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Eye movements in baboons performing a matching-to-sample task presented in a divided-field format

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Abstract

We examined eye saccades in a baboon solving a video-formatted matching-to-sample (MTS) task. In that task, the animal had to place a cursor by way of joystick manipulation within the boundaries of a fixation point (FP) displayed on a monitor. A sample stimulus was then flashed in either the left or right of FP. Immediately thereafter, two comparison forms were displayed and the animal had to select the comparison form matching the sample. A new video technique requiring no specific head or body constraints was employed to monitor eye movements. Expt. 1 indicated that the gaze was centered on FP during the fixation procedure. However, some goal-directed express saccades, with mean latencies of 100 ms, were observed during sample presentation. Expt. 2 used an overlap procedure in which FP remained visible during sample presentation. Latencies of express saccades increased by approximatively 20 ms. Expt. 3 showed in four baboons that the overlap procedure did not affect scores. It is concluded that the computerized MTS task is a valuable tool for the assessment of hemispheric lateralization in visual processing in intact primates, as long as the sample is not displayed longer than 120 ms.

Key words: Express saccade; Overlap; Cerebral dominance; Matching-to-sample; Primate; Baboon

1. Introduction

The existence of functional asymmetries in non-human primates is central in the field of behavioral neurosciences. During the last decade, the interest for this problem has been concretized by an important literature on motor [1,17] and cognitive lateralization in several non-human species [12,13]. Questions underlying these studies are whether or not non-human primates show hemispheric lateralization, and if this phenomenon is similar to human lateralization.

Understanding of hemispheric lateralization in non-human primates could allow for the development of an animal model of hemispheric lateralization in humans. An important problem, however, for developing such a model is the lack of appropriate methods to test non-human primates in conditions comparable to those used with humans. To circumvent this difficulty, most studies with non-human primates (but see, Petersen et al. [18]) have used either lesion approaches [13] or have split the two cerebral hemispheres by cutting the corpus callosum and accompanying posterior and anterior commissures [8]. Such approaches provide insight about brain functioning, but tell little about the intact brain and are thus of a limited implication for our comprehension of normal subjects.

Studies with humans have often employed the tachistoscopic procedure [9] in order to assess the respective abilities of each cerebral hemisphere in the processing of visual information in intact subjects. The tachistoscopic procedure implies a gaze fixation on a fixation point (FP) followed by the display of a stimulus flashed in either the left or right visual half-field. Its rationale is that, given the anatomy of the visual system, visual information flashed to one side of the visual field projects to the visual cortex of the contralateral cerebral hemisphere [16].

Hopkins et al. [12] have recently developed a procedure for studying visual lateralization in non-human primates, which has several characteristics in common with the tachistoscopic mode of stimulus presentation. With this technique, primates are initially trained to manipulate a

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joystick so as to displace a cursor in any direction on a computer monitor [23]. Subjects are then tested in a matching-to-sample (MTS) task in which the sample form is presented in either the left or the right of a fixation point (FP) for a duration shorter than the latency to initiate a saccade. To ensure that the sample form is presented in one visual half-field only, fixation is imposed by having the subject to place and to maintain the cursor on FP before the display of the sample form. Therefore, this technique is analogous to the tachistoscopic mode to stimulus presentation in that it restricts the visual input in one visual half-field only in order to direct the information to the contralateral hemisphere.

The divided-field MTS task has been used so far in baboons [2,10,22], rhesus monkeys [12], chimpanzees [12] and humans [12,22]. A related task with the same fixation procedure was also employed with chimpanzees [11]. Although these studies addressed different questions and consequently used different stimuli and procedures, results are striking in the sense that they all indicate the existence of hemispheric lateralization. Moreover, other convergences have emerged. For example, a right hemispheric advantage was found both in baboons [2] and chimpanzees [12] when novel stimuli were used during testing.

2. Experiment 1

The aim of Expt. 1 was to analyse patterns of eye movements in the aforementioned video MTS task. This experiment was designed to address the following two questions. First, given the lack of empirical evidence showing the effectiveness of the procedure to have the animal looking at FP, we wanted to determine where the animal was looking at during the fixation procedure. Secondly, this study was designed to collect both temporal and spatial information on eye movements during the display of the sample form. It is of note that the latency for saccadic eye movements in monkeys remains a controversial topic. Whilst it is often said that saccade latencies in monkeys range from 180 to 220 ms [6], Fischer and Boch [3] and Fischer and Weber [5] reported in monkeys the existence of Express-saccades (E-saccades) with latencies as short as 70–90 ms. According to Fischer et al. [4], the occurrence of E-saccades would increase with practice. Thus, the divided-field video-task, which requires a large amount of training, could favor the emergence of E-saccades. If E-saccades are performed in the divided-field MTS task, it would then be needed to display the sample form during 70–90 ms only, that is for a duration shorter than that employed in previous studies (i.e. 100–150 ms [2,10,12,22]).

