Dissecting errors of the exogenously-driven and endogenously-driven saccadic tasks in the common marmosets

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Abstract

Various saccadic tasks used traditionally in oculomotor research, including both exogenously-driven and endogenously-driven saccades, have been proposed as clinical diagnostic for human movement disorders. Recently, common marmosets have been proven to be a good primate model for these movement disorders. However, whether similar saccadic measurements can be used for marmosets was not tested. Here, we trained three marmosets on the gap task, an exogenously-driven saccadic task, and the oculomotor delayed response (ODR) task, an endogenously-driven saccadic task. We demonstrated that with long-term training, they were able to learn and switch between the two tasks. The marmosets showed undershooting tendency in the gap and both under- and overshooting tendency in the ODR task when they made saccades to the target. We also categorized the error trails into distractive, impulsive, and visuomotor errors, depending on when a false saccade happened concerning the task progression, and interpreted possible causes of errors based on the saccade response time and the task history. Each error category may indicate specific failures in a particular aspect of cognitive or sensorimotor processes. Finally, and critically, we found that saccades from successful trials exhibited the highest saccade peak velocity and the shortest saccade duration comparing to the same saccade amplitude from error trials. Taken together, we showed the potential of training the same marmoset on conflicting oculomotor tasks simultaneously. We documented the baseline performance and compared successful and error trials in both gap and ODR tasks from the same animals. We propose that analyzing the error trials in sync with successful trials could provide a further understanding of the marmosets' cognitive and sensorimotor processes in both healthy and disease conditions.

1 Introduction

Saccades are conjugated rapid eye movements that primates use to bring their fovea to the target of interest (Yarbus, 1967; Zee and Leigh, 1983). These movements exhibit stereotypic kinematics with a fixed relationship between saccade amplitude, velocity, and duration (Bahill et al., 1975; Lebedev et al., 1996). Besides studying the characteristics of saccade kinematics *per se*, various saccade paradigms have been developed to probe different neuronal mechanisms (Gooding and Basso, 2008). Several studies have also demonstrated that the saccade kinematics and the measurements of saccade paradigms can be useful in clinical diagnostics of neurological diseases (Leigh and Kennard, 2004; Ramat et al., 2007), including movement disorders (Termsarasab et al., 2015; Waldthaler et al., 2021; Fukushima et al., 2017), psychiatric diseases (Bittencourt et al., 2013; Morita et al., 2020), and neurodegenerative diseases (Antoniades and Kennard, 2015; Opwonya et al., 2021).

To faithfully reproduce these neurological diseases with human-like behavioral symptoms, there are pressing needs to develop animal models using non-human primates (Verdier et al., 2015; Qiu and Li, 2017). The common marmosets (*Callithrix jacchus*), a new world monkey, has been proposed as a possible primate model for these diseases because of their availability in transgenic tools (Sasaki et al., 2009; Izpisua Belmonte et al., 2015; Park et al., 2016), their smooth brain surface for pinpoint intracranial injection (Lin et al., 2019; Mundinano et al., 2016) and their ability to be trained on behavioral paradigms (Okano, 2021). The marmosets can learn to perform a variety of visual and cognitive tasks under head unrestrained conditions (Spinelli et al., 2004; Clarke et al., 2011; Yamazaki et al., 2011; Jendritza et al., 2021). Their short lifespan also makes them suitable candidates for long-term behavioral observation with the progression of neurological diseases (Tardif et al., 2011). In fact, several neurological models of marmosets have been successfully generated using various methods (Eslamboli et al., 2007; Tomioka et al., 2017; Lin et al., 2019; Jenner et al., 1984; Fox et al., 2010; Emborg, 2017).

The marmosets can also be trained to perform various saccadic paradigms under head restrained conditions (Mitchell et al., 2014), for example, step task (Sedaghat-Nejad et al., 2019; Chen et al., 2021) and gap task (Johnston et al., 2018; Chen et al., 2021). Both tasks are exogenously-driven saccadic tasks because the saccade was initiated in response to a visible visual stimulus. With some modification of the task design, one report has shown successful training for marmosets saccading to a less salient saccade target (anti-saccade task, (Johnston et al., 2019)). However, the endogenously-driven saccadic tasks, such as oculomotor delayed response (ODR) task or memory-guided saccade task, where the target is only briefly presented and the saccade is initiated to the target location that is no longer visually available (Hikosaka and Wurtz, 1983; Funahashi et al., 1989), were not reported successfully trained on marmosets (but see Carney et al., 2019). Since both exogenously-driven and endogenously-driven saccadic paradigms are important in the clinical diagnostic and for probing different aspects of neurological diseases in humans, the primate model selected for these diseases would be more ideal if the same animal can perform both types of tasks concurrently.

In the current study, we trained three marmosets in two different saccadic paradigms, the gap, and the ODR tasks. We aimed to see if it is possible to achieve a stable performance on the standardized exogenously-driven and endogenously-driven saccade tasks in the same animals. By comparing the task performance, and the saccade kinematics of the two tasks, and identifying the characteristics of the error trials, we have established a baseline measurement to pave the way for future studies of neurological disorders using marmosets as animal models.

2 Materials and Methods

2.1 Animal ethics

All marmosets (*Callithrix jacchus*) used in this study were born in the breeding colony of Kyoto University Animal Research Facility. The experiments followed the guideline of the Japan Neuroscience Society and the Science Council of Japan. Animal Ethics Committee at Kyoto University, Japan approved all experimental procedures.

2.2 Animal preparation and surgical procedure

Three adult marmosets were used in this study; marmoset S: male 2.5 years, 390 g; marmoset N: female 2.5 years, 370 g; and marmoset M: male 2 years, 340 g. All marmosets started with one week of transportation cage adaptation followed by two weeks of chair training. After achieving a stable performance in the chair, marmosets underwent surgery of headpost implantation for preparation of head-fixing training. Induction of anesthesia was achieved using 14 mg/kg ketamine and 0.14 mg/kg medetomidine along with 0.07 mg/kg atropine, 0.5 mg/kg dexamethasone, and 1.5 mg/kg gentamicin to prevent excessive salivation, relieve pain, and prevent infection. Under 1.5 % isoflurane, each marmoset was aseptically mounted with its own custom-made headpost that we designed based on MRI reconstruction of their skulls (Chen et al., 2021). The headposts were 3D-printed using Dental SG Resin (Form2, Formlabs, U.S.A.), and they were attached to marmosets' skulls using dental resin, Super-Bound (Sun Medical Co., Ltd., Japan). After the surgery, marmosets received 4 days of antibiotics; ampicillin, 30 mg/kg, and anti-inflammatory and analgesics medication; ketoprofen, 0.8 mg/kg. After medical treatment, the marmosets were given an additional week for recovery.

2.3 Eye tracking and calibration

Eyelink 1000 Plus (SR Research, Canada) was used to track marmosets' eyes binocularly with a sampling frequency of 500 Hz. We used both pupil and corneal reflection information for accurate tracking. We calibrated the eyes' position with the same method described in (Chen et al., 2021). Briefly, for online calibration, we used marmoset face photos presented randomly on the screen and the marmosets were free to look at the photos for 10 seconds per trial. We then used a graphical user interface to examine the photos that were presented and the corresponding marmosets' gaze. We manually adjusted the x and y gain and the x and y offset of the eye positions for each marmoset individually. This calibration was done once for each marmoset after the first time sitting in front of the eye tracker. Then, based on the task performance of the marmosets, slight changes in the gain and offset were made manually each day.

2.4 Monitor Setup

We used a 1280 X 1024 pixels resolution LCD monitor at the refresh rate of 60 Hz (Dell P1917S). The visual distance was 40 cm, and the background where the tasks were presented was a grey background with a luminance of 80.81 cd/m^2. The experimental software used to control the stimuli display was PsychoPy 3.6 (Peirce et al., 2019).

2.5 Saccadic paradigms

2.5.1 Gap task

In the gap task (**Figure 1A**), a 1-degree-radius marmoset face picture was presented as a fixation stimulus over a grey background at the center of the screen for up to 1000 ms at the beginning of a trial. The marmosets were trained to initiate the trial by fixating at the fixation stimulus and staying within a 2-degree-radius invisible window centered at the fixation stimulus (**Figure 1A**, dashed

circle). The trial started if their gaze entered the window. If they successfully stayed within the window for 200 ms, a gap period was initiated, where the fixation stimulus was removed and only the grey background was presented. During this gap period, the marmosets were trained to keep their gaze within the 2-degree invisible window centered at the removed fixation stimulus. The gap period (0 to 400 ms) was predetermined randomly for each session. After successfully finishing the gap period, a peripheral stimulus (1-degree marmoset face) was shown as the saccade target. The target location was randomly picked from eight potential locations separated equally by a 45-degree radial visual angle from the horizontal meridian with predetermined eccentricity (4, 5, 6, 7, 8, or 9 degrees) before session initiation. The marmosets were required to make a saccade toward the target and stay within a 2-degree invisible window centered at the saccade target location for 200 ms to attain a drop (0.05 ml) of the reward. The reward was prepared by mixing baby supplement banana pudding (Kewpie Corp., Japan) with banana-flavored Mei-balance (Meiji Holdings Co., Japan). A 1000 ms was given to the marmosets to make a response, otherwise, the trial was terminated. One session was either 24 successful trails or 48 trials (maximum trial number per session). The marmosets were able to perform 3.20 ± 0.37 (mean ± standard deviation) sessions per day.

2.5.2 Oculomotor delayed response (ODR) task

In the ODR task (**Figure 1B**), the marmosets were trained to initiate the trial with similar criteria used in the gap task. After trial initiation, a saccade target was flashed for around 67 ms and the target location was randomly picked from either right or left relative to the fixation stimulus using predetermined eccentricity (4, 5, 6, 7, or 8 degrees) before the session started. A delay period followed immediately after the peripheral saccade target ranging from 100 to 400 ms (predetermined at session start) in which the marmosets were still required to keep fixating at the fixation stimulus. After the delay period, the fixation stimulus was removed, and the marmosets were trained to make a saccade toward the remembered saccade target location and stay within the 2-degree invisible window centered at the invisible saccade target for 183 ms to be rewarded. The same response time window of the gap task (1000 ms) was also used here. We used a different fixation and target stimulus (a white circle enclosed by a black arena, total 1-degree-radius, indicated in **Figure 1B**) than in the gap task to make it easier for the marmosets to learn and to associate each stimulus with each task. One session was terminated if the marmosets reached either 16 successful trails or 32 trials (maximum trial number per session). The marmosets were able to perform 4.05 ± 1.71 (mean ± standard deviation) sessions per day. The gap task was performed first during training.

2.6 Saccade detection

We used U’n’Eye, a deep neural network developed for eye movement detection and classification, to detect saccades in our study (Bellet et al., 2019). The eye data were first preprocessed and the ground-truth saccade dataset was first labeled and manually checked following the same procedure and criteria as (Chen et al., 2021). After labeling around 200 trials per animal, the data were gathered and fed into U’n’Eye for network training and validation to get optimal performance for the marmosets. After training, the rest of the preprocessed eye data were fed into the trained network for saccade labeling and the results were inspected manually to check for mislabeling.

2.7 Successful and error trials definition

We divided the total trials into either successful or error trials. Successful trials were defined as the trials that the marmosets made saccades toward the target and stayed within a 2-degree invisible window centered at the saccade target location for 200 ms or 183 ms in the gap or ODR tasks, respectively, and obtained the reward at the end of the trials. Alternatively, error trials were defined

as the trials that the marmosets failed to get the reward at the end of the trials. A detailed definition of the error trials is mentioned in the Result section.

