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Analysis of microsaccades during extended practice of a visual discrimination task in the macaque monkey

Milena Raffi, Andrea Meoni, Alessandro Piras

Department of Biomedical and Neuromotor Sciences, University of Bologna, Bologna, Italy

Corresponding Author:

Milena Raffi
Department of Biomedical and Neuromotor Sciences
University of Bologna
Piazza di Porta San Donato 2
40126 Bologna, Italy
Email address: milena.raffi@unibo.it

Abstract

The spatial location indicated by a visual cue can bias microsaccades directions towards or away from the cue. Aim of this work was to evaluate the microsaccades characteristics during the monkey's training, investigating the relationship between a shift of attention and practice. The monkey was trained to press a lever at a target onset, then an expanding optic flow stimulus appeared to the right of the target. After a variable time delay, a visual cue appeared within the optic flow stimulus and the monkey had to release the lever in a maximum reaction time (RT) of 700 ms. In the control task no visual cue appeared and the monkey had to attend a change in the target color. Data were recorded in 9 months. Results revealed that the RTs at the control task changed significantly across time. The microsaccades directions were significantly clustered toward the visual cue, suggesting that the animal developed an attentional bias toward the visual space where the cue appeared. The microsaccades amplitude differed significantly across time. The microsaccades peak velocity differed significantly both across time and within the time delays, indicating that the monkey made faster microsaccades when it expected the cue to appear. The microsaccades number was significantly higher in the control task with respect to discrimination. The lack of change in microsaccades rate, duration, number and direction across time indicates that the experience acquired during practicing the task did not influence microsaccades generation.

Introduction

The sensory systems continuously receive signals, which cannot be simultaneously analyzed at the conscious level. Raja Parasuraman [18] identified three different components of attention: 1) selective attention (or selection), which determines the processing of peculiar information; 2) vigilance, the ability to maintain attention over time; 3) control, the ability to plan and coordinate different activities. Attentional processes vary in relation to the object of attention, the way in which attention is expressed and the time periods in which these mechanisms occur. Spatial attention represents a submodality of attention, which participates in all attentional processes. Spatial attention allows the observer to selectively analyze visual information, prioritizing a specific region of the visual field; information coming from the specific region then receives further processing.

Our eyes are never still. Small eye movements, called, microsaccades, change the position of the eyes [15]. Previous studies linked microsaccades to perception [14, 16] and determined the key interactions between the dynamics of microsaccades and cognitive processes, especially regarding the location of attention [5, 8, 20-23]. The spatial position indicated by an attentional signal can influence the direction of the microsaccades towards or away from that signal: endogenous stimuli tend to shift attention towards the signal, while exogenous stimuli tend to remove it [7].

The relationship between attention and microsaccades has been extensively studied both in human subjects and in non-human primates using attentional, cued or discrimination tasks. However, little is known about the time course of the microsaccades during the entire process of learning and practicing a visual task that requires the orientation of attention. In the last decade, a number of studies showed that specific conditions modulate microsaccades, like exogenous emotional stimuli [11], multisensory integration [33] and cognitive processing load [4, 6]. These studies encouraged us to evaluate if the consolidation of a learning process, which requires different cognitive processing loads across time, influences the microsaccades generation.

Materials & Methods

The experiments were performed on one male macaque monkey (*M. fascicularis*). All experimental procedures received the approval of the Committee on Ethics in Animal Experimentation of the University of Bologna and of the Italian Ministry (approval n. 258/2015-PR).

Surgical procedures

Before the beginning of the training, three metal skull pins for restraining the head were implanted by using titanium screws. Surgical procedures were performed under general anesthesia (Thiopenthotal Sodium 15 mg/Kg i.v.). Analgesic and antibiotics were given for several days after surgery (Ketorolac tromethamine, 30 mg/die i.m.; Benzathine Benzylpenicillin 0.1 ml/Kg i.m.) following the same protocol used in previous studies [25-30]. During the experiments, the head was restrained using a halo head fixation system similar to that describer by Azimi et al. [1]. After recovering from surgery, the monkey started the training procedure.