For the purpose of the present research, we have integrated within a single experiment the video MTS task assessment of hemispheric lateralization and the method, initially developed by Wilde [24], for eye movement recording. Contrary to other existing methods available for monkeys [7], this approach allows to test the animal while the head is not firmly maintained in a still position (e.g. by way of a primate chair). Moreover, this method does not require adjunctive elements implanted on eye balls, such as a scleral search coil [14] or other equipments fixed on the skull of the animal. Consequently, we were able to monitor eye movements during the MTS task in conditions very similar to those used in previous published experiments [2,10,12,22].

2.1. Material and methods

2.1.1. Subject

The subject was a neurologically intact 5-year-old wild-caught female baboon (*Papio papio*) raised in a social group of 8 animals within the animal facilities at the C.N.R.S., Marseille, France. Prior to testing, the baboon has been trained on a psychomotor task involving the use of a joystick [23]. It was also used in a series of behavioral experiments on pattern discrimination [2], and rotational invariance problem solving [10,22]. The subject was not food deprived during the experiment but received its daily food ration (fruit, monkey chow and vegetables) at the end of the day and thus, after the completion of the experimental test sessions.

2.1.2. Apparatus

The testing environment is depicted in Fig. 1. The set-up comprised an experimental cage ($68 \times 50 \times 72$ cm) equipped on its front with a face mask and two hand ports. The face mask consisted of an 14.5×14.5 cm infra-red filter, impermeable to wavelengths shorter than 800 nm, in which a small 2.0×8.2 cm view port was cut. The infra-red filter was mounted on the cage between two sheets of plexiglas. A 14-inches computer color monitor, driven by a PC-AT computer, was installed at eye level 48 cm from the view port in front of the experimental cage. An analogue joystick was centrally positioned 18 cm from the hand ports. Also centrally positioned, but 5 cm from the hand ports, was a touch sensitive pad (11.5×10.0 cm) that served to initiate trials by lying one hand on it. The testing cage was fitted with a food dispenser for the delivery of 190 mg food pellets on the floor of the cage when correct responses were made. Timing of stimulus presentation and recording of response times were controlled at a one millisecond sampling rate by a software program written in Turbo Pascal 5.0.

In order to record eye movements, two infra-red CCD video cameras (Panasonic WV-BL202) with zoom lenses

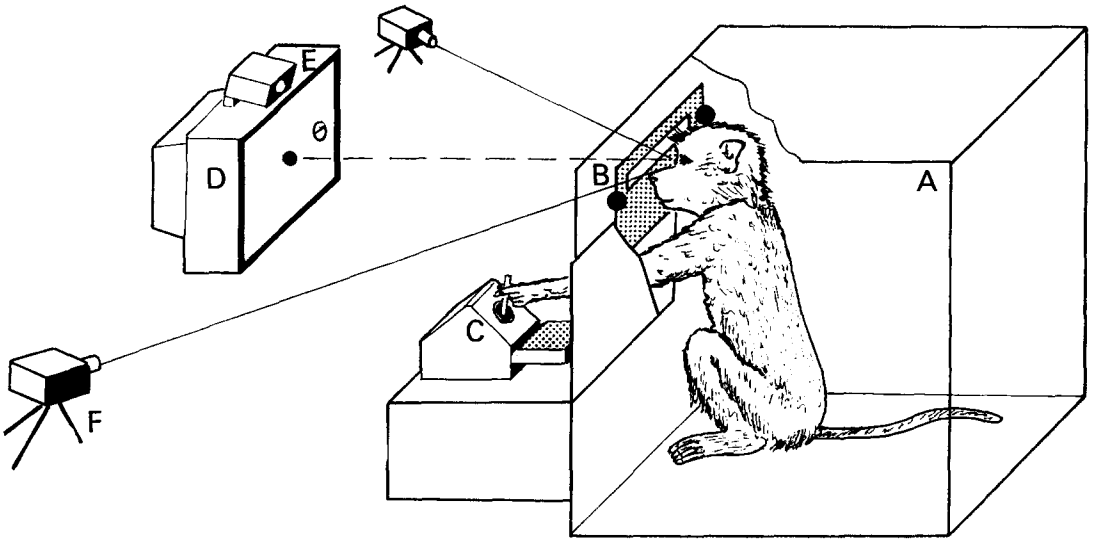

Fig. 1. Schematic view of the setup showing the testing cage (A), the infra-red filter with the view port (B), the joystick (C), the computer monitor (D), the infra-red light (E) and the two infra-red cameras (F).

set at approximatively 65 mm were mounted in a symmetrical arrangement on tripods at the view port level on both sides of the computer monitor. The cameras, which were sensitive to the infra-red light, pictured all essential parts of the monkey's face, while it had to look through the view port. Cameras were focused on the origin of a 3-dimensional (3D) coordinate system which was referring to for the computation of eye movements. The origin of the 3D system of coordinates was located about 3.0 cm behind the view port inside the experimental cage (see Fig. 1). The distance between the two cameras was 89.6 cm, and their optical axis sustained an angle of 45.6 degrees at the location of the origin of the system of coordinates. Each video camera was connected to one videotape recorder (Panasonic NV-H75) so as to register images at the rate of 50 pictures per second (i.e. one image every 20 ms). For a sharp recording of the monkey's face and eye movements (see Fig. 2), the face was illuminated by a 50 W infra-red light. The distance between the face and the lamp was 65.0 cm. Two infra-red diodes were fixed on each side of the view port. The diodes provided visual synchronization signals in order to map eye movements on the video-images with stimulus presentation on the computer screen. In summary, both the whole face of the animal and the synchronization diodes were recorded on the video-images of the two cameras. The face of the subject was videotaped through the infra-red filter in which the view port was cut. Subject's head position was kept