2.8 Data analysis

2.8.1 Task performance and stability

To compare the improvement of each task before and after long-term training, we calculated the success rate of the first and the last month of training for the gap task with each gap period and the ODR task with each delay period regardless of the target eccentricities for each marmoset. We further analyzed if the success rate was dependent on target eccentricity by separating the successful trials into the first and the latter half according to the training period for each task and each animal regardless of the gap or delay period. We then took the difference between the first the latter half of the success rate and combined the result of the three marmosets to analyze if the performance improvement was correlated with the target eccentricity for each task. The same practices were performed to determine if the success rate changed with the gap or the delay period for each task and whether the improvement was correlated with the gap or delay period.

To analyze the performance stability, we also compared the standard deviation (std) of the success rate of the first and the last month of training for the gap task with each gap period and the ODR task with each delay period regardless of the target eccentricities for each marmoset. We took the difference of the std calculated according to the target eccentricity between the first and the latter half of the training period again to check if the change in standard deviation was dependent on the target eccentricity for each task. The same practice was again taken to determine the correlation between the change in std and the gap or delay period.

2.8.2 Radial distance from the saccade endpoint to the target location

To analyze whether the marmosets had any systematic saccade undershooting (hypometria) or overshooting (hypermetria) when they made their saccades towards the targets in each task, we measured the radial distance from the saccade endpoint to the target location. We first rotated all the target locations and the saccades after target onset in the gap task or fixation stimulus offset in the ODR task. The rotation angle was determined by the angle between the target location of the trial and the positive x-axis. Next, we subtracted the length of the saccade after rotation to the distance of the rotated target location to obtain the radial distance.

2.8.3 Saccade main sequence

To characterize the change of saccade kinematics for different trial categories, we looked at the saccade main sequence (Bahill et al., 1975; Chen et al., 2021). We first plotted the saccade amplitude (x) against the saccade peak velocity (f(x)). We then fitted the data with the following equation:

$$f(x) = a \times (x^n)$$

a and n are the fitting parameters representing the slope and the exponent.

We also plotted the saccade amplitude (x) against the saccade duration (f(x)) and fitted the data with the following equation:

$$f(x) = b \times (x) + c$$

b and c are the fitting parameters representing the slope and the intercept. All fitted curves were overlaid on the correspondent figure, color-coded with trial categories.

2.9 Statistical analysis

All statistical analysis is described in the Result section. Additional statistical analysis was performed and described in the Supplementary Figures. If not specifically mentioned, the result of the analysis was made by combining all three marmosets' data.

3 Result

3.1 Task performance improved after long-term training

All three marmosets were trained for eight months on both gap and oculomotor delayed response (ODR) tasks (**Figure 1**). To quantify the effect of training, we separated the trials into successful and error trials, based on if the marmosets were rewarded or not while performing the tasks (Materials and Methods). When the training just started for one month, the successful trials were on average 56.0 % across the marmosets in the gap task and 21.0 % in the ODR task (**Figure 2**). This indicates that likely the gap task was intrinsically easier than the ODR task for the marmosets. At the last month of training, the successful trials increased on average to 75.7 % in the gap task (marmoset S: $p = 0.004$; marmoset N: $p = 0.08$; marmoset M: $p = 2x10^{-13}$, Wilcoxon rank sum test). However, the successful trials did not increase significantly in the ODR task (average, 24.0% marmoset S: $p = 0.6$; marmoset N: $p = 0.2$; marmoset M: $p = 0.1$, Wilcoxon rank sum test). There were no clear correlation between the success rate and the target eccentricity either in the first 4 months (gap: marmoset S: rho = -0.8, $p = 0.06$; marmoset N: rho = -0.9, $p = 0.02$; marmoset M: rho = -0.6, $p = 0.2$, ODR: marmoset S: rho = -0.2, $p = 0.9$; marmoset N: rho = 0.5, $p = 1$; marmoset M: rho = 0.5, $p = 1$; Spearman Rank coefficient) or in the latter 4 months of training, in both tasks (gap: marmoset S: rho = -0.3, $p = 0.7$; marmoset N: rho = 0.09, $p = 0.9$; marmoset M: rho = -0.9, $p = 0.03$, ODR: marmoset S: rho = -0.6, $p = 0.4$; marmoset N: rho = 1, $p = 0.3$; marmoset M: rho = 1, $p = 0. 3$; Spearman Rank coefficient). The improvement comparing the first half of the training to the latter half was also not correlated with the target eccentricity (gap: rho = 0.3, $p = 0.2$, ODR: rho = 0.3, $p = 0.5$; Spearman Rank coefficient). Similarly, the correlation between the success rate and the gap or the delay period was weak in the first half (gap: marmoset S: rho = -0.1, $p = 0.8$; marmoset N: rho = 0.5, $p = 0.4$; marmoset M: rho = -0.2, $p = 0.4$; Spearman Rank coefficient, ODR: marmoset S: rho = -1, $p = 0.003$; marmoset N: rho = -0.7, $p = 0.2$; marmoset M: rho = 0.03, $p = 1$; Spearman Rank coefficient) and also in the later half, (gap: marmoset S: rho = 0, $p = 1$; marmoset N: rho = -0.6 $p = 0.2$; marmoset M: rho =-0.8, $p = 8.3x10^{-4}$, ODR: marmoset S: rho = -0.9, $p = 0.007$; marmoset N: rho = -0.4, $p = 0.5$; marmoset M: rho = -0.8, $p = 0.03$; Spearman Rank coefficient) of the training. However, the improvement between the first and the latter half of the training was correlated with the gap period and was weaker in longer gap period in the gap task (rho = -0.6, $p = 0. 02$; Spearman Rank coefficient). In the ODR task, the improvement was not correlated with the delay period (rho = -0.13, $p = 0.6$; Spearman Rank coefficient). We also found that the averaged standard deviation (std) of the success rate decreased from 22.4 to 17 in the gap task (marmoset S: $p = 2.3x10^{-19}$, marmoset N: $p = 0.6$, marmoset M: $p = 3x10^{-21}$, Two-sample F-test) and 16.3 to 10.6 in the ODR task (marmoset S: $p = 3x10^{-4}$; marmoset N: $p = 0.6$; marmoset M: $p = 9.2x10^{-5}$, Two-sample F-test) comparing the first to the last month of the training period (**Figure 2**). This indicates that the task performance became more stable after long-term training for both tasks. The decrease in std was not correlated with either the target eccentricity (gap, rho = -0.3, $p = 0.3$, ODR, rho = 0.4, $p = 0.4$, Spearman Rank coefficient) or the gap/delay period (gap, rho = 0.14, $p = 0.6$; ODR, rho = -0.4, $p = 0.1$, Spearman Rank coefficient). Besides long-term training, another possible reason for the improvement in the task performance was that for

simplicity of training, we used only two possible target locations (horizontal left or right) in the ODR task instead of eight in the gap task (Materials and Methods). The marmosets could have memorized the possible target locations and randomly chose either one. Indeed, we found that in the error trials, there were 6.1 % of the trials where the marmosets picked the exact opposite side of the target location in the last month of training. This was higher than in the first training month (4.5 %). However, this probability was still lower than the success rate in the last month of training (24.0%). Based on the above evidence, we believe that the marmosets learned the task structure and the possible locations of the target, and they were using the cue as a guide instead of only guessing where the target would be in the ODR task. Hence, the marmosets started with relatively low and unstable task performance in both the gap and ODR tasks, but after long-term training, they improved their performance in both the success rate and the performance stability, especially in the gap task. They were also able to generalize such improvements in different task conditions, for instance, target eccentricity and gap/delay periods starting from the beginning of the training.

3.2 Hypometric saccades in both tasks but hypermetric saccades only in ODR task found

To further investigate how the marmosets reached the target in either task, we plotted the radial distance of their very first saccade after target onset in the gap task or fixation spot offset in the ODR task from the successful trials (**Figure 3A**). In the gap task, we found that most of these saccades landed within the target window (**Figure 3B**). However, a small portion of these saccades were hypometric and the portion increased with target eccentricity (rho = 0.9, $p = 1.9\text{x}10^{-9}$; Spearman Rank coefficient), but not with gap period (rho = 0.2, p = 0.2; Spearman Rank coefficient). If a second saccade was made following the first, the endpoint of the second saccade was in general closer to the target (**Figure 3B**, $p < 2.2\text{x}10^{-308}$; Wilcoxon rank-sum test). The occurrence of the second saccades were more frequent with larger eccentric target (rho = 0.8, $p = 2.8\text{x}10^{-4}$; Spearman Rank coefficient) and with longer gap period (rho = 0.4, p = 0.02; Spearman Rank coefficient). This means that in some trials, particularly for larger eccentric targets, the marmosets made several short saccades (hypometric saccades) to reach the target in the gap task.

In the ODR task, the hypometric saccades did not increase significantly either with target eccentricity (rho = 0.5 p = 0.1; Spearman Rank coefficient) or with the delay period (rho = -0.05, p = 0.8; Spearman Rank coefficient) (**Figure 3C**). On the other hand, hypermetric saccades were found (**Figure 3C**), which was not observed in the gap task. The percentage of hypermetric saccades was decreasing with the larger eccentric target (rho = -0.9, $p = 8.5\text{x}10^{-7}$; Spearman Rank coefficient). If a second saccade was made following the first, again, the endpoint of the second saccade was closer to the target than the first saccade ($p = 1.6\text{x}10^{-22}$; Wilcoxon rank-sum test). The occurrence of second saccades was not significantly correlated with target eccentricity (rho = -0.5, p = 0.09; Spearman Rank coefficient), but it was less frequent compared to the correspondent eccentricity in the gap task ($p = 2.4\text{x}10^{-4}$; Wilcoxon signed-rank test).

Having found successful trials with hypermetric and hypometric saccades, we further subdivided them into three subgroups: pure single saccade group, single saccade group, and multiple saccades group, based on how the marmosets reached the target (**Figure 4**). We next defined the saccade that started within the fixation window and ended within the target window as the “answering saccade” (from pure single saccade and single saccade group, **Figure 4A, Figure 3D**) and replotted the distance between the answering saccade endpoint to the target (**Figure 3E, F**). To assess the accuracy of these answering saccades, we calculated the half-width of the histograms in **Figure 3E, F** as a proxy of it. The half-width did not change with eccentricity in the gap task (rho = 0.5, p = 0.05; Spearman Rank coefficient) and was, in general, smaller than those in the ODR task (p = 0.02;

Wilcoxon signed-rank test). However, the half-width decreased with eccentricity in the ODR task (rho = -0.8, $p = 2.9x10^{-4}$; Spearman Rank coefficient), suggesting that the accuracy of the answering saccades was higher with larger eccentric targets. For the saccade following the answering saccade, again, we found that the endpoint of this saccade was closer to the target than the answering saccade (gap / ODR; $p < 2.2x10^{-308}$ / $p = 1.2x10^{-5}$; Wilcoxon rank-sum test), and the second saccades were less frequent in the ODR task than in the gap task ($P= 2.4x10^{-4}$; Wilcoxon rank-sum test). We also analyzed separately the x and y distance of the answering saccades endpoints and confirmed that x offsets were always larger than y offsets (**Supplementary Figure 1**).

3.3 Effects of gap period

After defining the answering saccades, we calculated the saccade response time (SRT) of saccades as the time difference between the target onset in the gap task or fixation offset in the ODR task and the starting time of the saccades. As indicated in **Figure 5A**, the SRT decreased with increasing gap period (rho = -0.4, p = 0.03; Spearman Rank coefficient). This comes in agreement with the gap effect phenomenon, defined as a temporal gap between fixation point offset and target onset that typically results in shorter saccadic latencies than if the fixation point remains on (Saslow, 1967; Reulen, 1984; Tam and Ono, 1994; Pratt et al., 1999; Chen et al., 2021). This effect was not dependent on the eccentricity of the target location (rho = -0.06, p = 0. 8; Spearman Rank coefficient). Furthermore, a detailed analysis of the SRT distributions for all three marmosets showed no express saccades in the gap task (**Supplementary Figure 2A**).