Experimental paradigm

The monkey sat in a primate chair in front of a TV monitor covering 62 x 51° of visual field. The screen was placed 57 cm from the monkey's eyes. The monkey was trained in looking at a fixation point (FP) formed by a red square (0.5° side), in a visual discrimination task. At the FP onset, the monkey pressed a lever and an expanding optic flow stimulus appeared to the right of the fixation point. After a variable delay of 750, 1000, 1250 or 1500 ms, a visual cue appeared within the optic flow stimulus and the monkey was trained to release the lever in a maximum RT of 700 ms. The optic flow stimulus was 8° in radius and the focus of expansion was positioned 15° of eccentricity from the FP. The visual cue was a small sphere composed of dots, which moved randomly within the sphere (Figure 1A). The sphere used as visual cue had a radius of 2°. The random movement of the dots made the sphere very visible because the dots of the optic flow stimulus moved in radial expansion. We used a control task in which no visual cue appeared within the optic flow stimulus and the monkey was trained to attend a change in the target color (Figure 1B). To avoid the effect of timing, the recordings were performed in random order. Visual stimuli were generated using the Matlab Psychophysical Toolbox. A drop of water was given as a reward for each correct trial. Eye movements were recorded binocularly by the EyeLink II (SR Research Ltd, Mississauga, Canada). Pupil tracking was performed at 500 samples/s, with a gaze resolution $<0,005°$ and noise limited to $<0.01°$. Trials with eye positions outside a 1° window around FP were discarded.

Data analysis

The RTs related to the control and discrimination task were analyzed for each data set. To analyze the potential RT changes through the entire training period of nine months, we divided the RT values into six epochs. Each epoch contained the same number of data (i.e. training days) corresponding to about 5-6 weeks of training. The monkey's RTs have been analyzed using a repeated measure analysis of variance (ANOVA) having the RTs of time delay (750, 1000, 1250, 1500 ms), task (discrimination, control) and epochs (month 1-9) as within subject factors. The data were analyzed with the SPSS v22.0 statistical software (SPSS, Chicago, IL, USA).

Microsaccades are defined as eye movements with an amplitude less than 1° and with a peak velocity up to 100°/s [34]. For the identification of microsaccades we used the algorithm of Engbert and Kliegl [5]. Partial and complete pupil occlusions, including the previous and subsequent 200 ms from the occlusion, were discarded. Microsaccades amplitude, peak velocity, number, rate, duration and direction were calculated and averaged in each task and in each time delay of each experiment. The frequency of the microsaccades was calculated considering only the time spent during the fixation period, dividing the number of microsaccades by the duration of the recording in seconds [17]. The potential variations of microsaccades across the entire period of training were assessed on each parameter (amplitude, peak velocity, number, rate and duration) using a repeated measure ANOVA having the time delay, task and epochs as within-subject factors.

The relationship between microsaccades amplitude and peak velocity (the main sequence), and the correlation between RT changes and variations of microsaccades across the six epochs were assessed using the Pearson correlation coefficient.

Microsaccades directions were analyzed in each epoch using circular statistics (Oriana® 4.0 for Windows, Kovach Computing Services, Anglesey, Wales). The uniformity of the mean vectors distribution was assessed with the Rayleigh test.

Results

Reaction times

Results of the repeated measure ANOVA on the RTs showed a significant main effect for task ($F_{1,1} = 777.66$; $p < 0.001$; $\eta_p^2 = 0.985$), time delay ($F_{1,3} = 26.63$; $p < 0.001$; $\eta_p^2 = 0.685$) and epochs ($F_{1,5} = 6.002$; $p < 0.001$; $\eta_p^2 = 0.333$). Moreover, significant interaction effects were observed for task x time delay ($F_{1,3} = 16.77$; $p < 0.001$; $\eta_p^2 = 0.583$), task x epochs ($F_{1,5} = 10.812$; $p < 0.001$; $\eta_p^2 = 0.474$), time delay x epochs ($F_{1,15} = 4.353$ $p < 0.001$; $\eta_p^2 = 0.266$) and for all factors: task x time delay x epochs ($F_{1,15} = 3.582$ $p < 0.001$; $\eta_p^2 = 0.23$) (Figure 2). The Bonferroni pairwise comparison showed that the RTs in the visual discrimination task were significantly longer than those of the control task ($p < 0.001$). Regarding the time delay, the Bonferroni pairwise comparison showed that the RTs of the 750 ms (the shorter fixation period) were significantly different than those of the other fixation times (750 vs 1000 $p = 0.003$; 750 vs 1250 $p < 0.001$; 750 vs 1500 $p < 0.001$). Regarding the epochs, significant differences were found between epochs 1 and 3 ($p = 0.003$), epochs 2 and 3 ($p = 0.001$) and epochs 3 and 6 ($p = 0.033$).

During the training, the monkey made very few errors. In the 750 ms delay, the correct trials were 6901 (92.5%), while the early releases of the key were 147 (2%) and the late releases 405 (5.5%). In the 1000 ms delay, the correct trials were 5992 (93%), the early releases 286 (4%) and the late releases 172 (3%). In the 1250 ms delay, the correct trials were 4956 (88%), the early releases 581 (10%) and the late releases 118 (2%). In the 1500 ms delay, the correct trials were 4476 (77.5%), the early releases 1185 (20.5%) and the late releases 103 (2%). The only notable result is in the increase in the early release of the key that increases with the increment of the time delay.