Fig. 2. Display of the face of the monkey as recorded during the study by the camera positioned at the left of the subject.

in a still position during trials by having the animal looking at the computer monitor through the view port cut in the filter.

2.1.3. Testing procedure

Two days prior to testing, the baboon was anesthetized with a light dose of Imalgene and a small mark of China ink was put on the median axis of the nose. This mark was later used to evaluate the position of the head during the analysis of eye movements.

A trial was started when the baboon placed one hand on the touch pad. This action led to the immediate display of a cursor (a green circle 0.5 cm in diameter) and of a fixation stimulus (0.5 × 0.5 cm white square) on the computer monitor. The cursor appeared in the center of the screen and the stationary FP was shown vertically 2.0 cm above or below the cursor. The subject had then to manipulate the joystick so as to place and maintain the cursor on FP for 35 ms. Once the cursor was located within the boundaries of FP, a sample stimulus (3.0 × 3.0 cm) appeared laterally during 140 ms in either the left or the right part of the screen[1].The inside edge of the sample stimulus was laterally displaced 5.1 cm left or right from the center of the fixation stimulus, corresponding for the animal to an eccentricity of 6.1° of visual angle.

Immediately after sample stimulus display, two 3.0 × 3.0 cm comparison forms appeared 3.5 cm above or below the cursor on the vertical axis of the computer screen. The subject was then required to touch with the cursor the comparison stimulus matching the sample. A correct response was recorded if the subject correctly chose the correct comparison form. An incorrect response was recorded when the subject touched with the cursor the comparison stimulus different from the sample stimulus. Correct responses were food reinforced with pellets and were accompanied by a tone. Incorrect responses were never food reinforced. They were followed by a low raucous tone and a time-out of 3 s.

The testing session consisted in 120 trials using five different white ASCII characters (e.g. M) as stimuli. Each stimulus was presented 12 times as the sample stimulus in both the left and right hemi-fields. The location of FP, either 2 cm above or below the cursor, was randomly selected by the test program on each trial. In the same way, the location of the correct comparison form (top or bottom of the screen) was balanced across trials. Eye movements were videotaped during the test. The outcome of the trials (success or failure) and response times were recorded by the computer. Prior to the test, the subject received 360 warming trials with the five stimuli employed in the actual testing.

2.1.4. Computation of eye movements

The method used to analyze eye movements is exposed in Wilde [24]. It is beyond the scope of this paper to present in detail any of the algorithms used with this technique, but intuitively, the direction of gaze during the test was estimated from the position of the head, and from the orientation of the left and right pupils by reference to the position of the head.

In order to monitor eye movements, video-images from both cameras were digitalized (768 × 576 pixels, 256 gray scales) and sychronized on a computer equipped with a digitizer hardware (Video-1000/256, Fricke, Berlin). The horizontal and vertical coordinates of five points in the face of the monkey (i.e. the outer corner of the left and right eyes, the dot on the nose, and the center of the left and right pupils) were obtained by marking them with the mouse cursor. X–Y coordinates expressed in pixels were firstly converted in a metric format. For that purpose, prior to the experiment, a scale was recorded by each camera in order to determine the factor of conversion for changing the distances in pixels to metric values. Then, on the basis of the pixel-metric conversion, the location of the five points was determined by reference to the origin of the three-dimensional system of coordinates[2].

The position of the head was defined by the location of the outer corners of the left and right eyes and by the location of the dot on the nose. For an accurate estimation of the gaze regardless of head position, the three points defining the position of the head were shifted along the axes and turned around the origin of the system of coordinates. In that standard position, the line between the outer corners of the eyes was laying on the X-axis of the system of coordinates, and its center point was located on the origin of the 3D system of coordinates. The point on the nose was laying on the Y-axis. From this position, the orientation of the eyes in relation to the position of the head was derived from the coordinates of the middle of the two pupils relative to the position of the head. Previous use of this technique with lion-tailed macaques [24] showed that it is accurate with a resolution of about 2 degrees in the vertical axis and about 1.5 degrees in the horizontal

[1] We have chosen a presentation time of 140 ms because this number is close to the values used in previous studies [2,10,12,22]. Additionally, 140 ms is a multiple of 20 ms, that is the inter-image time interval of the video system.