3.4 Potential capture of attention effect in ODR task

As for the ODR task (**Figure 5B**), a decreasing trend of SRT with increasing delay period was observed only in one marmoset (marmoset M: rho = -0.9, p = 0.02; Spearman Rank coefficient). However, the other two marmosets showed a decreasing trend of SRT up until 200 ms then a rebound of slower SRT at 250 ms. The averaged SRT across the three marmosets did not show a clear trend of decreasing SRT with increasing the delay period (rho = -0.1, p = 0. 6; Spearman Rank coefficient). Similar to the gap task, there was also no dependency of the SRT on the eccentricity of the target location (rho = -0.5, p = 0. 1; Spearman Rank coefficient). In addition, the averaged SRT of gap / ODR task was 155 / 149 ms for Marmoset S, 165 / 240 ms for Marmoset N, and 158 / 194 ms for Marmoset M. This result showed that the SRT in the ODR task was generally longer than that for the gap task for the same marmoset (marmoset S: $p = 1.5x10^{-21}$, marmoset N: $p = 1.6x10^{-80}$, marmoset M, $p = 5.6x10^{-37}$; Wilcoxon rank-sum test). We also noticed some ultra-short latency answering saccades exhibited in the ODR task (**Supplementary Figure 2B**), which was consistent across all three marmosets.

3.5 Different types of errors made by the marmosets

In addition to the successful trials, the marmosets also made many errors during the tasks (error rates; gap task: 37.7%, ODR task: 78.7%, averaged from three marmosets). Therefore, we decided to take benefit from these errors and try to interpret why the marmosets ended up not getting the reward. To do so, we divided the error trials into three categories, distractive error, impulsive error, and visuomotor error categories, based on when the marmosets made mistakes relative to the task monitor events **(Figure 6A)**. For the gap task, we first labeled the error trials based on three monitor events in a given trial, fixation stimulus onset, fixation stimulus offset, and target stimulus onset. If a trial ended after fixation stimulus onset and before fixation stimulus offset, it was defined as a distractive error trial. If a trial ended after fixation stimulus offset and before target stimulus onset, it was defined as an impulsive error trial. Finally, if a trial ended after target stimulus onset but without

a reward, it was defined as a visuomotor error trial. We then looked for the first saccade in the labeled trial which broke fixation (i.e., the first saccade started within the fixation window and ended outside the fixation window). This saccade was taken as the saccade that responded to the nearest monitor event for this trial, and the SRT was then calculated. In the gap task, anticipatory saccades were reported for marmosets (Chen et al., 2021). These anticipatory saccades are considered not responding to the nearest monitor event (target onset) because the response time was too short (< 70 ms). They are likely the slower saccades responding to the second nearest monitor event (fixation offset). Considering that, we redefined visuomotor error trials with SRT less than 70 ms to be impulsive error trials and redefined impulsive error trials with SRT less than 70 ms to be distractive error trials and recalculated the SRT based on the second nearest monitor events. If the marmoset never entered the fixation eye window after fixation stimulus onset, the trial was defined as a distractive error trial and no saccade or SRT was identified. Also, if the marmoset did not leave the fixation window after entering it, the trial was defined as a visuomotor error trial and no saccade or SRT was identified. Example trials are shown in **Figure 6B**.

The definitions of the error categories were similar in the ODR task **(Figure 6C)**. The three monitor events were identified as fixation stimulus onset, target stimulus onset, and fixation stimulus offset. Distractive error trails were then defined as the trials ended after fixation stimulus onset and before target stimulus onset. Impulsive error trials were defined as trials that ended after target stimulus onset and before fixation stimulus offset. Visuomotor error trials were defined as trials ended after fixation stimulus offset but without a reward. Again, the SRT was extracted for each trial. No anticipatory saccades were reported previously, so we did not relabel any trials. Example trials are shown in **Figure 6D**.

3.6 Distinct error rate and saccade response time for each category

We first compared the distractive error category in either task **(Figure 7)**. Because the marmosets were trained with different fixation stimulus configurations **(Figure 1A)**, they should be able to distinguish the tasks at the very beginning of the tasks. This was reflected by different distractive error rate. We expected that because the ODR task was more demanding and had a lower success rate, the distractive error rate in the ODR task should be higher. However, to our surprise, the result was the opposite: the distractive error rate was lower in all three marmosets in the ODR tasks (marmoset S: $chi^2 = 34.2$, $p = 5x10^{-9}$; marmoset N: $chi^2 = 1.3x10^{3,}$ $p < 2.2x10^{-308}$; marmoset M: $chi^2 = 677.5$, $p < 2.2x10^{-308}$; chi-square test).

For the impulsive error category, we found that the error rate was much higher in the ODR than in the gap task (**Figure 7**). This was probably because the upcoming target location was not provided during the gap period, whereas it was displayed briefly just before the delay period in the ODR task. The marmosets needed to actively suppress their reflexive response to the target, and failure to suppress such impulsivity would result in breaking fixation faster than in the gap task. Indeed, the SRT in the impulsive error category was shorter in the ODR than in the gap task (marmoset S: $p = 5x10^{-27}$, marmoset N: $p = 1x10^{-105}$, marmoset M, $p = 6.9x10^{-264}$; Wilcoxon rank-sum test) and was comparable with that in the successful trials of the gap task (**Figure 8**).

We also found that the visuomotor error rate was higher in the ODR than in the gap task (**Figure 7**), and the SRTs in the visuomotor error category were slower in the ODR than in the gap task (marmoset S: $p=9.3x10^{-119}$, marmoset N: $p = 7.7x10^{-92}$, marmoset M, $p= 1.5x10^{-153}$; Wilcoxon rank-sum test) (**Figure 8**). The SRTs were also longer in the visuomotor error trials than in the successful

trials (marmoset S: $p < 2.2x10^{-308}$, marmoset N: $p = 5.4x10^{-104}$, marmoset M, $p < 2.2x10^{-308}$; Wilcoxon rank-sum test) (**Figure 8**).

3.7 Marmosets repeated the same incorrect answer in the ODR task

To further investigate why the marmosets failed in each step of the ODR task, we separated the saccade vectors made relative to the target location in the impulsive and the visuomotor error categories (**Figure. 9A**). We found that across all three marmosets, saccades from the impulsive error trials were mainly directed towards the target stimulus. This implies that the marmosets were indeed incapable of suppressing their reflexive saccade toward the briefly presented target. From the visuomotor error trials, the main failure reason for saccades directed towards the target was the generation of hypometric saccades that did not reach the target window (**Figure. 9B**). However, the marmosets made more often, saccades away from the target stimulus (**Figure. 9A**). This was an unexpected result because if the marmosets forgot the target direction of the current trial, an equal bias of saccading toward or away from the target would've been seen. If the marmosets only remembered the rough target direction but not the exact location, the saccade direction should be made towards the target location. To tackle this question, we took the saccades directed away from the target, of the visuomotor error trial and named them as "current trial saccades" and inspected what the marmosets' previous responses were (**Figure 9C**). We found that if the previous trial was successful, the marmosets did not show any tendency to select the same or the opposite location of the target that they chose before (**Figure 9C**, left figure). However, if the previous trial was impulsive, the marmosets showed a tendency to saccade to the opposite side of what their previous choice was (**Figure 9C**, middle figure). This means that the marmoset actually made a saccade away from the target in the current visuomotor trial given that most of the impulsive error trails had saccades directed toward the target (**Figure 9A**). Finally, if the visuomotor error trail was preceded by another visuomotor trial, the marmosets tended to stick with the same answering direction of their choice (**Figure 9C**, right figure), which would be away from the target location.

3.8 High saccade peak velocity and short saccade duration for successful answering saccades

Finally, we compared the saccade kinematics across all categories for both tasks. We first looked at the relationship between saccade peak velocity and amplitude. As **Figure 10A, B** shows, in both the gap task and the ODR task, the peak velocity was similar in the successful trials and was also the highest comparing to saccades in other error categories. Furthermore, we found that the saccades' duration in the successful trials was the shortest compared to the error saccades in either task when looking at the relationship between saccade duration and amplitude (**Figure 10C, D**).

4 Discussion

We showed that the marmosets were able to learn two different saccadic paradigms, the gap, and the ODR task, and switch in between them. Regarding successful trials, we found hypometric saccades in the gap but both hypo- and hypermetric saccades in the ODR task. We also analyzed the SRT and confirmed the gap effect and potential capture of attention in either task from the marmosets. We further categorized and analyzed the error trials to interpret why the marmosets made mistakes in each task. We found that the marmosets had fewer distractive errors in the ODR task, however, the impulsive errors were more compared to the gap task. Although there were more visuomotor errors in the ODR than in the gap task, this was not an outcome of a previous answer influence. Rather, these errors might be the result of repetitively making the same mistake. In the end, we found that the successful trials had the highest saccade peak velocity and the shortest saccade duration under similar saccade amplitude in both tasks. To the best of our knowledge, no previous research has fully

documented the learning curve of the gap and ODR tasks and directly compared the two in the same marmoset. This is also the first time a detailed analysis was made in both the successful and the error trials to interpret the potential cognitive and sensory-motor processes while the marmosets were performing the tasks. We believe our approach can better evaluate the marmosets' behavior and pave the way to analyze the behavior in both healthy and disease model marmosets.

We started the comparison by looking at the success rate in each task. Our data showed clearly that the marmosets learned both tasks and were able to switch in between them. It is known that long-term training helps in improving the subject's ability to correctly respond to visual stimuli (Goldstone, 1998). But, if we cross-compared between the two tasks, the success rate was lower in the ODR task than in the gap task (**Figure 2**). We attribute this to the complete reliance on working memory in recalling the location of the previously presented target in the ODR task. Indeed, previous macaque monkey studies have shown that saccades made in response to a remembered target location are associated with larger errors than saccades made in response to a visually accessible target (Opris et al., 2003; Stanford and Sparks, 1994). There might be also interference between the exogenously-driven and endogenously-driven saccadic tasks being trained in parallel. The marmosets might have chosen to receive more rewards on the easier task but avoid doing the difficult one. However, in the ODR task, there was no clear avoidance behavior (for example, sudden performance drop), and after long-term training, there was a performance improvement, although not as dramatic as in the gap task.

Next, we looked at the accuracy of the first saccade and the answering saccade after target onset. As our data showed, the marmosets have the tendency to undershoot in their first saccade in the gap task, and they make a following saccade that corrects for it (**Figure 3**). This comes in line with the previous human research that visually guided saccade tasks tend to have answering saccade first undershooting and frequently followed by a corrective secondary saccade to line up the fovea with the target (Nuthmann et al., 2016). This undershooting is referred to as an attempt to reduce the saccade flight time (Harris, 1995). For the ODR task, less corrective saccade occurred because there was no visual target to align with. However, there was a clear saccadic range effect with saccades biased toward the center of the range, undershooting for furthest targets from the fixation center, and overshooting for closest targets to the fixation center. (Kapoula, 1985). This is mainly occurring due to the task condition. Nonetheless, if we looked at the half-width of the answering saccade distribution, we found that the 5 deg target was the narrowest. This may indicate that 5 deg target was the most precisely encoded target in the ODR task. Additionally, although previous research showed that memory-guided saccade is usually more hypometric than visually guided saccades (Nuthmann et al., 2016), a similar effect was not observed in our current study.

We did not find express saccade in gap task in the current study (**Figure 4**), in contrary to our previous study (Chen et al., 2021). Even though the training for gap task was almost identical to our previous report. We attribute this difference to two possible reasons, one is the interference from the ODR task, and the other is the use of multiple training eccentricities. Furthermore, not all marmosets showed express saccade after gap task training (Johnston et al., 2018). But we did observe the gap effect in the current study. On the other hand, ultra-short latency answering saccades were found in the ODR task, which can be a result of several possible cognitive elements such as predictions, knowledge, and strategies (Badler and Heinen, 2006; Heeman et al., 2019). In addition, when we compared the gap and ODR tasks, we found that in general, the SRT in the ODR task was longer than in the gap task in the same marmoset (**Figure 5**). This also comes in accordance with previous macaque studies which have shown that the response time of memory-guided saccades is longer and less accurate than visually guided saccades (Gnadt et al., 1991). We also found that the SRT from

two marmosets in the ODR task decreased until 200 ms and then increased. This is analogous to the capture of attention effect observed in the Posner paradigm (Posner, 1980). However, because the ODR task and the Posner paradigm are different, and not all marmoset showed the same response, it is hard to make a solid conclusion.

