Dissecting errors made in response to externally- and internally- driven visual tasks in the common marmosets and humans

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Keywords: Callithrix jacchus[1], gap saccade task[2], oculomotor delayed response task[3], error trials[4], task history[5].

ABSTRACT

Various visual paradigms in oculomotor research were proposed and proven effective for studying the neural processes of eye movement, cognitive control, attention and neurological disorders. However, oculomotor researchers usually analyse data collected from humans or over-trained non-human primates (NHPs), focusing only on successful records, whereas error records are usually excluded. In diseased conditions, these errors may repetitively show up but their interpretation would be difficult due to the absence of baseline records reported from healthy controls. In the current study, we aimed to analyse both failure and success and to compare marmosets and humans. We trained marmosets to perform the externally-driven gap saccade task and the internally-driven oculomotor delayed response task. We also collected data from human subjects who performed identical tasks. We categorised error trials into three different groups, depending on when the task instructions were violated, and interpreted possible causes based on saccade reaction time, saccade landing position and task history. We found that marmosets and humans showed remarkably similar behaviour in both error and success, despite the rareness of humans' failure. Finally, we found that successful saccades in gap saccade task had always the highest peak velocity in both species, reflecting faster sensorimotor processes for correct responses. Our results suggest that when performing oculomotor tasks, marmosets may share similarities to humans' neural processing of success and errors, making them a suitable model for studying humans. More importantly, analysing error trials in sync with successful ones provides further insights into the cognitive and sensorimotor processes.

INTRODUCTION

Saccades are conjugated rapid eye movements that primates make to bring the target of interest to the centre of the fovea (Yarbus, 1967; Weymouth et al. 1928). These movements exhibit stereotypic kinematics with a fixed relationship between saccade amplitude, velocity, and duration (Bahill et al., 1975; Lebedev et al., 1996; Robinson 1981), giving saccades valuable research and clinical means.

After the establishment of the first awake non-human primates (NHPs) preparation for measuring eye movements (Fuchs 1967; Fuchs and Robinson 1966), the NHPs, especially macaque monkeys -who can learn and master different types of saccadic tasks quickly with close-to-perfect performance- became and are still the primary entrance to study the cortical and subcortical control of saccades (for reviews, see Borra and Luppino 2019; Coiner et al. 2019; Schiller and Tehovnik 2009; Takahashi and Shinoda 2018). With the progression of

other research, the interdependency between the cortical saccadic system and attention, visual working memory, and visual decision-making was also discovered (Boshra and Kastner 2022; Hunt et al. 2019; Jonikaitis and Moore 2019; Spering 2022). Measuring the saccadic eye movement went beyond understanding the oculomotor system and became a window to observe and evaluate the cognitive processes of the brain (Beesley et al. 2019; Hafed et al. 2015; Liversedge et al. 2011; Wolf and Lappe 2021). Macaques have taken an important role here again, because of their high abilities to perform cognitive tasks. However, most of the saccade-related research considered and analysed only successful records, mainly due to the insufficiency of error records.

In the meantime, the visual paradigms and saccade measurements have been extended to the clinical means of investigation, evaluating different neurological disorders (Gooding and Basso 2008; Das et al. 2022; Everling and Fischer 1998; 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), and were proposed as an early behavioural measurement for these disorders. In those studies, patients showed significant errors while performing the tasks. Nonetheless, the inadequate understanding of how errors occur in healthy controls makes it challenging to further diagnose the potentially affected brain structures, relying on eye movements.

Although NHPs are a powerful tool for studying neurological disorders because of their similar brain structure and function to humans (Hutchison and Everling 2012) and indeed, several studies have successfully used macaque monkeys to reproduce the symptoms of various brain disorders (Qiu and Li 2017; Verdier et al. 2015; Sherman et al. 2021; Souder et al. 2021; Liu et al. 2016), still, the lack of error records makes it difficult to directly compare to patients' records obtained from the clinical studies.

Recently, the common marmosets (*Callithrix jacchus*), a new world monkey, have been proposed as an alternative NHP model with the advantages of easier transgenic manipulation (Izpisua Belmonte et al. 2015; Park et al. 2016; Sasaki et al. 2009), smoother brain surface for easier and more accurate intracranial manipulation (Lin et al., 2019; Mundinano et al., 2016) and a shorter lifespan for long-term behavioural follow-up with the progression of neurological diseases (Tardif et al. 2011). Several neurological disease models have also been successfully generated using various methods in marmosets (Eslamboli et al., 2007; Tomioka et al., 2017; Jenner et al., 1984; Fox et al., 2010; Emborg, 2017). Moreover, they can learn to perform a variety of visual and cognitive tasks under head unrestrained conditions (Clarke et al. 2011; Jendritza et al. 2021; Spinelli et al. 2004; Yamazaki et al. 2011; Okano 2021) and under head restrained conditions (Mitchell et al. 2014; Johnston et al., 2018; Chen et al., 2021; Sedaghat-Nejad et al. 2019), and they showed similar to human behaviour when they successfully performed oculomotor tasks.

Here, we hypothesized that not only success but also the error behaviour of marmosets would be similar to those of humans. Therefore, we trained three marmosets in two different visual paradigms, the externally-driven gap saccade task (in short, gap task) and the internally-driven oculomotor delayed response (ODR) task (Funahashi et al. 1989; Hikosaka and Wurtz 1983) concurrently, mimicking the clinical studies done on human patients. We collected both successful and error records and proposed a systematic way to categorize error trials based on the designed constraints of the task. We studied these different errors in-depth, analysed

their possible causes, and compared them between the two species. We aimed to establish the baseline of error profiles to pave the way for future studies of human neurological disorders using NHP models.

METHOD

Ethics Approval

All the 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.

Ethics committees at the Medical Faculty of Kyoto University approved human experiments. Subjects provided written, informed consent to join the experiment.

Animal Preparation and Surgical Procedure

Three adult marmosets participated 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 where they were allowed to enter and leave the transportation cage from their home cage as they wanted until they acclimated to it. This was followed by two weeks of chair training to familiarise the marmosets with the primate chair and the lab environment. Later, they underwent headpost implantation surgery to prepare for head-fixing training. Anaesthesia was induced using 14 mg/kg ketamine and 0.14 mg/kg medetomidine. In addition, 0.07 mg/kg atropine, 0.5 mg/kg dexamethasone, and 1.5 mg/kg gentamicin were administered to prevent excessive salivation, pain and infection respectively. Under 1.5 % isoflurane, each marmoset was aseptically mounted with its custom-designed headpost based on the MRI reconstruction of their skulls. The headposts were 3D-printed using Dental SG Resin (Form2, Formlabs, U.S.A.), and were attached to the marmosets' skulls using Super-Bound (Sun Medical Co., Ltd., Japan). After the surgery, marmosets were given the antibiotic ampicillin, 30 mg/kg, and the anti-inflammatory and analgesic medication ketoprofen, 0.8 mg/kg for 4 days. After the medical treatment, an additional week was given to allow for a full recovery.

Human Subjects

Three adult human subjects aged 29–37 participated in this study, two males (human C, H) and one female (human W). Humans' head position was stabilized using a custom-made chin rest.

Monitor Setup and Visual Stimulus Software

We used a 1280x1024 pixel resolution LCD monitor (Dell P1917S) with a refresh rate of 60 Hz for marmosets and a 1920x1080 pixel resolution LCD monitor (Dell AW2125HF) cropped to 1280x1024 pixel with the same refresh rate for humans. The visual distance was 41 cm, and the background where the tasks were presented was a grey background with a luminance of 80.81 cd/m^2 for marmosets, and 58.47 cd/m^2 for humans. The experimental software PsychoPy 3.6 was used to control the stimuli display and for online control of subjects' eye position (Peirce et al. 2019).

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 marmosets' face photos (8 images per trial, sizes ranging from 4 to 20.25 deg^2; distance from monitor centre to image centre ±12 deg horizontal and ±10 deg vertical) presented at random eccentricity 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' gazes. We used the interface to estimate the x and y gain and offset of the eye positions for each marmoset individually. This calibration was done once for each marmoset after sitting in front of the eye tracker for the first time. We validated the calibration result every day by taking the average eye position of the last 50 ms before the marmosets obtained their reward from the blocked gap task (described below) and calculated the offsets and gains using simple linear regression. The offset and gain results were updated to the online eye controller as needed. Eyelink 1000 (SR Research, Canada) was used for human subjects, but all the other eye tracker settings and calibration procedures were similar to those used for marmosets.