[2] The location of any point in the digitalized picture was derived from the values of two angles for both the horizontal and vertical planes. These angles were formed between the optical axes of the cameras, which focussed on the origin of the three-dimension system, and the straight lines between each camera and the point which position should be estimated. The searched cordinates were obtained at the point of intersection between the two straight lines connecting the two cameras to the point which location must be determined.

axis. Although this method is precise in time and space, analysis of the video-tapes is very time consuming (0.5–1 h per trial), which limits the number of trials that can be investigated.

2.2. Results

2.2.1. Overall accuracy and response time

The correct comparison form was selected on 70% of the trials. This level of performance demonstrates that responses were not chance driven, Chi square test, $\chi^2 = 19.2$, $P < 0.001$. On average, response times were equal to 767 ms (S.D. = 339). Response times were lower for the successful trials than for the unsuccessful trials (720 vs. 877 ms, respectively, $t_{118} = 2.37$, $P < 0.02$).

2.2.2. Horizontal component of the gaze

The horizontal component of the gaze was computed for the first 20 successful trials for which there was a sharp recording of the face. Special attention was given to the time (i.e. 140 ms) elapsed between the onset and the offset of the sample stimulus. Although video-images were collected at a rate of one image every 20 ms, on some trials ($n = 3$) only 6 instead of 7 images were recorded by each camera during sample presentation. This discrepancy appeared because shoots of video-images were not necessarily synchronized with the onset of the sample presentation. In the following analyses, eccentricities from 0 to 120 ms of sample presentation were computed on the trials ($n = 20$) for which at least 6 video-images were available. Eccentricities at 120–140 ms were derived from the subset of 17 trials for which 7 video-images were recorded.

Table 1 provides mean eccentricities between the location of the gaze and both the location of the FP and the inner side of the sample form. Remember that FP had already disappeared when the sample stimulus was displayed. In Table 1, positive values correspond to gaze locations within the hemi-screen of sample stimulus presentation. By contrast, values are negative when the gaze was located within the hemi-screen contralateral to the sample stimulus. Results show that the gaze remained in the vicinity of FP from 0 to 100 ms. During that time span, average eccentricities between the FP and the gaze ranged from −0.12° to 0.33°, which was not statistically different from 0°, that is the eccentricity for an exact centration of the gaze on FP. For 100–120 ms and 120–140 ms, the gaze deviated on average from the FP, as demonstrated by the significant two-tailed t-tests.

Similarly, during the initial 100 ms of sample presentation, lateral eccentricity relative to the inner side of the sample form ranged from 6.54° to 5.77°. These values were all significantly greater than 2.5°, that being the minimal eccentricity required for a perception of the sample form in peripheral vision [16]. After 100 ms of stimulus presentation, the gaze shifted toward the sample form, as revealed by reduced eccentricities between the gaze and the sample stimulus. For the two last series of measurements (i.e. 100–120 and 120–140 ms), horizontal eccentricities between the gaze and the inner side of the form were no more significantly different from 2.5°. Thus, on average, the subject effectively perceived the sample form in peripheral vision during the first 100 ms of its presentation. Later, the lateral eccentricity was no more sufficient to ensure a perception of the sample stimulus by the peripheral retina.

A close look at the results suggests some important inter-trials differences in the pattern of eye movements. In effect, two different types of trials were observed. On some trials, the lateral eccentricity between the location of the gaze and the inner side of the sample stimulus always

Table 1
Expt. 1: average horizontal eccentricities (in degrees) of the gaze relative to (1) the location of FP, and (2) the inner side of the sample stimulus for every 20 ms of sample presentation

	Fixation point			Sample stimulus	
	Mean	S.D.	t	Mean	t
0–20 ms	−0.12	2.45	$t_{19} = 0.22$, ns	6.22	$t_{19} = 6.25$, $P < 0.001$
20–40 ms	−0.44	1.94	$t_{19} = 1.02$, ns	6.54	$t_{19} = 9.31$, $P < 0.001$
40–60 ms	−0.33	1.96	$t_{19} = 0.75$, ns	6.43	$t_{19} = 8.98$, $P < 0.001$
60–80 ms	−0.24	1.97	$t_{19} = 0.55$, ns	6.34	$t_{19} = 8.69$, $P < 0.001$
80–100 ms	0.33	2.34	$t_{19} = 0.64$, ns	5.77	$t_{19} = 6.25$, $P < 0.001$
100–120 ms	3.04	3.01	$t_{19} = 4.52$, $P < 0.001$	3.06	$t_{19} = 0.83$, ns
120–140 ms	4.41	2.06	$t_{16} = 8.83$, $P < 0.001$	1.69	$t_{16} = 1.62$, ns

For eccentricities relative to FP, ts and associate probabilities derived from the computation of two-tailed t-tests for a difference between a sample mean and a theoretical value of 0, which corresponded to an exact centration of the gaze on FP. For eccentricities relative to the location of the sample stimulus, ts and associate probabilities derived from two-tailed t-tests for a difference between a sample mean and the theoretical value of 2.5°, that being the minimal eccentricity required for a perception of the sample form in peripheral vision[16]. ns = non-significant difference.