One important point of the current study was to extend the analysis to include the error trials and to interpret how the marmosets made mistakes (**Figure 6**). First, we found that the distractive error rate was lower in the ODR task in contrast to the gap task (**Figure 7**). This is similar to "mind-wandering", where attention is generally directed to task-irrelevant internal thoughts for easy and repetitive tasks (Reichle et al., 2010). Moreover, many other studies proposed that whenever internal cognition is activated, eyes are disengaged from the external stimulus in order to guard the internal thoughts against external events (Smallwood et al., 2007). To successfully execute a demanding task, it is a must to stay concentrated on the current ongoing task and not going to the mind-wandering state (Benedek et al., 2017). Therefore, the lower distractive error in the ODR task might be due to the higher demands of the task, which activates more cognitive processes. However, the gap task is mainly driven by external stimulus and could lead to a mind-wandering state easily. We also found that the impulsive error rate was higher in the ODR task. During the gap period, there was no information about the target, hence, the impulsive error rate was lower in the gap task. Even if there was an impulsive error, because the marmosets did not know where to saccade to, the SRT was much slower than the ODR task. Yet, the SRT of the impulsive errors in the ODR task was similar to the SRT of the answering saccades in the gap task. This might be because the marmosets reflexively made saccades towards the flashed target, and they ignored the fixation spot almost completely (**Figure 8**). This could be a consequence of our parallel training of both tasks. Furthermore, the visuomotor error rate was higher in the ODR task. This could be related to the task design. Because in the gap task, the final stage was to make an exogenous saccade to a target stimulus, whereas in the ODR task, marmosets must rely on their working memory to recall the location of the target and generate an endogenous saccade towards an invisible stimulus. Because of this, the SRT was also slower in the ODR task for visuomotor errors. At last, we noticed that a good proportion of the successful answering saccades and the saccades in visuomotor errors in the ODR task had very short response times, but not in the gap task. This might be due to the strategy that the marmosets used to answer in the ODR task. In particular, the same delay period was used in the same session, which may have reinforced the marmosets to count the time.

We noticed that in the ODR task, visuomotor error trials' SRTs were consistently longer than successful trials' SRTs. This might indicate that the marmosets did not remember the target location and hesitated in making a saccade to the invisible target. Therefore, we further dissected how the marmosets made a visuomotor error in the ODR task by considering their previous decision (**Figure 9**). Since the target was either presented left or right and to prevent the marmosets from picking only one side to get the reward, the failed trial in our task repeated itself until the marmosets successfully answered it, we wondered if their decision in the previous trial might have influenced their current responses. However, we did not find evidence that the previous successful trial affected the marmoset's upcoming decision. However, if the marmosets made a visuomotor error previously, they tended to repeat the same answer. This may be similar to an effect called "recurring mistakes" (Kuvaldina et al., 2019) where the same mistakes are repetitively made after the first mistake. Although the neuronal pathway of recurring mistakes is still not clear, our experiment suggests that the marmosets might be useful to identify the neuronal bases of this psychological phenomenon using the ODR task.

The main sequence relationships are believed to reflect optimization of the trade-off between saccade duration and accuracy (Harris and Wolpert, 2006). It is commonly known that there is a fixed relationship between the saccade amplitude to the peak velocity and duration (Fuchs, 1967; Bahill et al., 1975). But when comparing visually guided and memory-guided saccades in macaque, it has been shown that saccades made in response to remembered locations have lower peak velocities and longer durations than saccades made in response to a visible stimulus (Gnadt and Andersen, 1988; Powers et al., 2013). In our results (**Figure 10**), we found that the previous statement is true only for saccades with small amplitude, however, as saccade amplitude got larger, answering saccades made in the ODR task had higher peak velocities and shorter durations than the amplitude of the same saccade made in the gap task. Our data also showed that the amplitude vs duration relationship had a slope smaller in the ODR task than in the gap task. This could be due to motivation, arousal, or advanced motor planning. It has been recently noticed that saccade peak velocity is not just dependent on saccade amplitude, but also on motivation, arousal, and inter and intra-individual variations (Muhammed et al., 2020). In addition, for advanced motor preparation, the expected value comes with great significance and, various studies have shown that saccade velocity can actually increase if a high reward was anticipated (Di Stasi et al., 2011; Chen et al., 2013). We think that motivation and advanced motor planning play crucial roles in modulating saccade velocity, especially in the ODR task. What was striking was that the answering saccades had the highest peak velocity and the shortest saccade duration comparing to error categories as if the marmosets knew whether they would answer correctly or not. This may be reflecting the confidence of the marmosets in making the saccades (Seideman et al., 2018).

Finally, we strongly recommend maintaining a high motivation level for the marmosets during behavior training. Because if they experienced continuous episodes of failure and no reward, they lose their enthusiasm and eventually give up on doing the task. In agreement with that, previous macaque monkey study has shown that when monkeys were given the choice to do or abandon a task with high difficulty, they choose to opt out of the task (Smith et al., 1998).

5 Conflict of Interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

6 Author Contributions

WA was responsible for the behavioural training, data collection, formal analysis, and the writing of the first draft. CC was involved in guiding the research and editing the manuscript. HO was involved in the marmosets' MRI imaging and surgeries. The project was overseen and supervised by TI. All authors shaped the final version of the manuscript and approved the submitted version.

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10 Data Availability Statement

Data presented in this paper are available upon reasonable request.

11 Figure legends

Figure 1 Task illustration. (A) Gap task. A 1-degree-diameter marmoset face was used as both fixation stimulus and target stimulus. **(B)** Oculomotor delayed response (ODR) task. A 1-degree-diameter white dot with black surrounding was used as both fixation stimulus and target stimulus. The 2-deg-diameter eye window was indicated with a dashed circle in each task. Marmoset's gaze fixation was indicated as a red arrowhead and the saccade that they made to acquire the reward was indicated as a blue arrow.

Figure 2 Change in success rate over the training period. (A) Gap task. The success rate for each session was plotted in relation to the cumulative training sessions, separated by the gap period. The data here was platted regardless of the target eccentricity. We selected 0 ms (left column), 150 ms (middle column), and 300 ms (right column) as examples. **(B)** Similar plots were generated for the ODR task. We selected 150 ms (left column) and 300 ms (right column) as examples. The black line in each plot is the moving average of the success rate with a window size of 10 sessions and moving at 1 session step.

Figure 3 Radial distance between the target location and the saccade. (A) Definition of first saccades. We analyzed the radial distance of the first saccade after target onset in gap task or fixation offset in ODR task regardless of whether the saccade vector was toward the target or not, from the successful trials. **(B)** Radial distance between the target location in the gap task and the first saccade. 4-degree and 6-degree target eccentricities are plotted here as examples from all marmosets. An example of undershooting (hypometric) saccade with less than 2-degree is indicated by an arrowhead. **(C)** Radial distance between the target location in the ODR task and the first saccade. 4-degree and 6-degree target eccentricities are plotted here as examples for all marmosets. An example of overshooting (hypermetric) saccade with radial distance more than 2-degree is indicated by an arrowhead. **(D)** Definition of answering saccades. We further constrained the saccades with start point and endpoint all within the eye window and defined them as answering saccades (also see **Figure 4A**). **(E)** Radial distance between the target location in the gap task and the answering saccade. **(F)** Radial distance between the target location in the ODR task and the answering saccade. The median of the radial distance is indicated in each figure.

Figure 4 Subgroups from the successful trials. (A) Definition of the answering saccade and subgroups from the successful trials. By definition, answering saccades are found only in trials of

pure single and single group, not in the multiple group. **(B)** Percentage of trials in each subgroup from the successful trials. Note that in the ODR task, the pure single group was higher in both marmoset S and marmoset M than in the gap task. The multiple groups have a lower percentage of trials in the ODR task than in the gap task for all marmosets.

Figure 5 Saccade response time (SRT) from the successful trials of gap and ODR task. Only answering saccades were included for SRT calculation. **(A)** Averaged SRT of gap task. Note that the SRT for all marmosets continued to decrease for the gap period 0 to 150 ms. **(B)** Averaged SRT of ODR task. No consistent SRT change was observed across the delay period. Data shown here were collected regardless of the target eccentricity. Shaded areas around the colored lines indicate the standard error mean (S.E.M.) of the SRT. The black solid line in each plot indicates the mean SRT from the three marmosets.

Figure 6 Description of the error categories in the gap and ODR tasks. (A) Definition of error categories in the gap task. Error trials consist of three types of error, defined according to when the trial was aborted. The eye position shown here represents a visuomotor error trial with saccade response time (SRT) extracted. If the SRT was less than 70 ms, the trial was relabeled as an impulsive error trial and the SRT would be recalculated based on the second nearest monitor event (in this case, fixation stimulus offset). The black dashed lines around the eye position indicate eye windowing for monitoring the marmosets' eye position. **(B)** Example saccades extracted in each error category from the gap task. Here we plotted randomly selected error trials from marmoset S for each error category. For comparison, we also plotted randomly selected successful trials from the same marmoset. Dashed circles indicate the eye windowing size and locations of potential target stimuli. **(C)** Definition of error categories in the ODR task. A similar convention is used as in (A). **(D)** Example of saccades extracted from each error category from the ODR task. Here we plotted randomly selected trials from marmoset S for each category. A similar convention is used as in (B).

Figure 7 Percentage of trials in each category of gap and ODR task. After separating the error trials into proper error categories (distractive, impulsive, or visuomotor), we plotted the percentage of each category including successful trials collected from the beginning of training regardless of target eccentricity or gap/delay period. **(A)** Gap task. **(B)** ODR task.

Figure 8 Saccade response time (SRT) from all categories of gap and ODR task. SRTs were plotted for each error and successful trials regardless of target eccentricity or gap/delay period for either gap or ODR task. **(A)** SRT of distractive error category. Zero in the x-axis indicates fixation stimulus onset time for both tasks. **(B)** SRT of impulsive error category. Zero in the x-axis indicates fixation stimulus offset time in the gap and target stimulus onset in ODR task. **(C)** SRT of visuomotor error category. Zero in the x-axis indicates target stimulus onset time in gap and fixation stimulus offset time in ODR task. **(D)** SRT of successful category. Zero in the x-axis indicates target stimulus onset time in gap and fixation stimulus offset time in ODR task. Similar to **Figure 5**, only answering saccade was used to calculate SRT. The median of SRT for each task is indicated in the figure with a vertical line and an actual number of correspondent colors.

Figure 9 Current error saccade and previous decision in the ODR task. (A) Saccades direction of the current error trials. We separated the saccades vector and calculated if the saccade direction was toward the target location or away from it. **(B)** Reasons for failure of saccade toward the target in visuomotor trials. We found most of the saccades were undershooting saccades and did not reach the target eye window. A small portion of the saccades was overshooting. Another small portion of the saccades was that the marmoset did not stay enough time in the target eye window. **(C)** Previous trial

type and saccade direction relative to current saccade direction. We took only visuomotor error trials with saccade away from the target in this analysis. We found a similar percentage of the same and the opposite saccade direction comparing previous to current trial if the previous trial was a successful trial. However, if the previous trial was an impulsive trial, the marmosets tend to switch their saccade direction. If the previous trial was also a visuomotor trial, the marmosets tend to keep the same saccade direction.