Visual Tasks

Blocked Gap Task

In gap task (**Fig. 1A**), target eccentricity (4, 6 or 8 degrees) and gap period (0-400 ms with 50 ms increment) were predetermined randomly before the session onset and fixed for each session to facilitate training. The target location was randomly selected for every session from one of the eight different locations equally spaced by a 45-degree radial visual angle.

A trial started by presenting a 1-degree-radius marmoset face as the fixation stimulus at the centre of the monitor over a grey background for up to 1000 ms. The marmosets were trained to hold their gaze within a 2-degree-radius invisible window centred at the fixation stimulus (**Fig. 1A**, dashed circle in the top graph). If the gaze was successfully maintained within the window for 200 ms, the fixation stimulus was removed, allowing the beginning of the gap period (**Fig. 1A**, middle graph). During the gap period, marmosets were trained to hold their gaze within the same invisible window at the centre of the screen. If the gaze was successfully maintained, a peripheral stimulus (1-degree marmoset face) was shown as the target stimulus and the marmosets were required to make a saccade towards it within 1000 ms and to hold their gaze within a 2-degree invisible window centred at the target location for 200 ms to attain a drop (0.05 ml) of the reward. After every successful answer, a rewarding photo was also displayed at the target location (**Fig. 1A**, bottom graph). The trial was aborted if the subject failed to initiate fixation within the defined time after trial initiation, if the gaze escaped from the fixation window before the target onset during the fixation or gap periods, if the gaze escaped from the target window before the time allowed so (insufficient fixation) or if no or incorrect responses were made within 1000 ms. A one-frame red screen flash was presented as an indication of a trial failure. One session was terminated if either 24 successful trials (see Result section) were collected or if a maximum of 48 trials (including error) were collected. Human subjects performed the same task albeit without the liquid reward.

Figure 1 approx. here

Blocked Oculomotor Delayed Response Task (ODR)

In ODR task (**Fig. 1B**), target eccentricity (4 or 6 degrees) and delay period (100-400 ms with 50 ms increment, (similar to Andersen et al. 1990; Massendari et al. 2018; Willeke et al. 2019; Angelo V. Colmenero 2021) were predetermined before the session onset. Similar to gap task, these parameters were fixed for each session to facilitate training. But here, a different fixation and target stimuli were used (a black dot with a white centre, total 1-degree-radius, indicated in **Fig. 1B**) to make it easier for the marmosets to distinguish between the tasks.

Marmosets were trained to initiate the trial with similar criteria used in gap task (**Fig. 1B**, top graph). After successful initial fixation, a peripheral target was flashed either to the right or left of the centre fixation stimulus for around 67 ms (**Fig. 1B**, second graph, similar target presentation duration (Hikosaka and Wurtz 1983; Kato et al. 1995; Rivaud-Péchoux et al. 2000; Takikawa et al. 2002; Loe et al. 2012; Willeke et al. 2019). A delay period then followed, during which the marmosets were required to hold their gaze at the fixation stimulus (**Fig. 1B**, third graph). Following the end of the delay period, and the fixation stimulus offset, the marmosets were required to make a saccade toward the flashed/remembered target location within 1000 ms and keep their gaze within the 2-degree invisible window centred at the invisible target for 17 ms to be rewarded (**Fig. 1B**, bottom graph). After every successful answer, a rewarding photo was also displayed. The trial was aborted for similar reasons as in gap task and a one-frame red screen flash was presented as an indication of a trial failure. One session was terminated if either 16 successful trials (see Result section) were collected or if a maximum of 32 trials (including error) were collected. Human subjects performed the same task albeit without the liquid reward.

The number of sessions per day was determined based on the level of willingness to work of the marmosets, but in general, an average of 4 sessions of gap and 4 sessions of ODR tasks were performed a day and each session was structured with a different gap/delay period and a different target eccentricity. The liquid reward used for marmosets was prepared by mixing baby supplement banana pudding (Kewpie Corp., Japan) with banana-flavoured Mei-balance (Meiji Holdings Co., Japan).

Saccades Detection

For saccades detection, we used U'n'Eye, a deep neural network developed for eye movement detection and classification (Bellet et al. 2019). The eye data were first pre-processed and the ground-truth saccade dataset was labelled and manually checked following the same procedure and criteria as (Chen et al. 2021). After labelling around 200 trials, the data were gathered and fed into U'n'Eye for network training and validation to get optimal detection. After training, the rest of the pre-processed eye data were fed into the trained network for saccade labelling and the results were inspected by the experimenter to check for mislabelling.

Data Analysis

Definitions of Successful Trials, Error Trials and Saccade Reaction Time

Total trials were first separated into either successful or error trials for each task (**Fig. 2)**. A trial was defined as successful if a saccade was generated after target onset or fixation offset in gap or ODR tasks, respectively, the target was reached regardless using a single saccade or more, and the trial ended with reward delivery and reward photo display. On the contrary, a trial was defined as an error if it ended with a one-frame red screen flash presentation.

We further divided successful trials into either a single saccade group or multiple saccades group. A trial was defined as a single saccade trial if the saccade started from within the 2-degree invisible window centred around the fixation stimulus, and landed within the 2-degree invisible window centred at the target location, regardless of whether the saccade was escorted with microsaccades or not **(Fig. 2A,** left**)**. Alternatively, a trial was defined as a multiple saccades trial if multiple saccades were generated to reach the target stimulus, provided that the first saccade to leave the fixation stimulus meets the fixation criteria and the last saccade to reach the target stimulus meets the successful saccade landing criteria **(Fig. 2A,** right**)**. Saccade reaction time (SRT) was calculated as the time between target onset or fixation offset in gap or ODR tasks and the onset of the saccade (**Fig. 2B, 2D**, yellow eye traces). We used the single saccade group only for SRT and main sequence analysis because it wasn't clear which saccade was the one intended to answer in the multiple saccades group.

On the other hand, the error trials were divided into three sub-groups, distractive error, impulsive error, and visuomotor (VM) error, based on when a trial was terminated relative to the monitor events in each task **(Fig. 2B, 2D)**. For gap task, error trials were labelled based on three monitor events, 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 (**Fig. 2B**, red eye traces). If a trial ended after fixation stimulus offset and before target stimulus onset, it was defined as an impulsive error trial (**Fig. 2B**, blue eye traces). Finally, if a trial ended after target stimulus onset but with the one-frame red screen flash, it was defined as a VM error trial (**Fig. 2B**, purple eye traces). We then looked for the last saccade in the labelled trial that broke fixation (i.e., the saccade started within the fixation window and ended outside the fixation window) **(Fig. 2B)**. This saccade was taken as the saccade that responded to the nearest monitor event in this trial **(Fig. 2C)**, and the SRT was calculated. To be more specific, impulsive error SRT was calculated as the time between fixation offset and the onset of the saccade and VM error SRT was calculated as the time between target onset and the onset of the saccade. 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. Furthermore, if the marmoset did not leave the fixation window after entering it, the trial was defined as a VM error trial and no saccade or SRT was identified.

However, anticipatory saccades from successful records were reported for marmosets performing the gap task (Chen et al. 2021). Because the SRT of anticipatory saccades was short (< 70 ms), they were likely to be the saccades responding to the fixation stimulus offset (the second nearest monitor event). Considering that, we redefined successful trials and VM error trials with SRT less than 70 ms to be impulsive error trials and 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 **(Fig. 2B)**. An example of saccades extracted from the different error trials and successful trials from marmoset S are shown in **Fig. 2C**.

The definitions of the error trials and SRT calculation for the ODR task were similar to those of gap task **(Fig. 2D)**. The three monitor events were identified as fixation stimulus onset, target stimulus onset, and fixation stimulus offset. Distractive error trials were defined as the trials that ended after fixation stimulus onset and before target stimulus onset (**Fig. 2D**, red eye traces). Impulsive error trials were defined as the trials that ended after target stimulus onset and before fixation stimulus offset (**Fig. 2D**, blue eye traces). VM error trials were defined as the trials that ended after fixation stimulus offset but with the one-frame red screen

flash presentation (**Fig. 2D**, purple eye traces). Again, the SRT was extracted for each trial. Impulsive error SRT was calculated as the time between target onset and the onset of the saccade whereas VM error SRT was calculated as the time between fixation offset and the onset of the saccade. No anticipatory saccades were reported previously, so we did not redefine any trials. An example of saccades extracted from the different error trials and successful trials from marmoset S are shown in **Fig. 2E**.

Fig 2 approx. here

Identification of Saccades Towards and Away from the Target

To categorize saccades as being directed towards or away from the target, a line through the origin and perpendicular to the extension line connecting the origin and the target coordinates was drawn, dividing the Cartesian coordinate plan into two equal parts. If a saccade endpoint was on the same side as the target coordinates, it was defined as towards the target, whereas if the saccade endpoint was on the side opposite to the target coordinates, it was defined as away from the target.