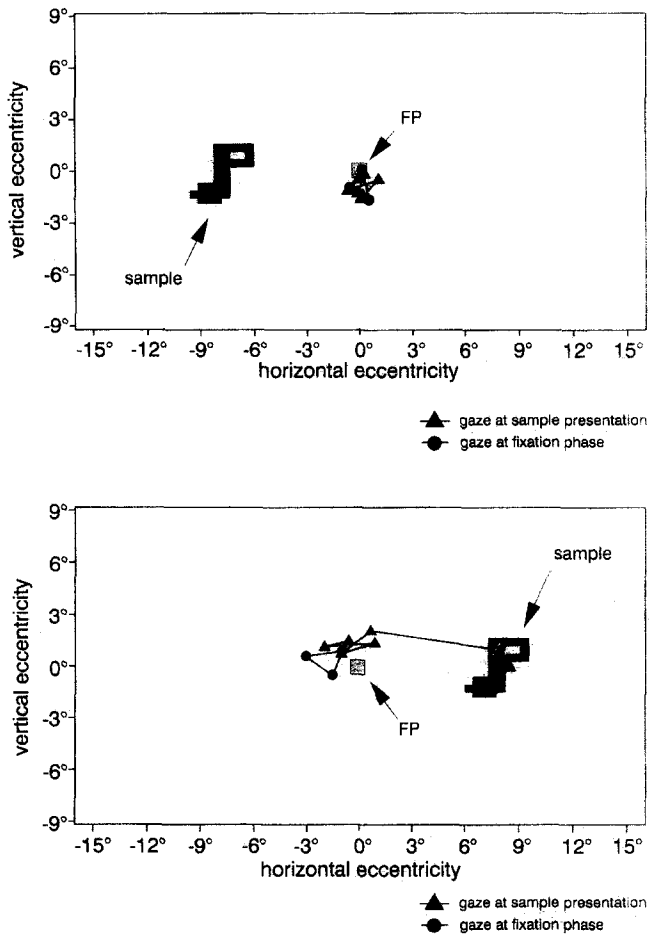

Fig. 3. Top: eye movements in a single trial in which the gaze was maintained in the vicinity of FP during the entire duration of sample presentation (i.e. 140 ms). Bottom: eye movements in a single trial in which the subject performed an E-saccade towards the sample form at 00 ms of its presentation. Note that gaze location was determined every 0 ms. Open circles = gaze location during the 60 last milliseconds of the xation period. Triangles = gaze location during sample presentation.

emained greater than 2.5°. This type of trials is illustrated n the top of Fig. 3. Such an eccentricity suggests that the aboon perceived the sample in peripheral vision. The econd type of trials is illustrated on the bottom of Fig. 3. n that case, the subject made goal-directed saccades toward the sample stimulus after 100 ms or 120 ms. Overall, the gaze eccentricity relative to the inner side of the ample form was smaller than 2.5° for 1, 0, 0, 0, 1, 8, and 0 trials respectively for each time span from 0–20 to 20–140 ms.

.2.3. Vertical component of the gaze

The analysis of the vertical component of the gaze was erformed on the same 20 correct trials as previously. For hose trials, vertical eccentricities were computed taking nto account the location of FP on the vertical axis of the omputer monitor (i.e. either 2.0 cm above or below the enter of the screen). Table 2 shows, for every 20 ms of

Table 2
Expt. 1: average vertical eccentricities of the gaze (in degrees) relative to the location of FP for every 20 ms of the sample stimulus presentation

	Mean	S.D.	t
0–20 ms	0.71	2.65	$t_{20} = 1.19$, ns
20–40 ms	0.46	2.65	$t_{19} = 0.77$, ns
40–60 ms	0.67	2.65	$t_{19} = 1.13$, ns
60–80 ms	0.39	2.62	$t_{19} = 0.67$, ns
80–100 ms	0.28	2.47	$t_{19} = 0.50$, ns
100–120 ms	0.00	2.83	$t_{19} = 0.00$, ns
120–140 ms	0.09	2.56	$t_{16} = 1.54$, ns

ts and associate probabilities derived from two-tailed t tests for a difference between a sample mean and the theoretical mean of 0°, that was the mean for an exact centration of the gaze on FP. ns = nonsignificant difference.

sample presentation, average vertical eccentricities relative to FP. Positive values in Table 2 correspond to gaze positioning above FP, and negative values depict gaze positioning below FP. Very few vertical variations in eye movements were found during the display of the sample form (range 0° to −0.71°).

2.2.4. Analysis of errors

Given that eye movements could differ between successful and unsuccessful trials, eye saccades were examined in the 20 first incorrect trials of the testing session. Time elapsed from the onset of the sample form to the first visible saccade was estimated from the number of frames that were counted from the video-tape. The direction of the saccade (left or right) was also recorded. In one of the 20 trials, the subject was not looking at the screen during sample presentation. In the remaining 19 trials, the mean latency of E-saccades was 117.8 ms (range 100–160 ms) which is in the range of the latencies of E-saccades for correct trials. Note also that all the saccades in error trials were accurate in direction, which suggests that they were goal-directed. Hence, patterns of eye movements for incorrect trials appeared to be very similar in latency and direction to those of correct trials.