Figure 10 Comparing saccade main sequence across error and successful categories. (A) Saccade amplitude against saccade peak velocity. We plotted saccades extracted from each error and successful trials for gap task. Fitting parameters are: Marmoset S: distractive: a= 84.6, n= 0.817; impulsive: a= 64.08, n= 0.967; visuomotor: a= 48.98, n= 1.135; successful: a= 118, n= 0.768; Marmoset N: distractive: a= 81.45, n= 0.84; impulsive: a= 67.58, n= 0.94; visuomotor: a= 57.85, n= 1.003; successful: a= 105, n= 0.854; Marmoset M: distractive: a= 80.68, n= 0.897; impulsive: a= 73.85, n= 0.955; visuomotor: a= 58.47, n= 1.096; successful: a= 123.8, n= 0.789. **(B)** Saccade amplitude against saccade peak velocity. Here we plotted saccades extracted from each error and successful trials for ODR task. Fitting parameters are: Marmoset S: distractive: a= 42.54, n= 1.13; impulsive: a= 89.57, n= 0.9077; visuomotor: a= 66.9, n= 0.978; successful: a= 80.11, n= 0.989; Marmoset N: impulsive: a= 106, n= 0.756; visuomotor: a= 58.97, n= 0.974; successful: a= 53.07, n= 1.21; Marmoset M: distractive: a= 92.12, n= 0.872; impulsive: a= 108.3, n= 0.851; visuomotor: a= 81.34, n= 0.904; successful: a= 89.45, n= 0.984. **(C)** Saccade amplitude against saccade duration. Here we plotted saccades extracted from each error and successful trials for gap task. Fitting parameters are: Marmoset S: distractive: b= 2.47, c= 23.24; impulsive: b= 1.67, c= 29.76; visuomotor: b= 1.448, c= 31.39; successful: b= 1.73, c= 20.7; Marmoset N: distractive: b= 2.33, c= 24.09; impulsive: b= 1.77, c= 27.17; visuomotor: b= 1.68, c= 30.1; successful: b= 1.09, c= 22.3; Marmoset M: distractive: b= 2.05, c= 26.57; impulsive: b= 1.63, c= 28.03; visuomotor: b= 1.19, c= 30.39; successful: b= 1.31, c= 20.6. **(D)** Saccade amplitude against saccade duration. Here we plotted saccades extracted from each error and successful trials for ODR task. Fitting parameters are: Marmoset S: distractive: b= 2.83, c= 28.69; impulsive: b= 0.86, c= 26.56; visuomotor: b= 1.63, c= 29.26; successful: b= 0.39, c= 28.59; Marmoset N: impulsive: b= 2.19, c= 21.36; visuomotor: b= 2.09, c= 29.20; successful: b= -0.52, c= 34.69; Marmoset M: distractive: b= 2.17, c= 29.25; impulsive: b= 1.44, c= 21.97; visuomotor: b= 1.96, c= 27.05; successful: b= 0.37, c= 26.82. Solid curves indicate the fitted curve.

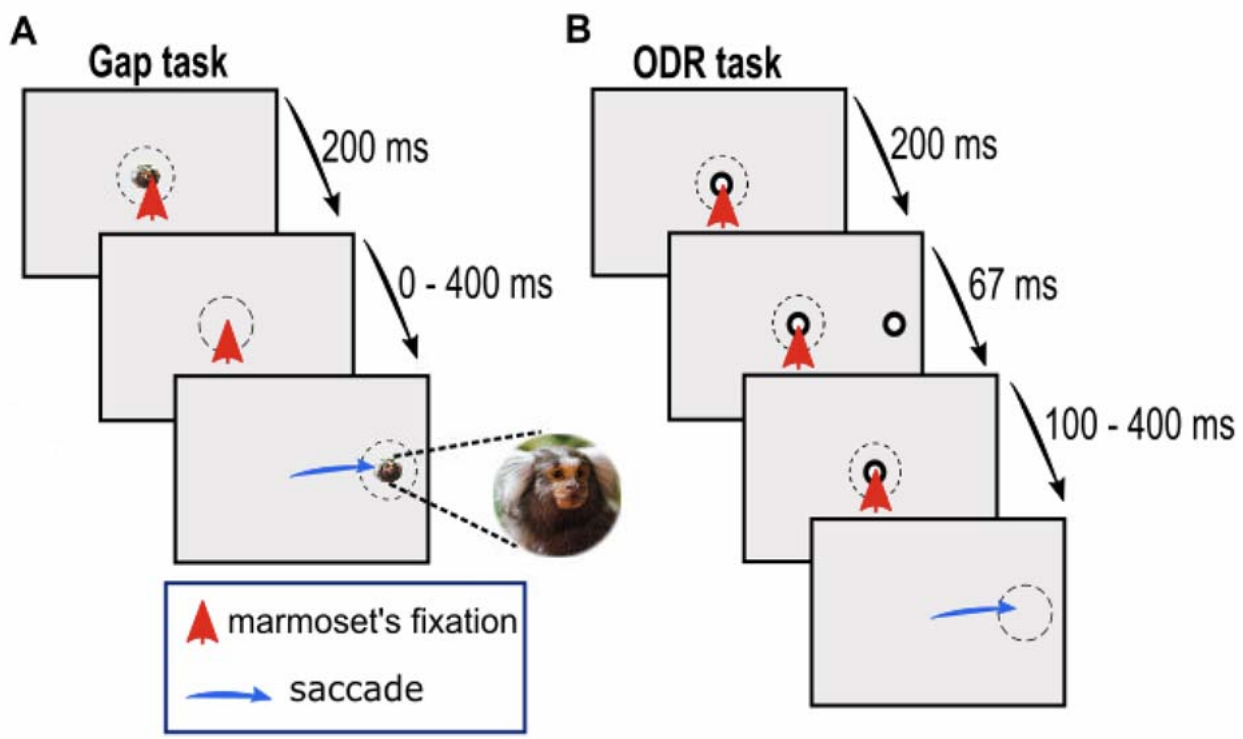

A
Gap task
200 ms
0 - 400 ms
B
ODR task
200 ms
67 ms
100 - 400 ms
marmoset's fixation
saccade

Figure 1

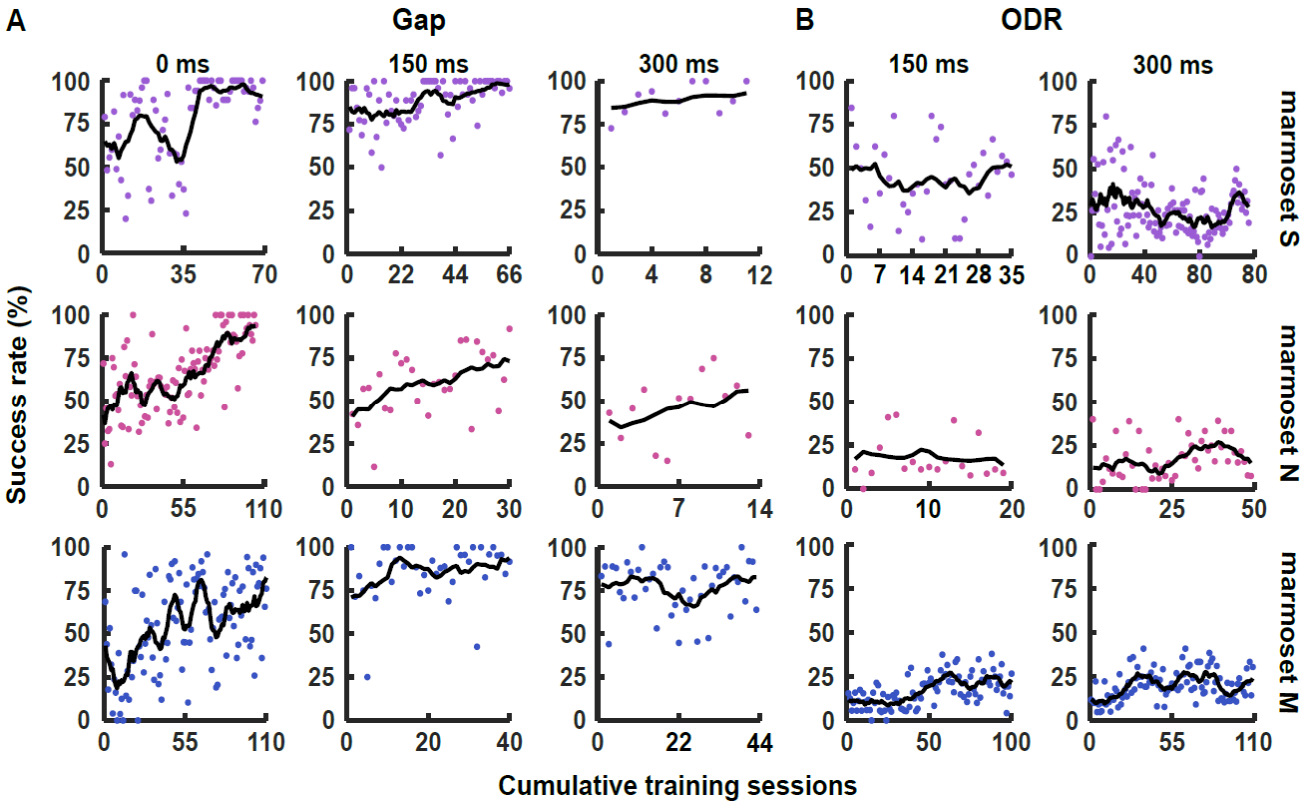

A
Gap
0 ms
150 ms
300 ms
B
ODR
150 ms
300 ms
marmoset S
marmoset N
marmoset M
Success rate (%)
Cumulative training sessions

