introduction

In order to explore the visual environment, observers plan and execute rapid eye movements called saccades that shift gaze from one fixation point to another. Visual information initially available in retinal coordinates must be transformed into motor commands through a series of operations known as sensorimotor transformations. In the laboratory, the majority of studies that examine saccadic planning focus on single saccades that shift gaze from one simple target, like a short duration dot, to the other. For such saccades, the saccadic vector might be computed directly from the retinal coordinates of the target, defined by the eccentricity between the actual eye position and the target location. However, our visual environment is full of spatially-extended objects and in many real-life tasks, such as reading or scanning a visual scene, the observer executes saccade sequences, some saccades shifting the gaze to a new object and others shifting the gaze elsewhere in the same object. Previous studies have identified the relevance of this distinction (based on the action

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to be performed) for saccade planning (e.g. Vergilino and Beauvillain, 2001; Vergilino-Perez and Findlay, 2003; Beauvillain et al., 2005; Vergilino-Perez and Findlay, 2006). By contrasting the second saccade as a function of the action goal – to aim for a new object or to explore the same object – the authors showed the use of specific reference frames for each action. Within-object saccades were coded in an oculocentric reference frame as a fixed motor vector applied irrespective of the initial landing position on the object. The second saccade motor vector was planned before the execution of the first saccade and computed as a function of the object size integrated in the periphery: the longer the object, the longer the size of the motor vector (Vergilino and Beauvillain, 2000). The sensorimotor transformation processes for the second saccade occur before the execution of the whole sequence, the within-object motor vector being encoded in a motor memory during the execution of the first saccade. Alternatively, between-object saccades would be coded in a retinocentric reference frame in which the second object location is encoded in spatial memory before the execution of the first saccade and updated afterward as a function of the new eye position. Therefore, the sensorimotor transformation for the second saccade occurs after the execution of the first saccade. The updating process during fixation on the first object can explain why between-object saccade latencies are longer than within-object saccade latencies. Overall, these studies showed that the goal of the action determines which spatial information – the location or the size of the object – is relevant for saccadic planning. Therefore, the visual information relative to the structure of the peripheral stimuli appears to be crucial in the selection of the appropriate reference frame. The question then arises as to whether the use of a specific reference frame for second saccade planning (oculo-versus retinocentric) depends on the time available for the integration of peripheral visual information before the execution of the saccade sequence.

A great number of studies have demonstrated that information presented before first saccade onset can be used to drive the second saccade (e.g. Becker and Jürgens, 1979; Findlay and Harris, 1984; Aslin and Shea, 1987; Walker and McSorley, 2006). For example electrophysiological evidence for temporal overlap of first and second saccade planning was provided by a study measuring the neural activity in monkey superior colliculus, and showing that for fast sequences of saccades, motor activity related to the second saccade goal increased before first saccade onset and was maintained during its execution (McPeek and Keller, 2002). Also, the time course of visual information accrual that guides the first and second saccades in a visual search task was examined (Caspi et al., 2004). The results revealed that visual information was being accumulated simultaneously for the first and the second saccade before the execution of the first saccade. Integration of visual information for the planning of the second saccade begins after integration of visual information for first saccade planning but continues during the first saccade's dead time (i.e. the interval time immediately preceding the saccade execution during which metric changes can no longer be obtained).

In Vergilino-Perez and colleagues' work, parallel planning of saccades depended on the visual object structure obtained in parafoveal vision and on the action to be performed on the object (to aim for a new object or to explore the same object). It is possible that the coding of saccade sequences in specific reference frames depends on the time interval available before first saccade onset, during which parafoveal visual information can be extracted and used to guide action planning. Because the natural variability of the first saccade latency is not large enough to examine this question, we chose to decrease or increase it with the use of the gap and overlap paradigms (Saslow, 1967). The introduction of a gap period without any stimulation reduces the latency of the saccade, up to "express" saccades with latencies around 100 ms (Fischer and Breitmeyer, 1987). On the contrary, in the overlap paradigm, the foveal fixation cross and the target stimulus remain present together on the screen, the extinction of the cross being the start signal for the saccade. Mean latency is around 220 ms (Becker, 1989). In the present experiments, we used Gap-200, Gap-0 and Overlap-600 ms procedures in order to examine the role of the time available for parafoveal visual integration in the planning of two-saccade sequences.

Another way to manipulate the time available for saccade preparation is to load the saccadic system with additional processes that have to be carried out in conjunction with motor planning. The antisaccade task, in which subject were required to make an eye movement away from a visual target, involves such supplementary processes. The system has to first inhibit the reflexive prosaccade toward the visual target and then to program the voluntary antisaccade to the opposite direction (see Munoz and Everling, 2004 for a review). These supplementary processes could explain why antisaccade latencies are longer than prosaccade latencies. In the two experiments described here, we examined sequences of two pro-or anti-saccades in order to investigate whether the reference frames involved in saccade sequence planning are preserved when concurrent processes are involved during saccade planning.

The experiments presented here examined the coding of a sequence of two saccades, the second saccade being directed to a new object or within the same object (see Fig. 1, left panel). The total length of the stimuli could be of 10 or 12 crosses and for one total length, the single long object or the two separate objects both occupied the same space. Three delays of presentation of the objects in periphery were introduced: a Gap-0 and an Overlap-600 ms delay in Experiment 1 and a Gap-200 ms delay in Experiment 2. With gap paradigms, the time interval available for sequence planning is the first saccade latency, whereas with the overlap procedure, the saccadic system should benefit from additional 600 ms to encode the visual stimulation and plan the saccades. For both experiments, we examined two saccade sequences in both prosaccade and antisaccade tasks, in separate sessions.

For the prosaccade task, we expected that the two-saccade sequence would be planned in a specific reference frame according to the action (to aim for two separate objects or to explore the same object) in both Gap-0 ms and Overlap-600 ms (Exp1), as previously found with similar procedures (e.g. Beauvillain et al., 2005). The motor planning of a two-prosaccade sequence has never been tested with a Gap-200 ms delay (Exp 2). It is possible that in this time-pressured situation the saccadic system would not have enough time to encode the visual stimulation and plan the sequence in a

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