2.3. Discussion

The aim of Expt. 1 was to record eye movements in a divided-field MTS task that is analogous to the tachistoscopic mode of stimulus presentation. Four conclusions can be drawn from this study. First, the behavioral procedure to have the animal looking at the fixation point, namely the adjustment of a cursor on FP, effectively implied a centration of the gaze on FP. This result is attested by the minimal lateral eccentricity of the gaze (i.e. −0.12°) relative to FP, during the very first 20 ms of sample

presentation (see Table 1). Second, no goal-directed saccades were observed from 0 to 100 ms, suggesting that the sample was at least initially perceived in peripheral vision. Third, on almost half of the trials, goal-directed saccades toward the sample stimulus were observed with latencies as short as 100 or 120 ms. Fourth, saccades for incorrect trials had latencies in the same range as those of correct trials. Expt. 1 thus validates the divided-field procedure, as long as the sample stimulus is not presented for durations longer than 100 ms.

3. Experiment 2

In Expt. 1, the fastest saccades had latencies ranging from 100 to 120 ms. This finding is at variance with the latencies, ranging from 180 to 250 ms, generally reported in the literature [6]. Although performed with extremely short latencies, saccades observed after 100–120 ms of sample display were accurate in direction. They were thus goal-directed instead of random in direction, due for instance to some anticipations.

Several studies have reported that goal-directed E-saccades can be found with latencies as short as 100 ms for humans [4,5], or even 70 ms for monkeys [3,5]. According to Fischer & Weber [5], the frequency of E-saccades depends on the temporal and spatial parameters of the fixation procedure. Specifically, E-saccades would increase in frequency in gap trials, that is when FP disappears from the screen before the onset of the stimulus. Conversely, E-saccades would decrease in frequency in overlap trials, that being when FP remains visible during sample presentation [19,20,21]. The aim of Expt. 2 was to test if the mean latency of the saccades would increase, and their frequency decrease, when FP remains visible during sample stimulus presentation (i.e. in overlap trials).

3.1. Material and methods

3.1.1. Subject, apparatus and procedure

The same baboon as previously was tested. All the experimental conditions were similar to those of Expt. 1. The unique change in the procedure concerned the temporal attributes of FP. In this experiment, instead of disappearing when the sample form appeared, FP remained visible during sample stimulus presentation. The baboon received 360 warming overlap trials in two consecutive days before the onset of the Expt. 2.

3.2. Results

3.2.1. Accuracy scores and response times

The baboon selected the correct comparison form 86 times (71.7%) over the series of 120 trials. This level of performance is significantly above chance as demonstrated by a Chi-square analysis, $\chi^2_1 = 22.5$, $P < 0.001$. In addition, accuracy in Expt. 2 was not statistically different from accuracy in Expt. 1, $t_{238} = 0.28$, ns.

Mean overall response time in Expt. 2 was 689.4 ms. As in Expt. 1, successful trials corresponded to shorter response times on average (630.9 ms) compared to unsuccessful trials (837.5 ms), $t_{118} = 2.9$, $P < 0.01$. No significant difference was found between response times for correct trials in Expt. 1 and Expt. 2, $t_{168} = 1.68$, ns. Hence, patterns of scores and response times were very similar in both experiments.

3.2.2. Horizontal component of the gaze

The first 20 correct trials for which a sharp recording of eye movements was available were analyzed. Table 3 provides mean eccentricities relative to the location of FP and the location of the sample form, for every 20 ms of presentation time. Positive values on Table 3 correspond to

Table 3
Expt. 2: average horizontal eccentricities (in degrees) of the gaze relative to (1) the location of FP, and (2) the inner side of the sample stimulus for every 20 ms of sample presentation

	Fixation point			Sample stimulus	
	Mean	S.D.	t	Mean	t
0–20 ms	0.35	1.58	$t_{19} = 0.98$, ns	5.75	$t_{19} = 9.20$, $P < 0.001$
20–40 ms	−0.05	1.04	$t_{19} = 0.21$, ns	6.15	$t_{19} = 15.65$, $P < 0.001$
40–60 ms	0.37	1.28	$t_{19} = 1.29$, ns	5.73	$t_{19} = 11.24$, $P < 0.001$
60–80 ms	0.39	1.00	$t_{19} = 1.73$, ns	5.71	$t_{19} = 14.41$, $P < 0.001$
80–100 ms	0.51	1.01	$t_{19} = 2.28$, $P < 0.05$	5.85	$t_{19} = 13.70$, $P < 0.001$
100–120 ms	2.25	2.69	$t_{19} = 3.75$, $P < 0.002$	3.85	$t_{19} = 2.24$, $P < 0.05$
120–140 ms	3.41	2.43	$t_8 = 4.26$, $P < 0.003$	2.69	$t_8 = 0.23$, ns

See legend of Table 1.

gazes within the hemi-screen in which the sample was presented. Because the shoots of video-images were not necessarily synchronized with the onset of sample presentation, 7 images were recorded for 9 trials, whereas 6 images were recorded for the 11 remaining trials. Hence, data from 0 to 120 ms derived from 20 trials, and 120–140 ms data were computed on the subset of 9 trials for which 7 video-images were available.