Figure 2

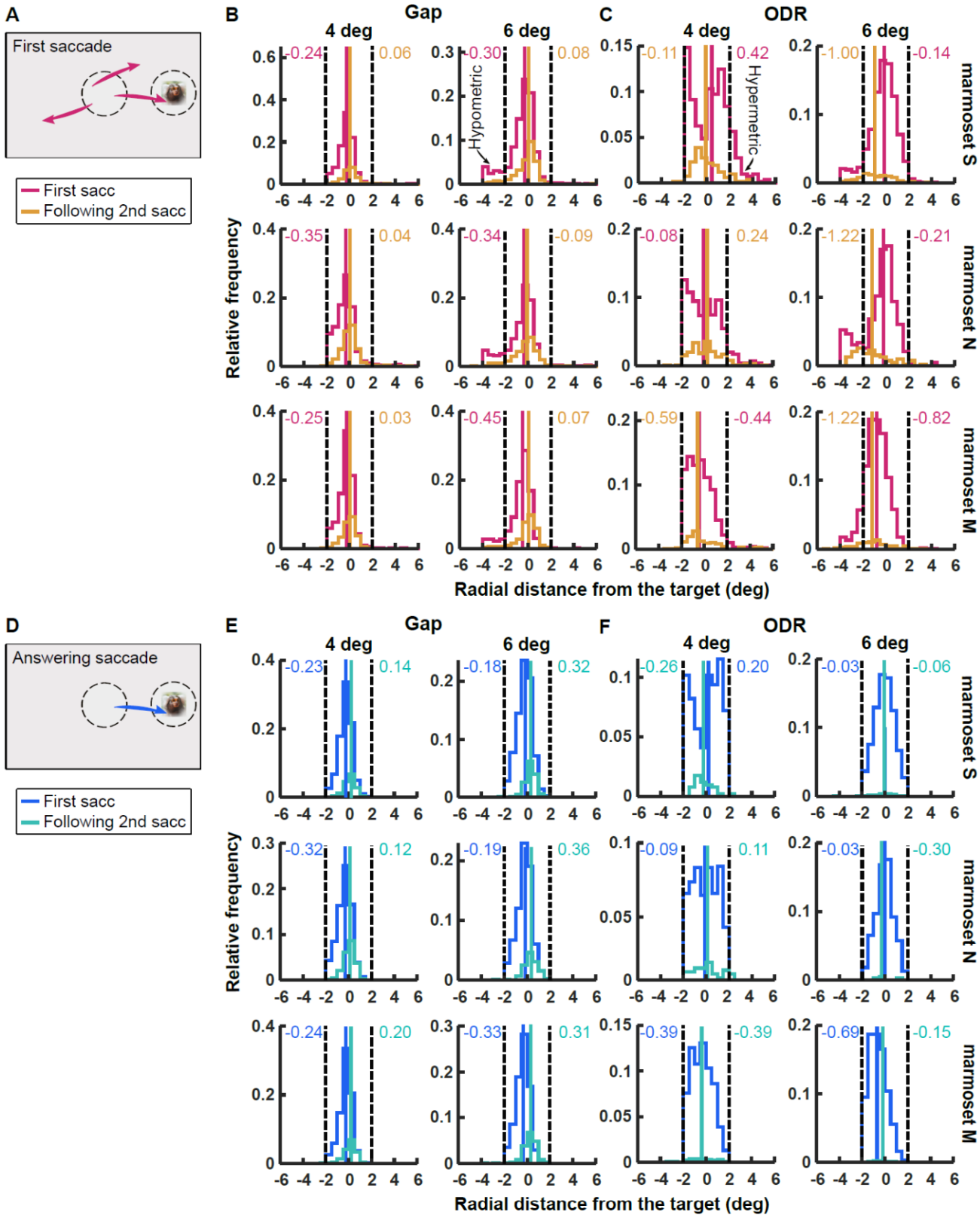

A
First saccade
First sacc
Following 2nd sacc
B
Gap
4 deg
6 deg
C
ODR
4 deg
6 deg
Hypometric
Hypermetric
marmoset S
marmoset N
marmoset M
Relative frequency
Radial distance from the target (deg)
D
Answering saccade
First sacc
Following 2nd sacc
E
Gap
4 deg
6 deg
F
ODR
4 deg
6 deg
marmoset S
marmoset N
marmoset M
Relative frequency
Radial distance from the target (deg)

Figure 3

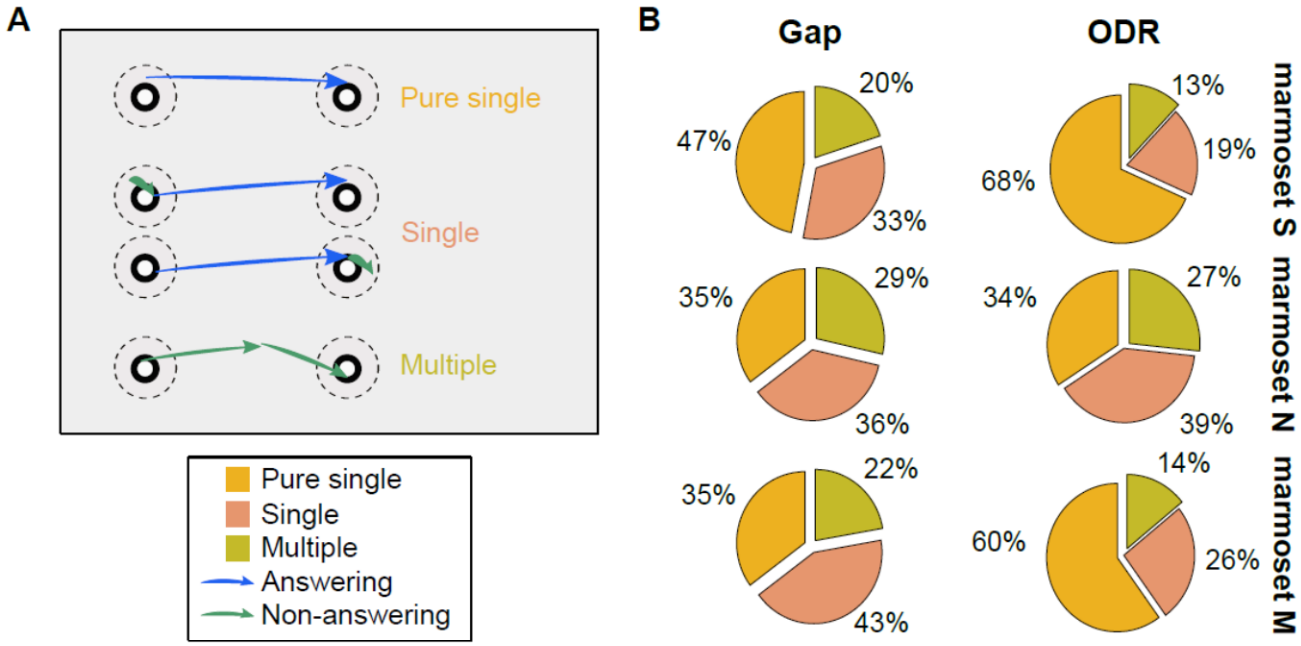

A
Pure single
Single
Multiple
Pure single
Single
Multiple
Answering
Non-answering
B
Gap
ODR
20%
47%
33%
13%
19%
68%
marmoset S
29%
35%
36%
27%
34%
39%
marmoset N
22%
35%
43%
14%
60%
26%
marmoset M

Figure 4

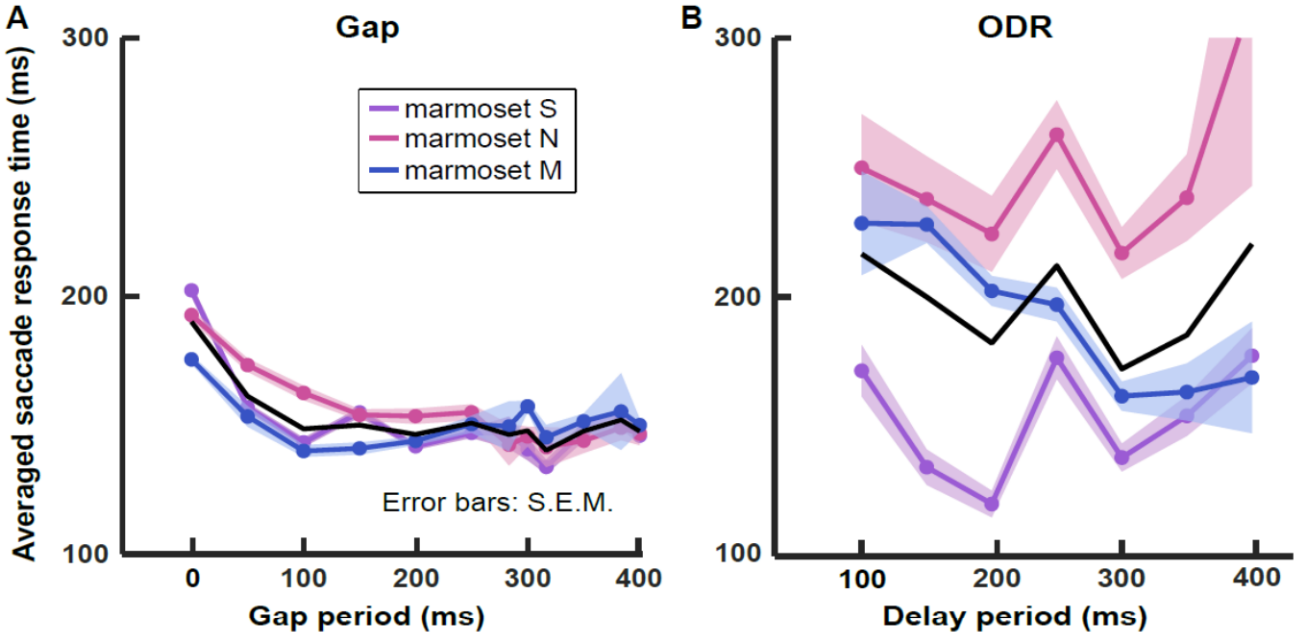

A
Gap
B
ODR
Averaged saccade response time (ms)
300
200
100
marmoset S
marmoset N
marmoset M
Error bars: S.E.M.
0
100
200
300
400
Gap period (ms)
Delay period (ms)

Figure 5

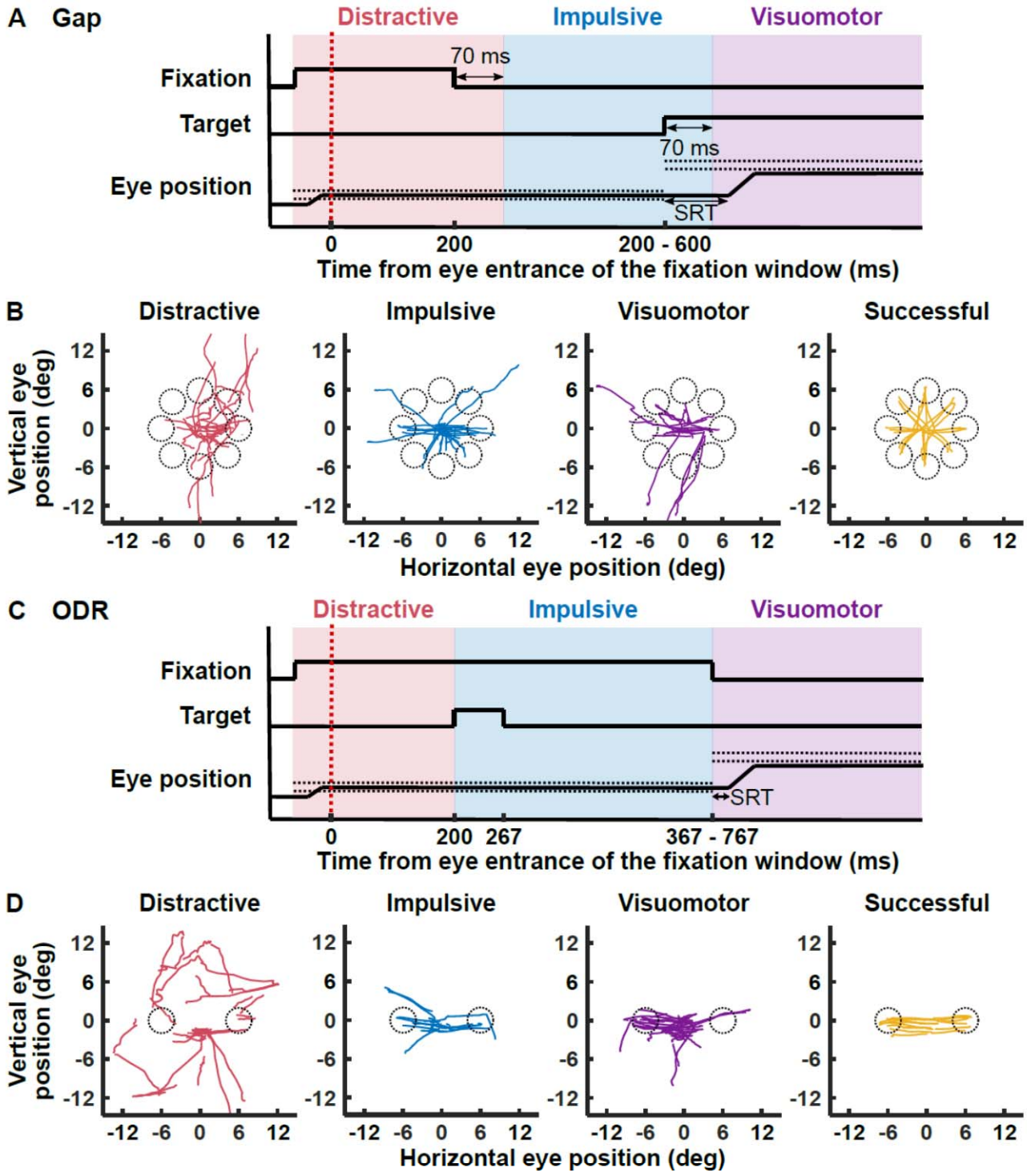

A Gap
Distractive
Impulsive
Visuomotor
70 ms
Fixation
Target
70 ms
Eye position
SRT
0
200
200 - 600
Time from eye entrance of the fixation window (ms)
B
Distractive
Impulsive
Visuomotor
Successful
Vertical eye position (deg)
12
6
0
-6
-12
-12 -6 0 6 12
Horizontal eye position (deg)
C ODR
Distractive
Impulsive
Visuomotor
Fixation
Target
Eye position
SRT
0
200 267
367 - 767
Time from eye entrance of the fixation window (ms)
D
Distractive
Impulsive
Visuomotor
Successful
Vertical eye position (deg)
Horizontal eye position (deg)