Microsaccades

The microsaccades main sequence, i.e. the relationship between amplitude and peak velocity, showed that the monkey made very fast microsaccades with large amplitude corresponding to the stimulus eccentricity (Figure 3). Analysis showed positive correlation coefficients between amplitude and peak velocity for both discrimination ($r = 0.53$, $p < 0,001$) and control task ($r = 0.52$, $p < 0,001$).

Results of the repeated measure ANOVA on the microsaccades peak velocity (Table 1) showed a significant main effect for epochs ($F_{1,5} = 9.43$; $p < 0.001$; $\eta_p^2 = 0.35$) and time delay ($F_{1,3} = 4.94$; $p = 0.004$; $\eta_p^2 = 0.22$) and a significant interaction effect of epochs x time delay ($F_{1,15} = 2.19$; $p = 0.007$; $\eta_p^2 = 0.11$). The Bonferroni pairwise comparison on the time delays showed few differences in the microsaccades peak velocity (1000 vs 1500 $p = 0.035$; 1250 vs 1500 $p = 0.049$). Regarding the epochs, significant differences were found between epochs 1 and 2 ($p = 0.048$), epochs 2 and 4 ($p = 0.009$), epochs 2 and 5 ($p = 0.037$), epochs 4 and 6 ($p = 0.005$) and epochs 5 and 6 ($p = 0.001$).

The analysis of the microsaccades amplitude (Table 1) showed a significant main effect for epochs ($F_{1,5} = 6.97$; $p < 0.001$; $\eta_p^2 = 0.29$). The Bonferroni pairwise comparison showed that all epochs differed significantly from each other (all significant values were smaller than 0.007).

The analysis of the microsaccades number (Table 1) showed a significant main effect for condition ($F_{1,1} = 50.16$; $p < 0.001$; $\eta_p^2 = 0.74$).

No significant differences were found for microsaccades rate and duration.

Results of the circular statistical analysis showed that microsaccades directions were significantly clustered toward the optic flow stimulus in all 6 epochs of the training period (Figure 4). The Rayleigh test of uniformity showed non-uniform significant distribution for both discrimination and control task ($p < 0.001$).

Correlation between microsaccades and RTs

We correlated the microsaccades values with the RTs at the discrimination task in the 6 epochs. In the 750 ms delay, in epoch 1 RTs were correlated with microsaccades duration ($r = 0.56$, $p = 0.049$), while in epoch 6 RTs were correlated with both amplitude ($r = 0.69$, $p = 0.009$) and duration ($r = 0.75$, $p = 0.003$). In the 1000 ms delay, in epoch 1 RTs were correlated with microsaccades number ($r = 0.62$, $p = 0.022$). In the 1250 ms delay, in epoch 3 RTs were correlated with microsaccades amplitude ($r = 0.68$, $p = 0.01$). In the 1500 ms delay, in epoch 1 RTs were negatively correlated with microsaccades amplitude ($R = -0.62$, $p = 0.022$) and rate ($r = -0.63$, $p = 0.018$), while in epoch 6 RTs were negatively correlated with microsaccades rate ($r = -0.71$, $p = 0.006$).

Discussion

Behavioral reaction times

The RTs in the control task were constantly shorter than those of the discrimination task, indicating that the perceptual processing of shifting attention toward the visual cue lasts about 150-200 ms. Results show that the monkey's strategy was very specific: we observed the longest RTs in the discrimination task during the shorter time delay (750 ms). RTs then reduced in all other conditions with longer cue presentation time suggesting that the monkey did not pay attention to the optic flow stimulus from the beginning of the task, but oriented its attention later in time.

The sudden onset of a visual stimulus draws attention toward the stimulus location enhancing perceptual sensitivity [19]. Krishna et al. found that manual reaction times on a detection task were slower when the attentional cue appears at a saccade goal [13]. In our study, eye movements outside the tolerance window of 1° caused the end of the trial, so the monkey was prevented to make a saccade toward the optic flow stimulus. However, the monkey's attentional requirements could have inhibited the eye-movement generation causing an increase in the attentional processing, and thus an increase in reaction times. This potential inhibitory process might be linked with the inhibition of return, where manual reaction times are slower in response to stimuli presented at previously cued locations [7, 12, 24]. We point out that the monkey continuously shifted its attention to the previous cued location, so that the slowdown of RTs in the shorter conditions can be explained by an inhibitory effect resulting from the necessity of suppressing the natural tendency to make a saccade toward a cue [2, 3, 12].