On average, the gaze remained in the vicinity of FP from 0 to 80 ms of sample presentation (see Table 3). After 80 ms of sample presentation, the gaze significantly deviated from FP. However, the deviation remained of reduced amplitude at 80–100 ms (mean = 0.51°), the maximal eccentricity being reached at 100–120 ms and 120–140 ms (2.25° and 3.41°, respectively). Table 3 also shows that, from 0 to 120 ms, mean lateral eccentricities between the gaze and the sample form were all significantly greater than 2.5°. At 120–140 ms, mean lateral eccentricities was 2.69°, which was not significantly different from 2.5°. One can thus conclude that the sample form was on average seen in peripheral vision during the initial 120 ms of its presentation. Later, lateral eccentricity were no more sufficient to ensure a perception of the sample form by the peripheral retina.

We have counted, for every 20 ms of sample presentation, the number of trials in which the gaze was positioned at a lateral eccentricity smaller than 2.5°. These numbers were equal to 1, 0, 0, 0, 0, 4 and 4, respectively for each 20 ms time span from 0 to 140 ms. At 100–120 ms, the number of observed saccades (i.e. 4/20) was half of the number found in Expt. 1 (i.e. 8/20). By contrast, the rate of saccades performed toward the sample at 120–140 ms was very similar in both experiments (Expt. 1: 10/17 trials; Expt. 2: 4/9). In conclusion, comparison of the data from Expt. 1 and Expt. 2 shows that the overlap procedure reduced the frequency of E-saccades with 100–120 ms of latency.

3.2.3. Vertical component of the gaze

Table 4 reports mean vertical eccentricities for Expt. 2. Data reported on Table 4 were computed by using the same procedure as for Table 2. On average, vertical variations of the gaze were minimal (range = −0.57°,0.02°, see Table 4)). Hence, the gaze remained at the level of FP during sample presentation.

3.2.4. Analysis of errors

Error trials were analyzed by counting the time (i.e. number of frames) elapsed from the onset of the sample form to the onset of the first visible saccade on the tape. As before, this analysis was performed on the 20 first trials in which the subject selected the incorrect comparison form. On 3 of those 20 incorrect trials, the subject was not looking at the screen during sample presentation. For the remaining trials, saccades were all accurate in direction. For those latter trials, mean latency was 136.5 ms (range 100–180 ms), which is about 20 ms longer than the mean latency (i.e. 120 ms) for incorrect trials in Expt. 1. Statistical analyses indicated a trend for longer latencies in Expt. 2 compared to Expt. 1, t-test, $t(34) = 1.95$, $P = 0.06$.

Table 4
Expt. 2: average vertical eccentricities of the gaze (in degrees) relative to the location of FP for every 20 ms of sample presentation

	Mean	S.D.	t
0–20 ms	−0.32	1.99	$t_{19} = 0.72$, ns
20–40 ms	−0.27	1.91	$t_{19} = 0.63$, ns
40–60 ms	−0.49	2.14	$t_{19} = 1.02$, ns
60–80 ms	−0.57	1.77	$t_{19} = 1.34$, ns
80–100 ms	−0.27	1.20	$t_{19} = 1.01$, ns
100–120 ms	−0.47	1.28	$t_{19} = 1.63$, ns
120–140 ms	0.02	1.30	$t_{19} = 0.05$, ns

See legend of Table II.

3.3. Discussion

Expt. 2 replicated the findings of Expt. 1 in that it demonstrated (1) the effectiveness of the fixation procedure in the divided-field MTS task, and (2) the existence of goal-directed saccades with short latencies. Moreover, Expt. 2 showed that introducing an overlap paradigm in the MTS task reduced the frequency of E-express with 100–120 ms of latency, for both correct and incorrect trials. Results of Expt. 2 thus suggest that the use of an overlap procedure can be beneficial, in that it can allow for a longer presentation of the sample form in the divided-field task. Its remains unclear however, from that experiment on a single subject, if the overlap procedure can affect accuracy and response times.

4. Experiment 3

The aim of Expt. 3 was to determine the possible effects of the overlap procedure on performance. In that experiment, a larger group of subjects was tested on both overlap and non-overlap conditions. Additionally, duration of sample presentation varied in order to indicate if presentation time could also affect performance.

4.1. Material and methods

4.1.1. Subjects and apparatus

Subjects were 4 wild-caught 5-year-old baboons (*Papio papio*), 1 male and 3 females, including the one used in the

two previous experiments. All subjects had the same living conditions, and were familiar with the matching-to-sample testing in the divided-field format, because they were used in previous experiments [2,10]. The apparatus was identical to that of Expt. 1.