Definition of Dysmetric Saccades

We further grouped VM error saccades directed towards the target into hypometric, hypermetric and orthogonal saccades based on the saccades' endpoints relative to the location of the presented target. To do so, we first identified a deviation vector to have its starting point as the target coordinates and its ending point as the actual saccade endpoint. We also identified a target vector to have its starting point as the origin and its endpoint as the target coordinates. We then calculated the angle between the deviation vector and the target vector. A saccade was defined as hypometric if the angle was within ±135°, and it was defined as hypermetric if the angle was within ±45°. Finally, a saccade was defined as orthogonal if the angle was outside the hypo/hypermetric saccades range of angles.

Saccade Main Sequence

We looked at the saccade main sequence to characterize the change of saccade kinematics for different trial groups (Bahill et al. 1975). 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 respectively.

Statistical Analysis

All statistical analyses were performed after we grouped the collected data according to gap/delay period as short (< 150 ms), intermediate (≥ 150 and < 300 ms) and long (≥ 300 ms) for each eccentricity used (4,6 or 8 deg in gap task and 4 or 6 deg in ODR task). The statistical tests and results are described in the figure legends.

RESULTS

Marmosets were More Prone to Making Mistakes than Humans

We first compared the performance and how often each error (Method, Fig. 2B, 2D) occurred between gap and ODR tasks in marmosets and humans. We collected a sufficient number of

trials from each subject performing the two tasks in parallel (averaged trials per marmoset: 3368 in gap task, 6649 in ODR task, per human: 4237 in gap task, 2650 in ODR task).

In marmosets, as indicated in **Fig. 3A, 3B**, the error trials ratio was higher in ODR task (77.7%, combined and averaged across marmosets) than in gap task (21%).

We further compared the frequency of each error type in both tasks. We expected to see a higher ratio of distractive error in ODR task as the task is more demanding and might induce more opt-outs than in gap task. However, the distractive error ratio was lower in all three marmosets in ODR task (on average 3.6% of the trials in ODR task vs 9.7% in gap task) **(Fig. 3A, 3B)**.

Fig 3 approx. here

As for the impulsive error, we hypothesized that the marmosets would be more susceptible to impulsive responses in ODR task because the target location was briefly displayed before the delay period in ODR task, whereas it was not provided yet during the gap period in gap task. **(Fig. 2C, 2E)**. Indeed, we found that the impulsive error ratio was higher in ODR task (36.3%) than in gap task (3.3%) (**Fig. 3A, 3B**). We also expected a higher VM error ratio in ODR task due to the absence of the visual target, and the results met our expectations (37.7% in ODR task vs 8% in gap task, **Fig. 3A, 3B**).

One important point to remark is that even though humans made scarce errors in both tasks (2.3% and 2.4% in gap and ODR task respectively) and we were unable to perform statistical comparisons between the tasks), a lower distractive error ratio (0.03% in ODR task vs 0.7% in gap task) and higher impulsive error ratio in ODR task (1.9% vs 0.4% in gap task) were observed, similar to marmosets.

On the other hand, we analysed how often successful trials were answered with a single saccade vs multiple saccades (**Method, Fig.2A**). We found that marmosets showed a higher probability to reach the target stimulus with a single saccade in both tasks. The likelihood of answering with either a single saccade or multiple saccades was not significantly different between the two tasks **(Fig. 3C, 3D)**. Humans showed similar preferences as well.

Marmosets Learned the ODR Task

Before proceeding further with dissecting the error characteristics, we were concerned that the overall marmosets' performance in ODR task was not as good as in gap task. We wondered if this was just a consequence of the higher task difficulty, or because the marmosets didn't comprehend the task requirements (i.e. when and where to make a response).

To first answer if the marmosets understood when to make a response, we plotted the relative frequency histogram and the cumulative probability distribution of the SRT for all the saccades made after the target onset (i.e. saccades collected from impulsive error, VM error and successful trials) from marmoset S as an example **(Fig. 4A)**. We also plotted the SRT distribution from human H **(Fig. 4B)** in the same manner as a reference, because the task was explained to human subjects before we started data collection.

Fig 4 approx. here

We identified four components in the relative frequency histogram (1-4, **Fig. 4A, 4B**, top-left illustration), two before and two after fixation stimulus offset (indicated in the magenta line). The most important components regarding our question are the ones around the fixation offset; the second and the third components, and they exhibited a strong discontinuity of the SRT distribution in both marmosets and humans.

The second component showed up in both species with delay periods of >= 250 ms. Because this component was time-locked on the fixation offset, we speculated that this component likely reflects the urgency to make a saccade. The third component coincides with fixation offset with a delay period of >= 150 ms in marmosets and >= 200 ms in humans. This is likely reflecting the prediction of the end of the delay period, likely because of our blocked task design (**Method**). These results indicate that the marmosets understood that the saccade should be made after fixation stimulus offset.

As for the other components, the first component showed up at around 120 ms after the target onset and appeared only in marmosets' data. Because this component was time-locked on the target onset regardless of the delay period, this is likely to be a reflexive response to the visual target. The fourth component showed up a while after fixation offset.

Interestingly, the SRT distribution after target onset from the marmosets captured most of the characteristics of the human subjects (SRT distribution components and the distribution discontinuity). Again, this discontinuity of the SRT distribution and the cumulative distribution around the fixation offset indicates that saccades before and after the magenta line are likely responding to different monitor events, signifying that the marmosets understood when to make a response.

We next examined whether the marmosets understood where to respond rather than just guessing either left or right. We looked at the VM error and successful saccades' landing positions for each marmoset **(Fig. 5)**. We mirrored the left targets and their corresponding saccades landing positions to the right side. The right solid circle in the figure represents the correct response whereas the left dashed circle represents the incorrect response. If the marmosets were guessing where was the target, a similar amount of saccades' landing positions should show up in both the solid and the dashed circles. As the figure shows, a significant majority of the saccades landed inside the right circle, signifying that the marmosets were not guessing but rather tried to answer according to the task instructions.

Fig 5 approx. here

The above results prove that the lower performance in ODR task was mainly due to the task difficulty and not because the marmosets didn't comprehend the task structure.

Longer Gap/Delay Periods Correlated with Higher Impulsive and Lower VM Error Frequency

Based on the previous results that confirmed that the marmosets learned ODR task, we were confident to proceed and investigate how the task conditions dictated the performance in both species **(Fig. 6)**.

The first condition that varied from session to session was the gap/ delay period in gap/ ODR tasks. By analysing the correlation between gap/delay period and the ratio of error or successful trials, we expected to see a positive correlation between gap/delay and impulsive error ratio because chances to break fixation increase with a longer waiting time. Indeed, we found that the impulsive error ratio increased with longer gap/delay periods in both tasks (**Fig. 6A**, second column). Interestingly, the VM error ratio showed a negative correlation with a longer gap/delay period (**Fig. 6A**, third column). Furthermore, we found that the success ratio didn't show consistent change with the gap period, however, it showed a significant negative correlation with the delay period in ODR task **(Fig. 6A**, last column**)**.

Although error trials were too less to perform statistical tests for humans, we observed a similar pattern to what we observed in marmosets. In other words, increasing impulsive error ratio with longer delay period in ODR, decreasing VM error ratio with longer gap/delay period in both tasks, decreasing success ratio with longer delay period in ODR task.

The second condition that varied from session to session was the target eccentricities. In marmosets, we didn't see much influence of the target eccentricity on either success or failure except for a positive correlation with VM error ratio in gap task and a negative correlation in ODR task **(Supplementary Fig. 1A,** third column**)**. In humans, a similar trend of increasing VM error ratio with farther eccentricities in both tasks was observed (**Fig. 6B, Supplementary Fig. 1B,** third column).

Fig 6 approx. here

Target Visibility Dictated Impulsive SRT in Both Tasks

Next, we examined how the task conditions altered the SRT. Because SRT reflects the time needed for the sensory-to-motor process -including decision- to take place, we wanted to investigate if such a process differs when different mistakes are executed or when correct vs incorrect responses are executed **(Fig. 7)**.

For both marmosets and humans, impulsive error SRT was, in general, shorter in ODR (marmoset: 100-200 ms; human: 200-300 ms) than in gap task (marmoset: 100-400 ms; human: 300-400 ms; **Fig. 7A, 7B,** left column). As described previously in **Fig. 4** for ODR task, this was due to the first two components in the SRT distribution, with the first being triggered by the flashed target and the second by the urgency to make a response. This could also explain why the saccades were mainly directed towards the target (**Fig. 8A**)**.** Whereas in gap task, all the impulsive error saccades were anticipatory, which natively happened after the peripheral target onset. Due to the above reasons, the impulsive error SRT of either gap or ODR task should have naturally a positive correlation with gap or delay period, respectively. These results indicate that the presence of a visually accessible target facilitates fixation disengagement and the urgency to make a response. We also noticed a significant negative correlation with successful SRT in both tasks and both species **(Fig. 7A, 7B,** right column**)**.