Figure 6

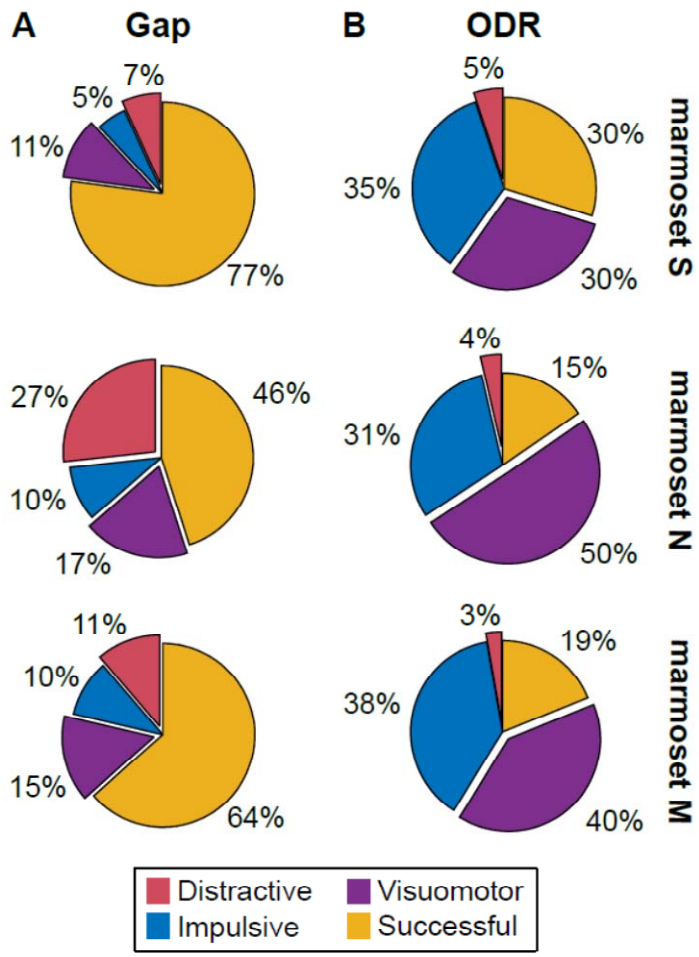

A
Gap
B
ODR
7%
5%
11%
77%
5%
30%
35%
30%
marmoset S
27%
46%
10%
17%
4%
15%
31%
50%
marmoset N
11%
10%
15%
64%
3%
19%
38%
40%
marmoset M
Distractive
Visuomotor
Impulsive
Successful

Figure 7

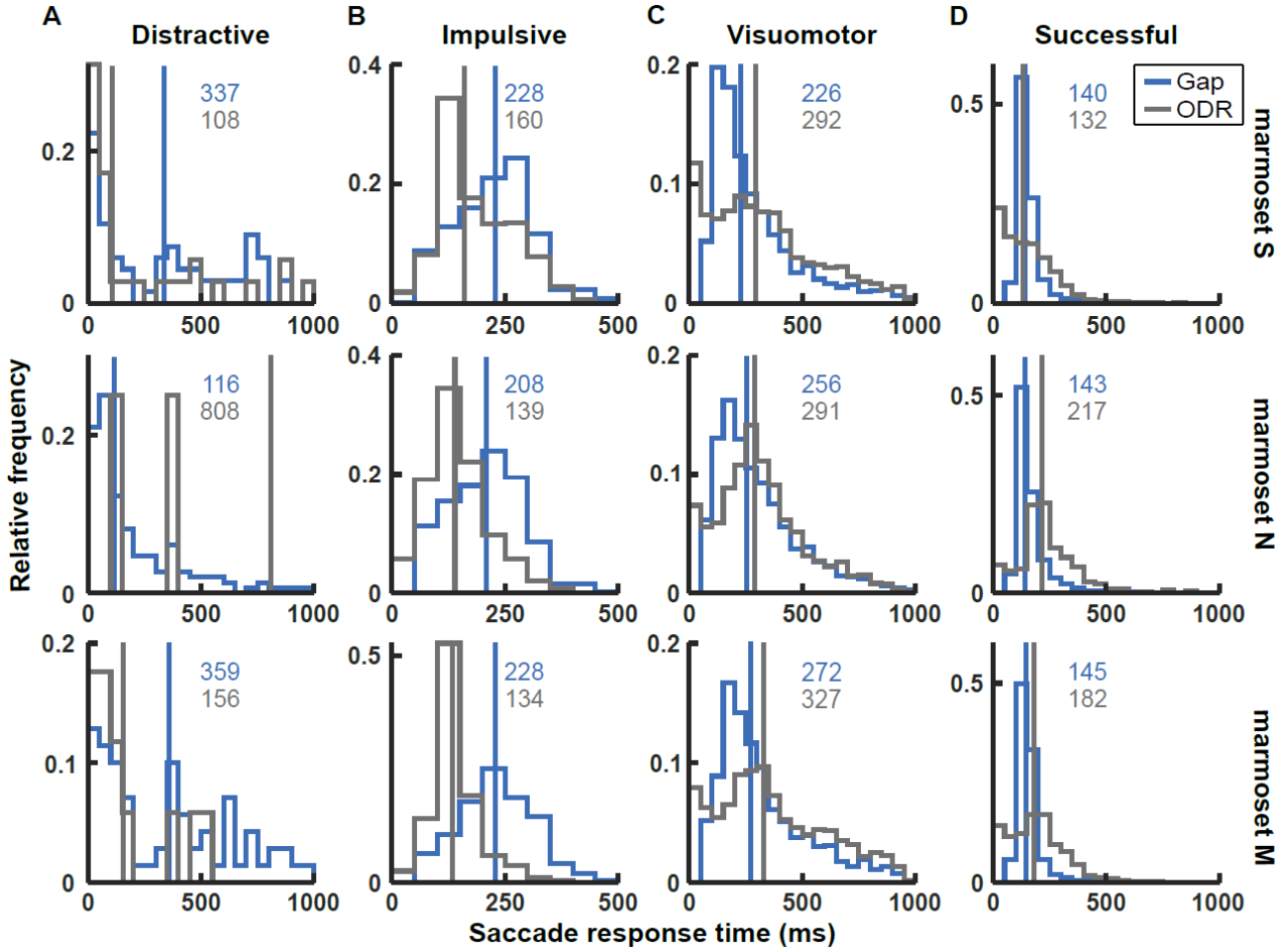

A
Distractive
B
Impulsive
C
Visuomotor
D
Successful
Gap
ODR
marmoset S
marmoset N
marmoset M
Relative frequency
Saccade response time (ms)
337
108
228
160
226
292
140
132
116
808
208
139
256
291
143
217
359
156
228
134
272
327
145
182

Figure 8

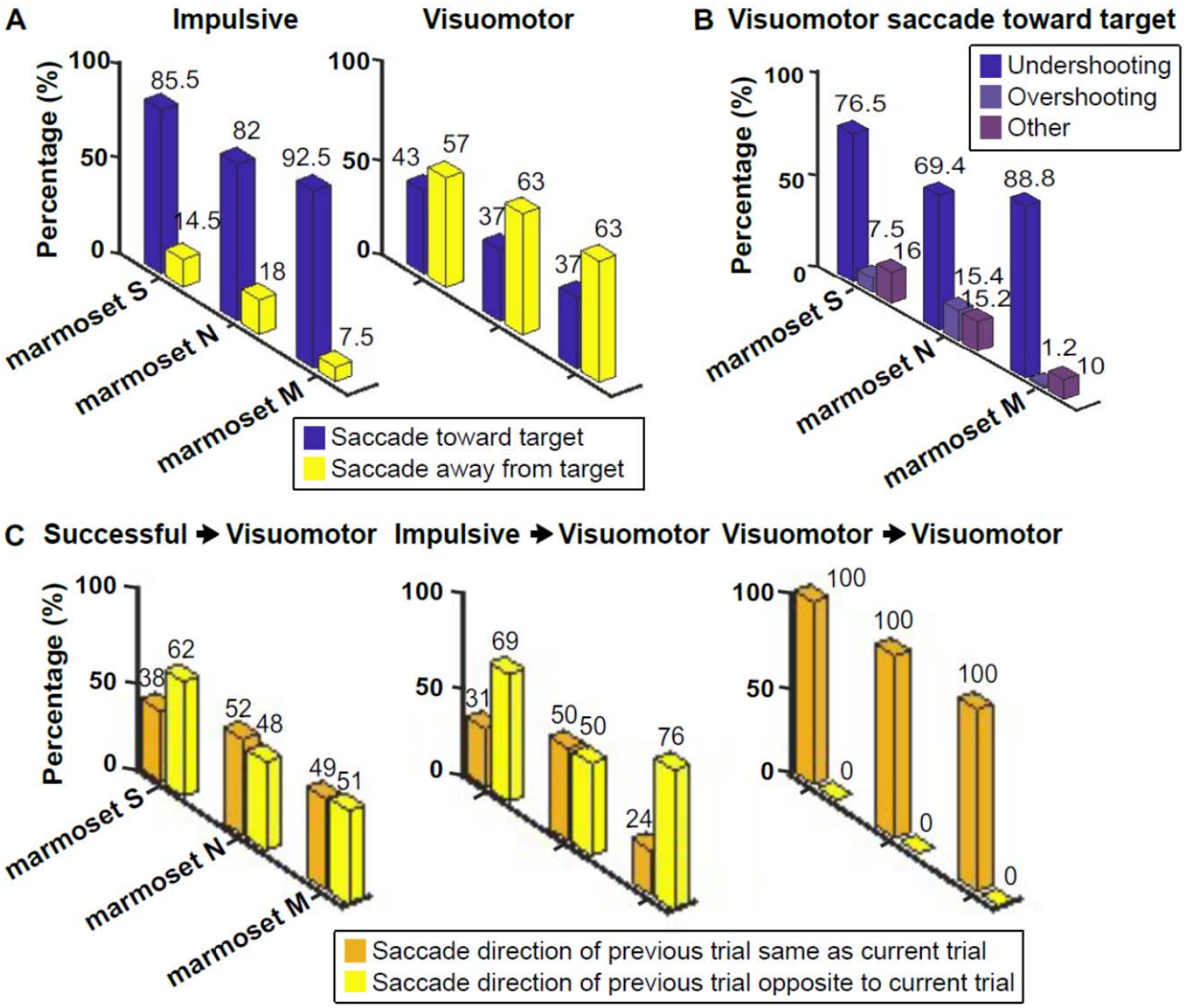

A
Impulsive
Visuomotor
Percentage (%)
100
50
0
85.5
14.5
82
18
92.5
7.5
43
57
37
63
37
63
marmoset S
marmoset N
marmoset M
Saccade toward target
Saccade away from target
B Visuomotor saccade toward target
Undershooting
Overshooting
Other
76.5
7.5
16
69.4
15.4
15.2
88.8
1.2
10
C Successful → Visuomotor
Impulsive → Visuomotor
Visuomotor → Visuomotor
38
62
52
48
49
51
31
69
50
50
24
76
100
0
100
0
100
0
Saccade direction of previous trial same as current trial
Saccade direction of previous trial opposite to current trial