The concept of attention is very complex as it involves many multi-channel sensorimotor systems [10]. The attentional strategy used by our monkey represents a good example of different sensory-motor processing, as it was slower with shorter presentation times and faster with longer presentation times. In our protocol, the monkey did not know if the trial would be discrimination or control. We see that the monkey always made microsaccades toward the optic flow stimulus but the RTs analysis seems to indicate that the change in color of the fixation point (from red to green) was a much stronger stimulus for lever release than the visual cue. Presumably, the monkey's attention was focused on the fixation point and the monkey continuously changed its strategy shifting attention to the optic flow stimulus to be able to perform the discrimination task. As already suggested by Krishna et al. [13], this strategy change could involve a greater engagement of endogenous attention.

Microsaccades characteristics

Microsaccades rate, duration, direction and number did not vary across the nine months of recordings, likely indicating that the monkey, to discriminate the stimulus, established a strategy at the beginning of the training, keeping it for the whole practice process. The lack of change in microsaccades production could be explained by the microsaccadic inhibition. This phenomenon was initially observed after the presentation of attentional cues, but it is now well known that microsaccades generation is affected by any transient stimulus, like the sudden appearance of an object or the change in contrast [5, 8, 31, 32]. Further, visual stimulus features can modulate the duration of the inhibition and/or the strength and latency of the subsequent rebound [9].

The time since the last microsaccade is indicative of the likelihood of an upcoming movement [9]. Using a neural network model, Hafed and Ignashchenkova explained that microsaccades can occur at specific phases of ongoing physiological α rhythms and these movements also exhibit signatures of oscillatory behavior. When such a rhythm is phase reset by stimulus onsets then the classic microsaccadic rate signature would be expected [9]. The stimuli used in the present study were presented to the monkey for nine months. It is possible to hypothesize that the microsaccades production did not change across time due to the identical stimulus features, which could have made such oscillatory behavior very constant. Future study could be designed to confirm this hypothesis changing the stimuli features, like contrast, spatial position (i.e. left-right or up-down) and optic flow direction. In this study protocol, we only used one optic flow stimulus without varying the focus of expansion eccentricity, the spatial position and the dot speed because changing such features would have complicated the monkey's training resulting in a misleading interpretation of the results.

The analysis of the main sequence showed that the monkey made very fast microsaccades with large amplitude corresponding to the stimulus eccentricity. Amplitude and peak velocity showed significant differences across the entire period of recordings, however, the microsaccades directions were clustered where the visual cue was expected to appear. This is in line with the strategy to make faster microsaccades when the monkey expected the cue to appear.

The microsaccades number was significantly higher in the control task in all conditions. This is interesting, as the monkey did not know if the trial would be discrimination or control until the cue onset or the change in target color. It is possible to hypothesize that the monkey focused more on the fixation point making more microsaccades toward the optic flow stimulus.

Lastly, the circular analysis showed that microsaccades directions have been clustered toward the optic flow stimulus for the entire training process. Such spatial asymmetry of the microsaccades suggests that the animal developed an attentional bias towards the place where the cue appeared in some trials. This result confirms that microsaccades directions could indicate the position of the attentional focus without significant variations during the training process. Note that the monkey was trained to press/release the lever with both hands, so to avoid any potential shift of attention due to the arm movement.

Conclusions

This study aimed at uncovering the relationship between microsaccades generation, attention and training. Results showed that the monkey was more focused on the fixation point, producing more microsaccades in the control task. The experience acquired during training did not change the microsaccades production, indicating that practicing a visual discrimination task does not affect microsaccadic circuitry. The correlation analysis showed very few significant relationships between RTs and microsaccades, confirming that the developed behavioral strategy and microsaccades generation seem to be independent processes.

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Figure legends

Figure 1. Task. **A.** Visual discrimination task. **B.** Control task. Note that the figure is not to scale, see Methods for stimuli and fixation point dimensions.

Figure 2. Frequency histograms of reaction times for both visual discrimination (grey) and control task (black) in each time delay in all epochs. Data are reported as mean values ± SE. **A.** Cue appeared after 750 ms from the target onset. **B.** Cue appeared after 1000 ms. **C.** Cue appeared after 1250 ms. **D.** Cue appeared after 1500 ms. Asterisks indicate significant effects (see Results for descriptions).

Figure 3. Main sequence of the microsaccades. **A.** Visual discrimination task. **B.** Control task.

Figure 4. Distributions of microsaccades directions in all epochs during the training period. **A.** Visual discrimination task. **B**. Control task. Mean vectors are computed for each trial. Solid line crossing each diagram indicates the significant mean vectors, curved line outside the circle indicate the circular SD. For each epoch n = 68. Bars are 20° width.

Table 1. Mean values of microsaccades parameter that showed significant differences across time or epochs. Data are shown as mean value ± SE (see Results for description of significant values).