Fig 7 approx. here

In addition, we provide the boxplot figure of the SRT **(Supplementary Fig. 2)** because most of the SRTs were not normally distributed (**Fig. 4**)**.** We also examined the correlation using

the median of the SRTs and the results were similar to that using the mean. Similar to what was shown in **Fig. 4**, we observed that both marmosets and humans showed a very short SRT (immediately following the fixation offset) for both VM error and successful trials in ODR task, indicating that the fixation stimulus offset prediction happened in both groups of trials (**Supplementary Fig. 2**).

As for the target eccentricity, it significantly influenced successful SRT in ODR task only (**Supplementary Fig. 3**).

Saccade Undershooting Correlated with Target Eccentricity

Although the positive correlation between the gap/delay period and the impulsive error met our expectations, the negative correlation with the VM error suggests other mechanisms behind making a mistake than merely not detecting the target in gap task or having memory fade out in ODR task **(Fig. 6, Supplementary Fig. 2)**, as both suggest an opposite outcome. To further investigate the underlying reasons, we separated those error groups based on if the saccade vector was directed towards or away from the target stimulus.

We found that across all three marmosets, impulsive error saccades made in gap task were directed 46% toward and 54% away from the target stimulus, with almost equal probability **(Method, Fig. 2C, Fig. 8A)**. We further confirmed that the saccades from the impulsive error trials were all anticipatory saccades. This is similar to a previous report that noted that anticipatory saccades with correct direction and direction errors should be equally frequent (Kalesnykas and Hallett 1987). Although saccades from the impulsive error trials in humans were also anticipatory saccades, they showed a higher tendency of going toward the target (84%). This result might be due to the scarcity of impulsive error trials (34 trials combining all three humans, vs 338 trials from all three marmosets).

On the other hand, impulsive error saccades made in ODR task showed a significant bias to go toward the target stimulus (76% towards, 24% away, **Fig. 8A**). This is likely because the target was briefly presented before the delay **(Fig. 1B)** and the marmosets were incapable of suppressing their reflexive saccades **(Fig. 4A)**. Humans showed similar results (100% towards), yet again, the number of impulsive error trials were scarce (148 trials combining all three humans).

Fig 8 approx. here

As for the VM error, the marmosets showed an almost equal probability of making a saccade towards (57%) or away (43%) from the target stimulus in gap task, whereas a significant proportion of saccades were directed away (64%) from the briefly presented target in ODR task **(Fig. 8B)**. Humans showed a higher tendency to make saccades directed towards the target in gap task (100%) and ODR task (92.5%). This might designate an interspecies variance, but the human trials count was very few to be ascertained. (157 trials in gap task, 36 trials in ODR task for humans, vs 870 trials in gap task, 7067 trials in ODR task trial).

To dissect VM errors, even more, we first examined the landing position of the VM error saccades directed towards different target eccentricities. Results showed that failure was attributed to dysmetria (overshooting, undershooting, orthogonal saccades) or insufficient fixation on the target (less than 200 ms in gap task or 17 ms in ODR task, **Fig. 8C, 8D**). Even

though human subjects didn't have many errors, among the collected ones, insufficient fixation was the main failure reason in both tasks **(Fig. 8C, 8D)**.

We also found that farther eccentricity was significantly correlated with more saccade undershooting in both tasks in marmosets. The same analysis in humans showed a similar trend, albeit without sufficient trials for statistical tests. And last, nearer eccentricity correlated with more overshooting only in ODR task in marmosets.

Marmosets Repeated the Same Incorrect Answer

The VM error saccades directed away from the target stimulus in marmosets were particularly puzzling to us **(Fig. 2B, 2E, 8B)**. In ODR task, if they forgot the target location, an equal bias of saccading towards or away from the target stimulus would've been seen, if they roughly remembered the exact target location, the saccade direction should've been made towards the target location (with dysmetria, as described previously). In gap task, the target was already visible by the time a VM error saccade was made. Then, how did this happen? We hypothesized that this could be related to the combination of our task design and the marmosets' answering strategy. To prevent the marmosets from favouring one spatial location over the others, if a previous trial was unsuccessful, the following trial will repeat the same target location. However, if the marmosets did not notice this implementation and decided to saccade in the opposite direction because they were not rewarded in the previous trial, a saccade away from target may occur. Therefore, we analysed the task history by inspecting the previous saccade direction that preceded the VM error saccade directed away from the target (i.e. consecutive trials only) to see if the previous experience affected their responses. (**Fig. 8E, 8F**).

We found that if the previous experience was successful, the previous and the next saccades were directed in the same or opposite direction of each other with almost equal probability in both tasks (48.5 and 47.5% same direction in gap and ODR tasks respectively), meaning that they didn't favour the direction that delivered the reward. However, if the previous trial was an impulsive error trial, the marmosets showed a preference to repeat the previous answer in gap task (78.5% same direction), whereas they showed a significant bias to change the answer from the previous one in ODR task (65.5% opposite direction). Finally, if the previous experience was a VM error, marmosets' decision was significantly biased towards repeating the same answer (away from the target), in both tasks (74.2% and 71% same direction in gap and ODR tasks respectively). To our surprise, instead of alternating their answer, the marmosets tend to repeat the same saccade direction in consecutive error trials.

Distinct Saccade Kinematics Between Success and Errors Observed

Finally, we investigated saccades' kinematics by analysing the saccade main sequence. It's known that the peak velocity and the amplitude of saccades are governed by a stereotyped relationship within the same subject. We wondered if such a relationship is also preserved between successful and unsuccessful defined saccades **(Fig. 9A, 9B)**. We found that in gap task, marmosets showed a higher slope and lower exponent of the fitted amplitude-peak velocity curve parameters for successful saccades compared to unsuccessful ones (**Method**, **Fig. 9C**). Similar result can also be observed in humans, although the impulsive error trials were too less causing the confidence intervals to be large **(Table 1)**. On the other hand, impulsive error saccades in ODR task had the highest fitted slope in marmosets, but the difference from other trial types is less obvious. The parameters in humans are not different

from each other **(Fig. 9D)**. The confidence intervals were large and overlapped due to the scarcity of error trials in humans.

Fig 9 approx. here

Table 1 approx. here

DISCUSSION

In this study, we showed that the marmosets were capable of performing gap saccade task (in short, gap task) and oculomotor delayed response (ODR) task. We categorized error trials into three groups based on our tasks' design and analysed them along with successful trials to interpret why the marmosets made such mistakes and compared them to humans' results.

We found that the marmosets had fewer distractive errors and more impulsive and visuomotor (VM) errors in ODR task compared to gap task. Although we were unable to collect enough error trials from humans to perform statistical analyses, we still observed very similar error profiles and saccade reaction time (SRT) trends in error and success compared to the marmosets. The high error ratio in marmosets could be partially explained by their tendency to repetitively reiterate the same saccade if the saccade was a VM error saccade directed away from the target. Finally, we found that the saccade main sequence differed between error and success in both tasks.

Dissecting Errors Revealed Similarities Between Marmosets and Humans

We started by looking at the overall performance in each task, and found that marmosets and humans made more errors in ODR task than in gap task (**Fig. 3A**). Although the possible target locations in gap task were more (gap: 8, ODR: 2 locations), relying on the working memory to recall the target location in ODR task was still more difficult than purely saccading to a visible target in gap task. Although only very few studies reported this difference between these two tasks, our results are still consistent with one previous report on humans (Brown et al. 2004).

In what follows, we discuss in detail the potential causes of the three error groups (distractive, impulsive, VM errors) based on our analysis in the result section and the new findings in successful trials.

Distractive Error

We found that the distractive error ratio was higher in gap task in contrast to ODR task (**Fig. 3A**). Despite the scarcity of other direct reports, similar results could be obtained by calculating the breakdown of the errors from (Brown et al. 2004). We refer to this more frequent distractive error as a potential "mind-wandering" state in gap task, 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, the eyes are disengaged from the external stimulus 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 go into the mind-wandering state (Benedek et al. 2017). Therefore, the lower distractive error in ODR task might be due to the higher task demands, which activates more cognitive processes. Alternatively, gap task is mainly driven by external stimuli and could lead to a mind-wandering state easily. Because such difference

should come from the essence of the tasks themselves, task conditions like gap/delay periods and target eccentricities should not correlate with the occurrence of the distractive error in either marmosets or humans, and indeed it did not (**Fig. 6, Supplementary Fig. 1**).