4.1.2. Testing conditions

The basic procedure was the same as before. The testing was composed of 4 sessions of 160 trials, using a set of 20 different 3×3 cm yellow ASCII characters serving as sample and comparison forms. Within a session of 160 trials, each stimulus served 4 times as the sample in the left and right visual-half field. For 2 of those 4 presentations, the correct comparison form was located on the top of the screen. It was presented on the bottom in the remaining 2 trials. On each trial, the comparison form was randomly selected among the 19 stimuli different from the sample. Note that subjects were familiar with the stimuli used in the test, because these stimuli have been used in previous trainings [2,10].

The sample was presented either 50 ms (two sessions) or 95 ms (two sessions). In one session per presentation time, an overlap procedure was adopted, whereas in the other session, there was no temporal overlap between the FP and the sample. Two baboons (one male, one female) used the right hand for joystick manipulation, the other two used the left hand. The order of sessions was balanced across subjects. The order of trial presentation within a session was randomly selected prior to the session; it was thus different from one session to the other, as well as from subjects to subjects.

4.2. Results

Overall accuracy was 70.4 percent correct. All subjects performed above chance as indicated by a Chi square analysis (all Ps < 0.05). Accuracy data were analyzed using a three-factor $2 \times 2 \times 2$ analysis of variance (ANOVA) with the visual-half field (left, right), the overlap condition (overlap, non-overlap), and the duration (50, 95 ms) serving as the within subject factors. Trials in which response times were lower than 100 ms or greater than 3 s were discarded from the ANOVA, because of the possibility that the subjects could anticipate the response or experience some difficulties in responding (e.g. because of distraction). These trials represented 11.9% of the total trials. The ANOVA indicated that the effect of field was significant ($F_{1,3} = 35.9$, $P < 0.01$), corresponding to greater scores for right-visual field/left hemisphere presentations (mean correct = 74.3%) than left-visual field/right hemisphere presentations (mean correct = 67.9%). Accuracy was slightly lower in the overlap condition (mean correct = 68.8%) compared to the non-overlap condition (mean correct = 72.0%), but the difference was not statistically significant. Other main effects or interactions did not reach significance.

In complement to the previous analyses, an ANOVA was performed on correct response times with the visual-field (left, right), overlap condition (overlap, non-overlap) and duration (50, 95 ms) serving as the unique within subject factors. Mean response time was 574 ms. No significant main effect or interaction emerged from the analysis of correct response times (mean overlap = 601 ms; mean non-overlap = 548 ms, ns).

5. General discussion

The data of this series of experiments constitute the first empirical evidence that the divided-field MTS task is an efficient way of restricting the visual input in one visual half-field only, which is a critical attribute of tasks devoted to the study of lateralization for visual processing in intact animals [9]. However, while our approach showed the efficiency of this MTS procedure, it also revealed some of its limits. Because of the existence of E-saccades, the data suggest that the sample form should not be presented for durations longer than 100 or 120 ms. This finding calls for two remarks. First, it should be kept in mind that the current data on eye movements (Expts. 1 and 2) derived from the study of a single subject. Thus, these two experiments provide no insight on the inter-individual variability in the latency or frequency of E-saccades. Second, as claimed by Fischer et al. [4], the rate and speed of E-saccades in monkeys is affected by the amount of practice, although E-saccades can be obtained in naive human subjects without training [5]. Prior to this experiment, the baboon used in Expts. 1 and 2 has involved during two years in several behavioral studies [2,10,22]. It is thus hypothesized that practice effects were at their maximum for that baboon.

In accordance with observations made by others [19,20,21], Expt. 2 demonstrated that the overlap procedure increased the latency of E-saccades. The overlap procedure had no direct effects on response times or accuracy scores, as demonstrated by the statistical comparison between Expts. 1 and 2 and by Expt 3. Methodologically, the use of the overlap procedure in conjunction with the divided-field MTS task appears to be advantageous, in that it allows for a longer presentation of the sample form. Hopkins and Morris [11] found in a related task, that accuracy scores increased with the increment of the sample presentation time. Such an effect was not observed in Expt. 3, perhaps because subjects were highly familiarized with the stimulus set.

However, the overlap procedure might not be the unique

way to delay the latencies of E-saccades. For example, in an experiment made with human subjects, Jüttner and Wolf [15] used catch trials mixed with regular trials, catch trials being defined as trials in which the sample form was not presented after the fixation of the eye on FP. These authors observed that, when catch trials increased in frequency, the probability of occurrence of E-saccades decreased and that of longer saccades rose. This effect was mostly apparent in trials that immediately followed catch trials. Hence, although to our knowledge this effect has not been investigated in monkeys, Jüttner and Wolf's [15] study calls for the additional introduction of the catch procedure in the divided-field MTS task, along with the use of the overlap procedure.

Finally, Expt. 3 revealed greater scores when the sample was shown in the left visual half field/right hemisphere compared to presentations in the contralateral right visual half field. This finding, which is in agreement with previous observations [2,11], suggests that the lateralization of the visual input might induce differential treatments in the left and right cerebral hemisphere. The divided-field MTS task is thus a useful and a valid technique to investigate hemispheric lateralization in intact primates, including humans.

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