Figure 9

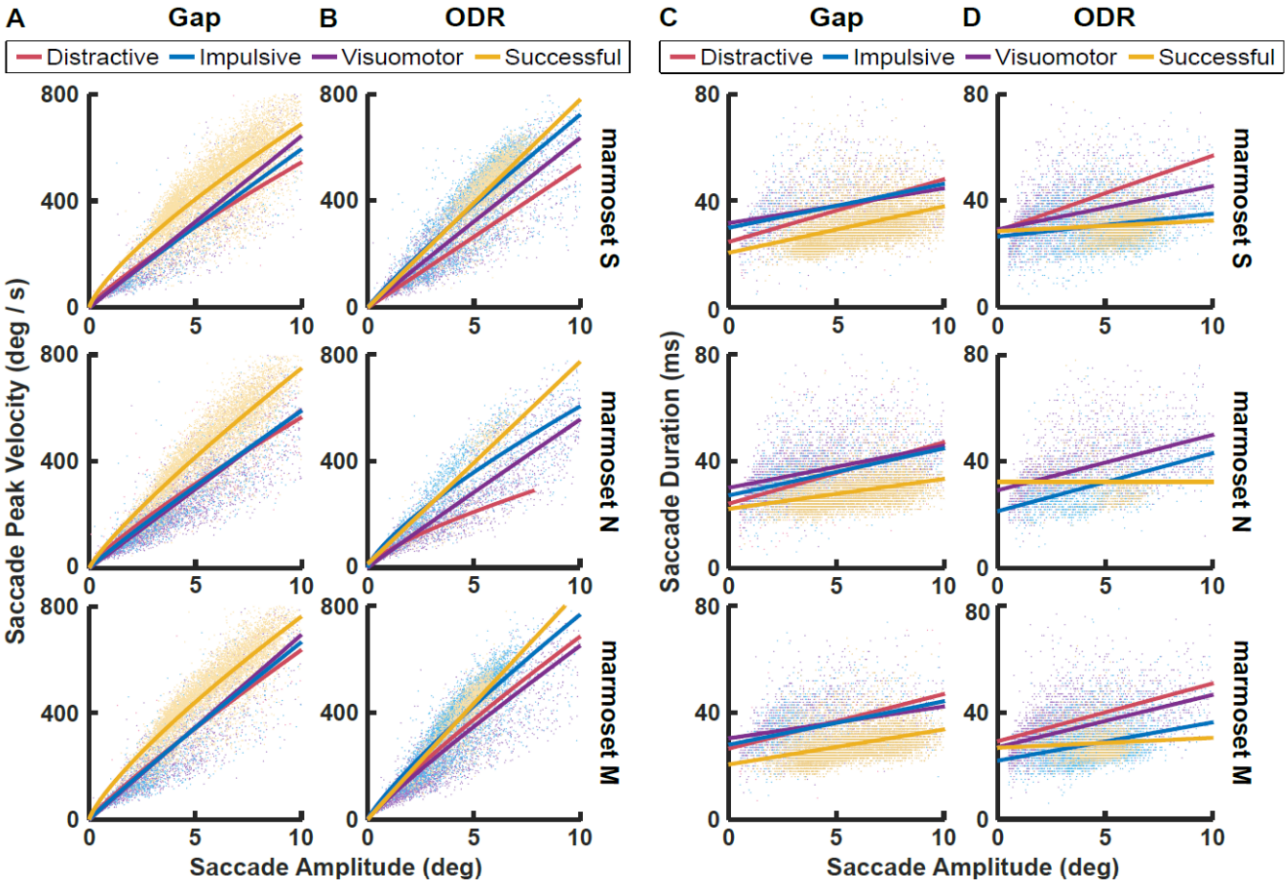
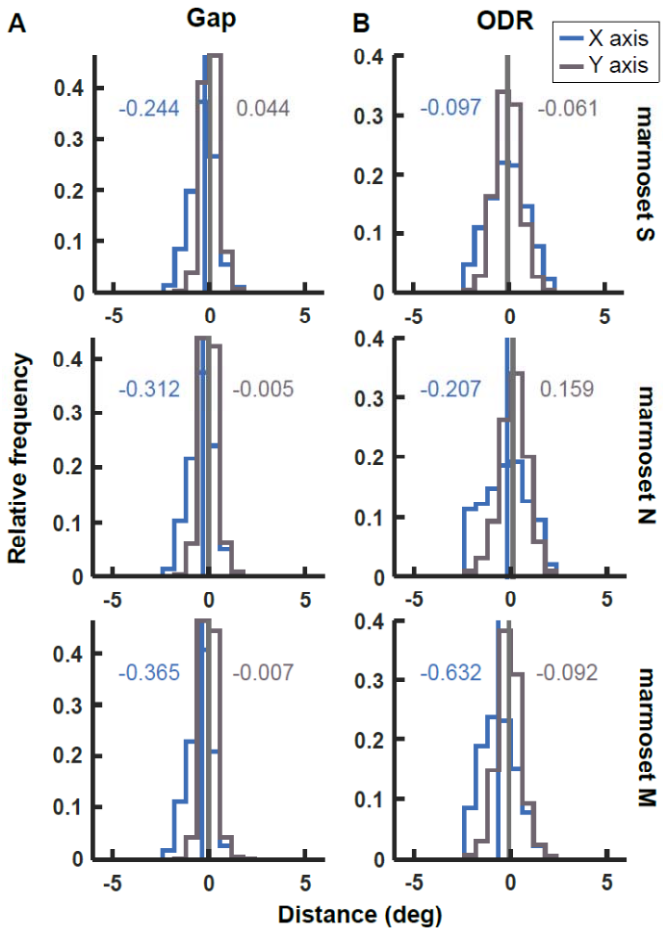
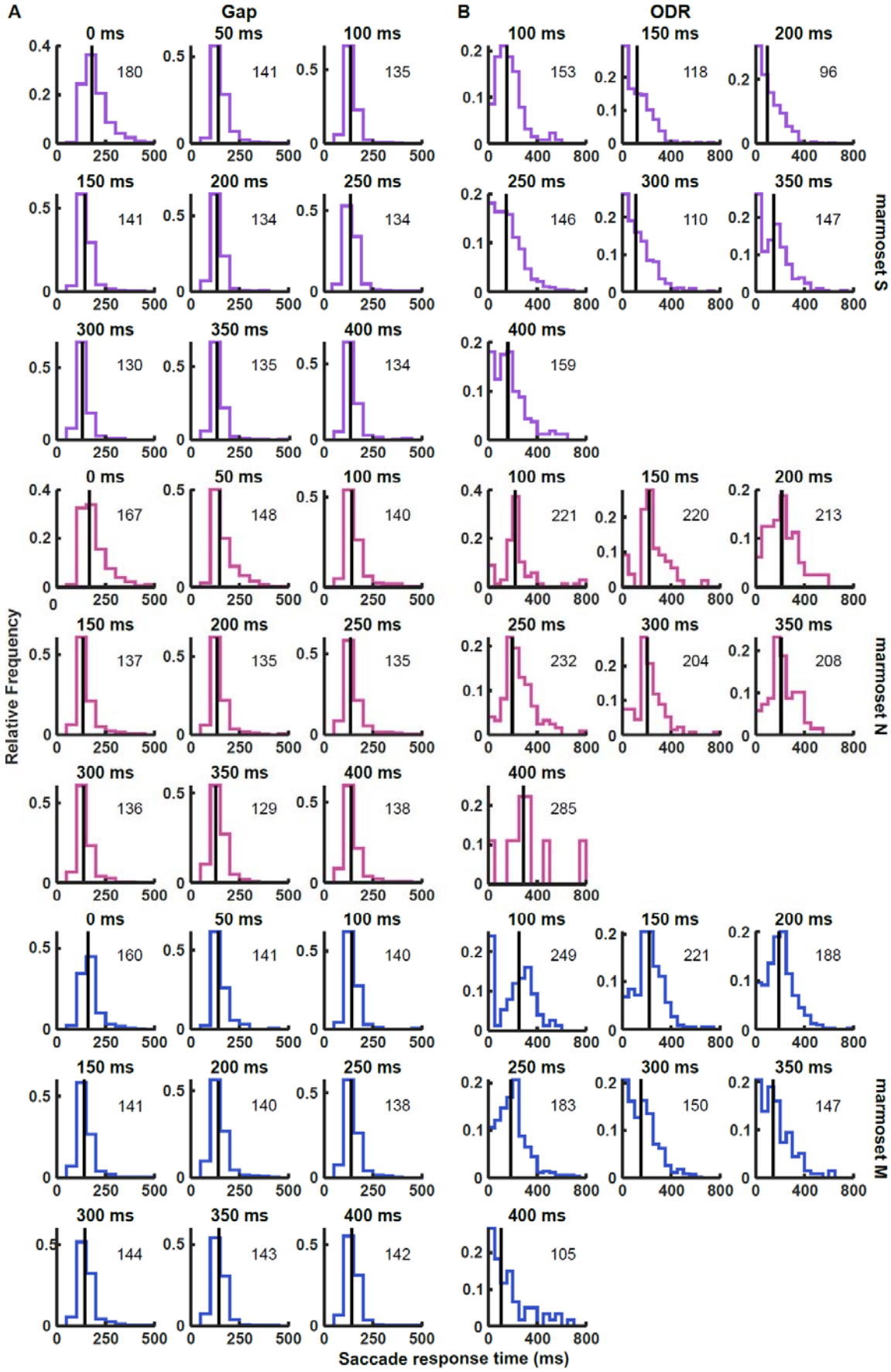

A
Gap
B
ODR
C
Gap
D
ODR
Distractive
Impulsive
Visuomotor
Successful
Saccade Peak Velocity (deg / s)
Saccade Duration (ms)
Saccade Amplitude (deg)
marmoset S
marmoset N
marmoset M

Figure 10



Supplementary Figure 1 Distance from the target location to answering saccade endpoint. In this figure, we combined all the answering saccades from successful trials regardless of the gap or delay period, or target eccentricity. Previously, an upward bias of the saccade trajectory and landing position was reported in both exogenously-driven and endogenously-driven saccadic tasks (White et al., 1994; Goffart et al., 2006). To preserve possible upward shift from our data set, we first flipped the target locations in the second and the third quadrant and the correspondent answering saccade along the x-axis. We then rotated all the target locations and the answering saccades to the positive x-axis. Finally, we took the difference between the target and the x and y coordinates of the saccade endpoint independently. **(A)** Result from gap task. **(B)** The result from ODR task. As can be seen, the undershooting on the x distance from the saccade endpoint to the target location was always more than the y distance for both tasks. (Gap: marmoset S: $p < 2.2\text{x}10^{-308}$, marmoset N: $p = 3.4\text{x}10^{-251}$, marmoset M, $p < 2.2\text{x}10^{-308}$; ODR: marmoset S: $p = 9.9\text{x}10^{-3}$, marmoset N: $p = 3.1\text{x}10^{-14}$, marmoset M, $p = 2.4\text{x}10^{-96}$; Wilcoxon rank sum test) and there was no systematic upward or downward bias in the y distance.


A
Gap
B
ODR
0 ms
50 ms
100 ms
150 ms
200 ms
250 ms
300 ms
350 ms
400 ms
180
141
135
153
118
96
141
134
134
146
110
147
130
135
134
159
167
148
140
221
220
213
137
135
135
232
204
208
136
129
138
285
160
141
140
249
221
188
141
140
138
183
150
147
144
143
142
105
marmoset S
marmoset N
marmoset M
Relative Frequency
Saccade response time (ms)

892

Supplementary Figure 2 Saccade response time (SRT) from the successful trials of each gap period for the gap task and each delay period for the ODR task. We plotted the SRT of the answering saccades of the successful trials regardless of the target eccentricity. **(A)** Gap task. Note that in all three marmosets, the SRT histogram for the 0 ms gap period had rather a long tail. When the gap period increased to 150 ms, the tail of the histogram got shorter. There was no express saccade observed in all three marmosets. **(B)** ODR task. Note that in all three marmosets, extra short-latency saccades (< 70 ms) were observed in all delay periods. The medians of the SRT for each plot were indicated in each plot in black.