Impulsive Error

We also found that the impulsive error ratio was higher in ODR than in gap task (**Fig. 3A**) (Brown et al. 2004), possibly due to the brief appearance of the target, which also caused the saccades to be directed more towards the target location (**Fig. 2E, 8A**). In the SRT distribution in marmosets (**Fig. 4**, before the magenta line), we found that there were two main components, with the first (component 1) being nicely time locked with the target onset where a very high ratio of the saccades directed towards the target (79.4%). This was observed in humans as well, although less frequent (33.3%, the rare saccades within 200 ms after target onset in **Fig. 4**). This result is very similar to humans' express saccade makers. They exhibited short latency (around 80 to 120 ms SRT) express saccades when performing gap task, but they were unable to suppress visually evoked saccades, or " brief glancing" as described in the previous report, while doing a visual memory task (Fischer and Ramsperger 1984; Biscaldi et al. 1996). This brief glancing is usually attributed to a weaker voluntarily control over saccade generation caused by a weaker fixation system either in the cortical or subcortical areas (Bon and Lucchetti 1992; Hafed et al. 2009; Munoz and Wurtz 1993).

The second component (component 2) appears in the delay period of more than 200 ms, and seems to be more time locked with fixation offset in both marmosets and humans (**Fig. 4**). This is referred to as the urgency to respond with a premature saccade before the go cue (Brown et al. 2004). Consistent with previous descriptions, these saccades were partially directed toward the target (marmosets: 50.9%, humans: 66.7%) (**Fig. 4**). For the ones that were not directed toward the target, we suspect that it is a counter-balance effect of programming an antisaccade to avoid making a saccade right after the target onset (Tian et al. 2018). Combining the two components, we observed an increase in impulsive error frequency and SRT with a longer delay period in both species (**Fig. 6, Fig. 7**).

For the impulsive error in gap task, we found that they were all the so-called "anticipatory saccades" as previously reported (Chen et al. 2021; Edelman and Keller 1996; Mayfrank et al. 1986). In both species, the anticipatory saccades frequency and the SRT were increasing with a longer gap period (**Fig. 6, Fig. 7**), and had no correlation with target eccentricity (**Supplementary Fig. 1, Supplementary Fig. 3**). These results are consistent with the previous interpretation that anticipatory saccades are the pre-target activities somehow crossing a theoretical saccade triggering threshold (Dias and Bruce 1994; Dorris and Munoz 1998; Munoz et al. 2000). Our results further propose that these activities are very sensitive to the temporal (**Fig. 6, Fig. 7**) but less sensitive to the spatial predictability (**Fig. 2C, Supplementary Fig. 1, Supplementary Fig. 3**). Furthermore, because the visual target information was not yet provided, the saccades were not all directed toward the target (**Fig. 8A),** similar to one previous report (Kalesnykas and Hallett 1987).

Visuomotor (VM) Error

VM error saccades directed towards the target stimulus failed to reach the target because of either saccade spatial error (hypometric or hypermetric saccade) or insufficient fixation (gaze left the eye window before the time allowed so). In gap task, saccade undershooting increased with target eccentricity (**Fig. 8C**), which is consistent with previously reported results in humans (Frost and Pöppel 1976; Gillen et al. 2013). However, this correlation was more

prominent in marmosets. This may be due to the smaller oculomotor range of the marmosets making the undershooting more apparent than in humans (Chen et al. 2021; Mitchell et al. 2014). On the other hand, an increase of saccade undershooting accompanied by a decrease of saccade overshooting in ODR task in marmosets seems to be reminiscent of the saccadic range effect previously reported in humans (**Fig. 8D**) (Kapoula 1985). In addition, previous research showed that memory-guided saccades are usually more hypometric than visually guided saccades (Nuthmann et al. 2016), which comes in agreement with our data from both marmosets and humans (**Fig. 8C, 8D**).

Another interesting result seen in marmosets was the substantial amount of VM error trials with saccades directed away from the target in both gap and ODR tasks (**Fig. 8B**). With further analysis, we found that the marmosets did not simply repeat their previous saccade direction every time, but only did so when consecutive VM error trials occurred (**Fig. 8E, 8F**). This perhaps mimics the so-called “recurring mistakes” effect (Kuvaldina et al. 2019) where the same mistakes are repetitively made after the first one. This is mainly described in humans when performing simple, repetitive tasks. Although the neuronal pathway of recurring mistakes is still unclear, our experiment suggests that the marmosets might be useful to identify the neuronal bases of this psychological phenomenon.

Successful Trials

For successful trials, SRTs decreased with increasing gap period is in agreement with the gap effect (reduction in the SRT to visual targets when the fixation offset is followed by a gap time before the target onset) (Saslow, 1967; Reulen, 1984; Tam and Ono, 1994; Pratt et al., 1999). However, SRT decreasing with increasing delay period in ODR task was not described before (**Fig. 7,** right column). Based on our data, we think this was facilitated by the ultra-fast saccades right after fixation offset (**Fig. 4,** the third component). The subjects were likely anticipating when to move because we fixed the delay period for each session. Interestingly, human subjects showed similar results and even showed a separate component in the SRT distribution (after fixation offset), which might indicate a similar neuronal mechanism behind the temporal execution of successful saccades **(Fig. 4, Supplementary Fig. 1)**.

Saccade Peak Velocity Changes When Error Happens

The main sequence relationship is 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 macaques, 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 (**Fig. 9**), we found that the previous statement is true for both marmosets (higher slopes in gap task) and humans (similar slope but higher exponent in gap task). Yet, what was striking was that even in a simple task like gap or ODR task, we found that successful saccades showed the highest peak velocity compared to saccades from error trials in both marmosets and humans, which is usually more related to choice confidence in decision-making tasks (Seideman et al. 2018).

Moreover, it has been recently noticed that the intrinsic value of the visual input comes with a substantial impact on the saccades motor commands, and that saccade peak velocity is not just dependent on saccade amplitude, but also on motivation, arousal, and inter and intra-individual variations (Xu-Wilson et al. 2009; 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 increase if a high reward was anticipated (Takikawa et al. 2002; Chen et al. 2013; Di Stasi et al. 2011). More studies are needed to determine the possible cause of this change in peak velocity.

CONCLUDING REMARKS

The current study proposed a generalizable way of grouping and analysing error trials in synchronous with successful trials in different visual tasks. We propose that the marmosets can be a good experimental candidate because they capture both the success and error properties of humans. Furthermore, analysing success and error records of behavioural data will help to understand neuronal mechanisms behind mistakes and to better interpret the cognitive state of a subject performing a task. More importantly, it will help to set up the behavioural baseline measurements for future NHP models to study different brain disorders (Scott and Bourne 2022).

GRANTS

The current study was supported by the Brains and Minds Project No. 19dm0207093h0001, Japan.

DISCLOUSURE

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.

AUTHORS CONTRIBUTION

W.A. did the behavioural training, data collection, data analysis, and drafted the manuscript. C.C. guided the research and edited and revised the manuscript. H.O. performed the marmosets' MRI imaging and surgeries. T.I supervised the project and approved the final manuscript. All authors shaped the final version of the manuscript and approved the submitted version.

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FIGURE LEGENDS

Figure 1. Tasks illustration.

A) In the gap task, a marmoset face was used as the stimulus. Each trial started with a fixation stimulus that appeared at the screen centre for the subject to fixate for 200 ms. Following the fixation stimulus offset, a gap period (0 - 400 ms with 50 ms increment) followed, and the gaze must be maintained at the centre. At the end of the gap period, a visual target appeared, and the subject must make a saccade towards the target and maintain the gaze for 200 ms. If the answer was correct, a rewarding photo was displayed but if the answer was incorrect, a one-frame red screen was flashed. **B)** In the ODR task, a black circle with a white centre was used as the stimulus. The fixation stimulus appeared at the screen centre for the subject to fixate for 200 ms. A peripheral target flashed for 67 ms after the initial fixation, and the gaze must be maintained at the centre. Then, a delay period (100 - 400 ms with 50 ms increment) followed and the gaze must be still maintained at the centre. At the end of the delay period, the fixation stimulus was turned off and the subject must make a saccade towards the remembered target location and maintain the gaze for around 17 ms. If the answer was correct, a rewarding photo was displayed but if the answer was incorrect, a one-frame red screen was flashed. Dashed circles indicate the eye window which was invisible to the subjects. Refer to **Method** for a detailed description.

Figure 2. Illustration of task events and the grouping of successful and error trials.

A) Successful trials were subdivided into a single saccade group (left) or multiple saccades group (right), based on how the subject reached the target stimulus. Dashed circles are the eye windows as described in Fig. 1. Red arrows illustrate saccades made after target onset. **B, D)** Illustration of how we defined successful and error trials in gap (B) or ODR (D) tasks based on when the mistake occurred relative to the monitor events. Black solid lines indicate fixation on time and target on time, and coloured lines indicate the relative eye position of the successful and error trial groups (distractive error in red, impulsive error in blue, visuomotor (VM) error in purple, and successful trial in yellow), top to bottom in the figure. Black dashed lines indicate the eye windowing position. The magenta dashed line indicates the time that the subject's eye position enters the fixation eye window. Illustrations of how we calculated the saccade reaction time (SRT) of the successful and the error trials are also indicated. **C, E)** Example saccade traces extracted from each error group (colour coded) and successful single saccade group in gap (C) or ODR (E) tasks. Saccade traces belong to marmoset S performing

the tasks at 6° target eccentricity and 400 ms gap or delay period. Dashed circles indicate potential target locations for each trial. In this example, only the trials where the target was on the right side (indicated as a green dashed circle) were plotted. Refer to **Method** for a more detailed explanation.

Figure 3. Percentage of each subgroup of successful and error trials in gap and ODR tasks.

Trials collected from all subjects are shown here. **A, B)** Success and error ratios are shown in (A) for gap task and (B) for ODR task. Comparing gap and ODR tasks, marmosets' data shows that the distractive error ratio was significantly higher in gap task ($p=0.01$). Impulsive and visuomotor (VM) errors were significantly higher in ODR task ($p=2.86\times10^{-8}$, 2.5×10^{-8} respectively), whereas the success ratio was significantly higher in gap task ($p=1.9\times10^{-8}$). Humans made very scarce errors and therefore, no statistical analysis was performed, but humans' success ratio in both gap and ODR tasks significantly outweighed that of marmosets ($p=9.98\text{x}10^{-10}$, $p=3.2\text{x}10^{-7}$ respectively). **C, D)** Subgroups of successful trials are shown for gap (C) and ODR (D) tasks. Single saccade or multiple saccades groups were not significantly different between the tasks in marmosets ($p=0.22$, 0.22 respectively) or humans ($p=0.38$, 0.94 respectively). Wilcoxon rank-sum test was used for statistical analyses.

Figure 4. Example saccade reaction times (SRTs) of impulsive error, visuomotor error and successful trials aligned on peripheral target onset from ODR task.

Four components were identified in the SRT distribution (illustration). The first component (1) represents impulsive responses to the visual target, the second component (2) represents urgency to make a saccade, the third component (3) represents successful predictions and the fourth component (4) represents the regular saccades responding to fixation offset. All the trials in ODR task belonging to marmoset S (A) and human H (B) are shown separated by the delay periods. For each sub-figure, the cyan line indicates target offset (67 ms) and the magenta line indicates fixation offset (end of the delay), the histogram (Y-axis on the left) indicates SRT frequency after target onset, and the orange curve (Y-axis on the right) indicates SRT cumulative probability after target onset. Illustration figures were replotted from the gap or delay period of 350 ms. As shown in the illustration, four SRT components, two before and two after fixation offset, were identified (1-4). Note that there is a break in the SRT histogram and a discontinuity of cumulative curve around the magenta line for all delay periods >100 ms in marmoset S and >150 ms in human H, meaning that saccades before and after the magenta line are likely responding to different monitor event (target flash and fixation off, respectively). Also, note that the ultrafast SRT immediately after the fixation offset for delay >100 ms in marmoset S and delay >150 ms in human H indicates that the subjects are probably counting (predicting) the time to make a response.

Figure 5. Marmosets' saccade landing positions in ODR task.

Heat maps show the normalized probability distribution of the saccade landing positions combining both the visuomotor error (VM) and the successful trials, separated by target eccentricities (top row: 4°, bottom row: 6°) for each marmoset. Saccades with the target on the left visual hemifield were mirrored so that the right solid circle represents the eye window around the correct choice whereas the left dashed circle represents the eye window around the incorrect choice. In each figure, the highest probability is normalized to 1. Landing positions inside the solid circle are all from successful trials. The dashed circle indicates the

mirror-image side used for statistics. A significant proportion of saccades landed inside the target eye window (solid circle) compared to saccades from visuomotor error trials landed within the opposite eye window (dashed circle), for both targets at 4° ($p= 1.1\times10^{-9}$, $p= 9.2\times10^{-4}$, and $p= 4.2\times10^{-9}$, for marmoset S, N and M) and 6° ($p=3.9\times10^{-50}$, $p= 8.3\times10^{-20}$, and $p= 2.1\times10^{-35}$, for marmoset S, N and M). Wilcoxon rank-sum test was used for statistical analysis.

Figure 6. Change in success and error ratios with gap or delay periods in marmosets and humans (B) in both tasks.

A) The trials proportions for impulsive and visuomotor (VM) error and successful trials against short (<150 ms), medium (150-250 ms), and long (> 250 ms) gap/delay periods were plotted for marmosets separating gap (top row) or ODR task (bottom row) to see the correlation. Statistics are provided in each subfigure and the ones with significant correlation are marked with *. **B)** The same analysis was also performed on humans' data. We didn't perform statistical tests on human errors due to the scarcity of error trials. But please note that a similar trend of increasing impulsive error and decreasing VM error with longer gap/delay periods was observed in both marmosets and humans. We found no correlation between the success ratio and gap period, whereas a negative correlation with the delay period was statistically confirmed in both species. Spearman linear correlation test was used for statistical analysis.

Figure 7. Change in saccade reaction time (SRT) of success and error subgroups with gap or delay periods in marmosets and humans in both tasks.

A) SRT of impulsive and visuomotor (VM) error and successful trials against short (<150 ms), medium (150-250 ms), and long (> 250 ms) gap/delay periods were plotted for marmosets, separating gap (top row) and ODR (bottom row) tasks to see the correlation. The Spearman linear correlation test results are provided in each subfigure and the ones with significant correlation are marked with *. We also compared the SRTs among success and error subgroups. SRT of impulsive error in the ODR task was shorter than in gap task ($p= 0.002$, Wilcoxon rank sum test). **B)** The same analysis was also performed on humans' data. We didn't perform correlation statistical tests on human errors due to the scarcity of error trials. But please note that a similar trend of increasing impulsive error SRTs with longer gap/delay periods was observed in both marmosets and humans. Decreasing successful SRTs with longer gap/delay periods in both tasks was statistically confirmed in both species.

Figure 8. Grouping of error trials according to the saccade direction relative to the target location or the previous trial decision.

Saccades from the impulsive and visuomotor (VM) error trials were plotted and analysed here for both marmosets and humans. Although we plotted the figure with all humans' results combined, the statistical tests were performed for them separately, similar to marmosets. **A)** In marmosets, saccades from impulsive error trials were separated based on going toward or away from the target and the marmosets showed an equal proportion of saccades in gap task but more saccades going toward the target in ODR task ($p=0.2$, $p=7.3\times10^{-7}$, respectively, Wilcoxon rank sum test). However, humans showed more saccades going towards the target in both gap and ODR tasks ($p=1.6\times10^{-6}$, $p=5.5\times10^{-6}$, respectively, Wilcoxon rank sum test). **B)** The same analysis on VM error trials in marmosets showed an equal proportion of saccades in gap but more saccades going away from the target in ODR task ($p=0.4$, $p= p=3.2\times10^{-7}$, respectively, Wilcoxon rank sum test), whereas again humans show more saccades going towards the target in both gap and ODR tasks ($p=1.3\times10^{-9}$, $p=5.1\times10^{-5}$, respectively, Wilcoxon

rank sum test). **C, D)** Further separation of saccades directed towards the target in the VM error trials into undershooting (under), overshooting (over), or orthogonal (ortho), or saccades landed within the eye window but with insufficient fixation. A positive correlation between the target eccentricity and saccade undershooting was observed in both gap and ODR tasks (rho=0.7, $p=2.2\times10^{-5}$, Spearman linear correlation test; p=0.004, Wilcoxon sign rank test, respectively) in marmosets. However, the correlation between the target eccentricity and saccade overshooting was only observed in ODR task (gap: rho=0.2, p=0.36, Spearman linear correlation test; ODR: p=0.008, Wilcoxon sign rank test, respectively). **E, F)** Further separation of saccades directed away from the target in the VM error trials based on the direction of the previous saccade. The total trial percentage combining the three marmosets is shown below each condition. If the VM trial was preceded by a VM experience, marmosets significantly repeated the same answer in ODR task (gap: p=0.02, ODR: $p= 3.2\times10^{-7}$, Wilcoxon rank sum test). If the VM trial was preceded by an impulsive error experience, the saccade from the previous trial was directed in the opposite direction of the current saccade in ODR task ($p=1.9\text{x}10^{-4}$, Wilcoxon rank sum test), but in the same direction in gap task (p=0.04, Wilcoxon rank sum test). Finally, if the VM trial was preceded by a successful experience, the previous and the next saccades were directed in the same or opposite direction of each other with almost equal probability, in both gap and ODR tasks (p=0.43, p=0.96, respectively, Wilcoxon rank sum test).

Figure 9. Saccade main sequence of the success and error subgroups in marmosets and humans.

A) Saccade peak velocities in gap task were plotted against saccade amplitudes and colour-coded, separating impulsive error, visuomotor (VM) error and successful trials. Marmoset's S (top) data was plotted as an example, and humans' data combined (bottom) due to the insufficient number of error trials. Saccade main sequences were fitted using the following fitting equation $f(x) = a * (x^n)$. **B)** The same analysis was performed also for ODR task. **C, D)** The fitting parameters (*a* and *n*, indicating the slope and the curvature, respectively) for each marmoset and combined humans' data were plotted for gap and ODR tasks. Error bars represent 95% of the confidence interval of the fitted parameter.

Table 1. The number of successful and error trials for each subject in both tasks.

The number of the trials in success and error categories used in saccade main sequence calculations are provided for each subject.

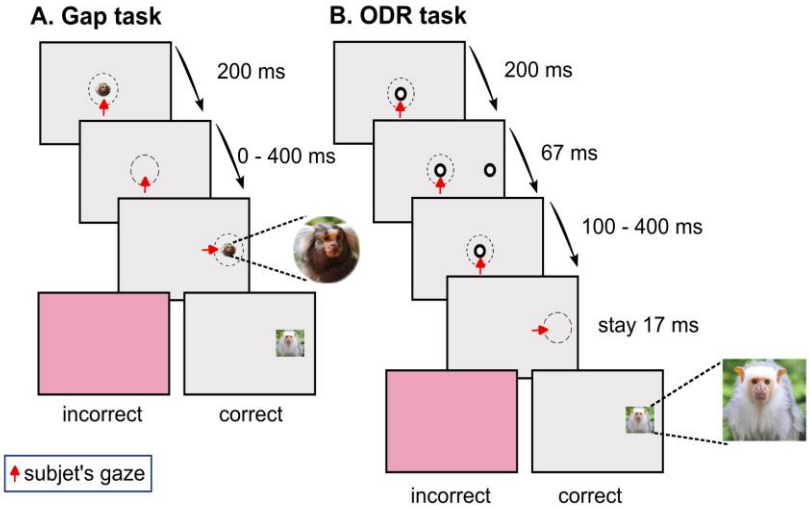
A. Gap task
200 ms
0 - 400 ms
incorrect
correct
subjet's gaze
B. ODR task
200 ms
67 ms
100 - 400 ms
stay 17 ms
incorrect
correct

Fig. 1

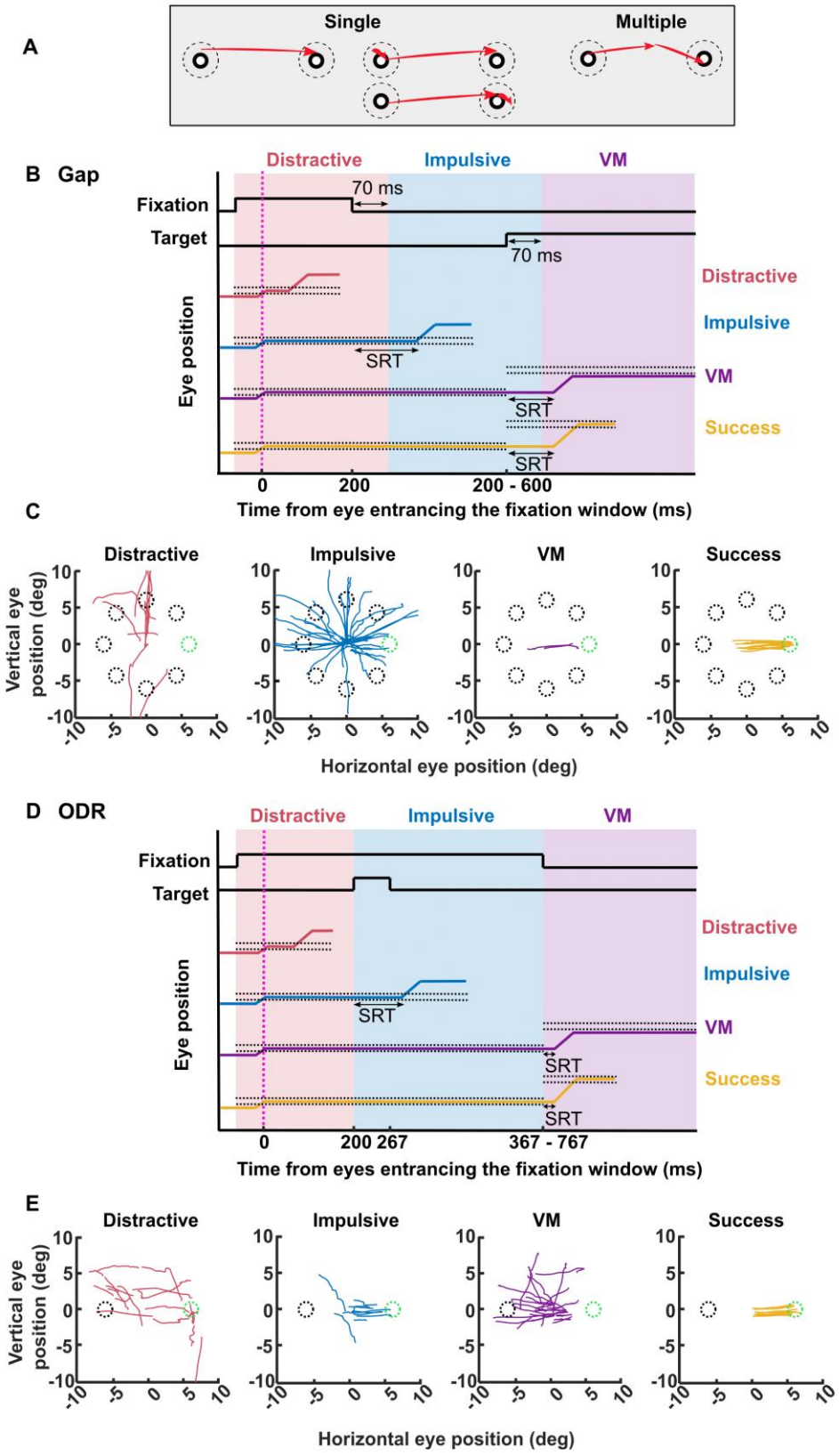
A
Single
Multiple
B Gap
Distractive
Impulsive
VM
Fixation
Target
70 ms
70 ms
Eye position
SRT
SRT
SRT
Distractive
Impulsive
VM
Success
0
200
200 - 600
Time from eye entrancing the fixation window (ms)
C
Distractive
Impulsive
VM
Success
Vertical eye position (deg)
Horizontal eye position (deg)
D ODR
Distractive
Impulsive
VM
Fixation
Target
Eye position
SRT
SRT
SRT
Distractive
Impulsive
VM
Success
0
200 267
367 - 767
Time from eyes entrancing the fixation window (ms)
E
Distractive
Impulsive
VM
Success
Vertical eye position (deg)
Horizontal eye position (deg)

Fig. 2

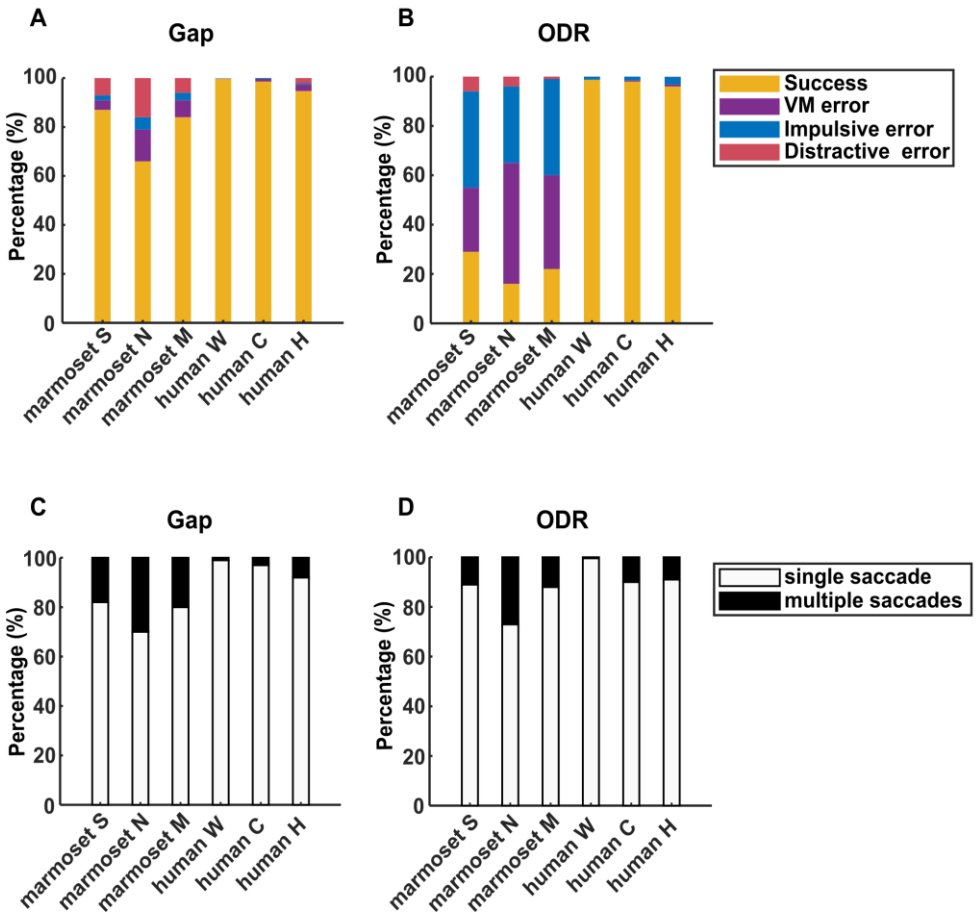
A
Gap
B
ODR
C
Gap
D
ODR
Percentage (%)
0
20
40
60
80
100
marmoset S
marmoset N
marmoset M
human W
human C
human H
Success
VM error
Impulsive error
Distractive error
single saccade
multiple saccades

Fig. 3

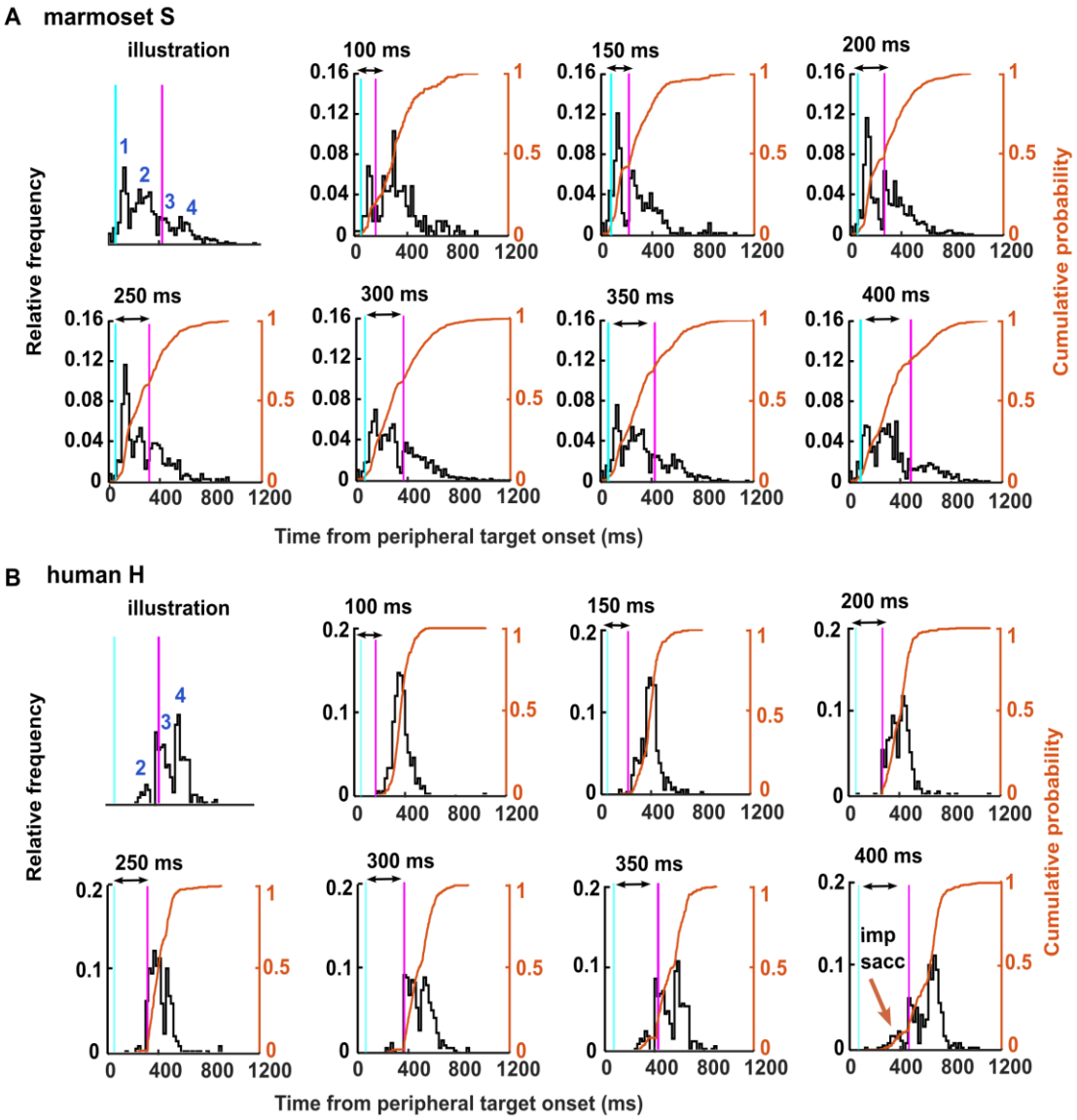
A marmoset S
illustration
100 ms
150 ms
200 ms
250 ms
300 ms
350 ms
400 ms
Relative frequency
Cumulative probability
Time from peripheral target onset (ms)
B human H
imp
sacc

Fig. 4

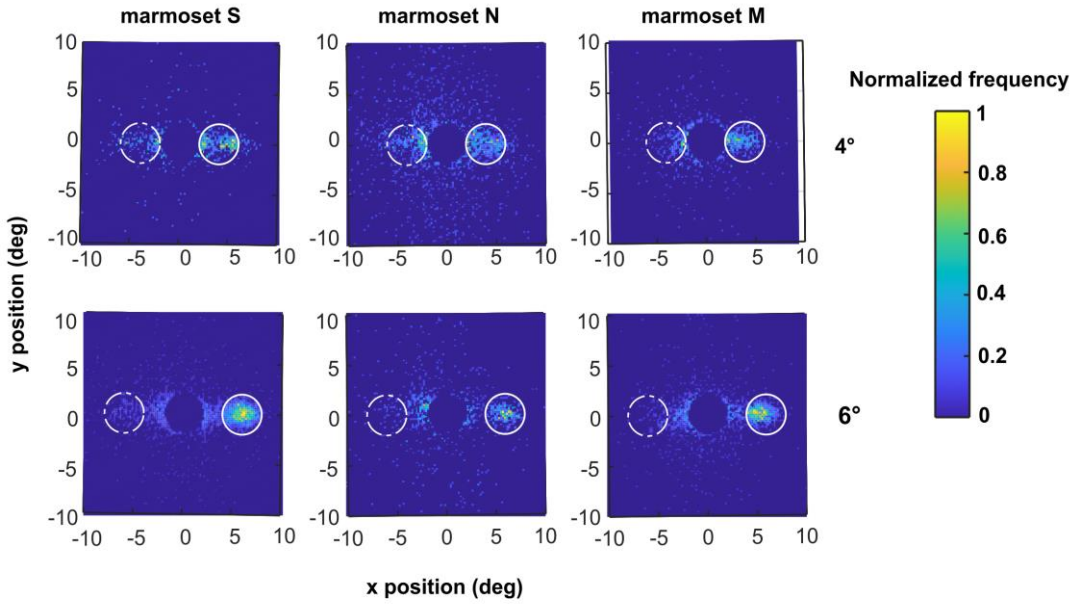
marmoset S
marmoset N
marmoset M
Normalized frequency
1
0.8
0.6
0.4
0.2
0
4°
6°
y position (deg)
x position (deg)
10
5
0
-5
-10

Fig. 5

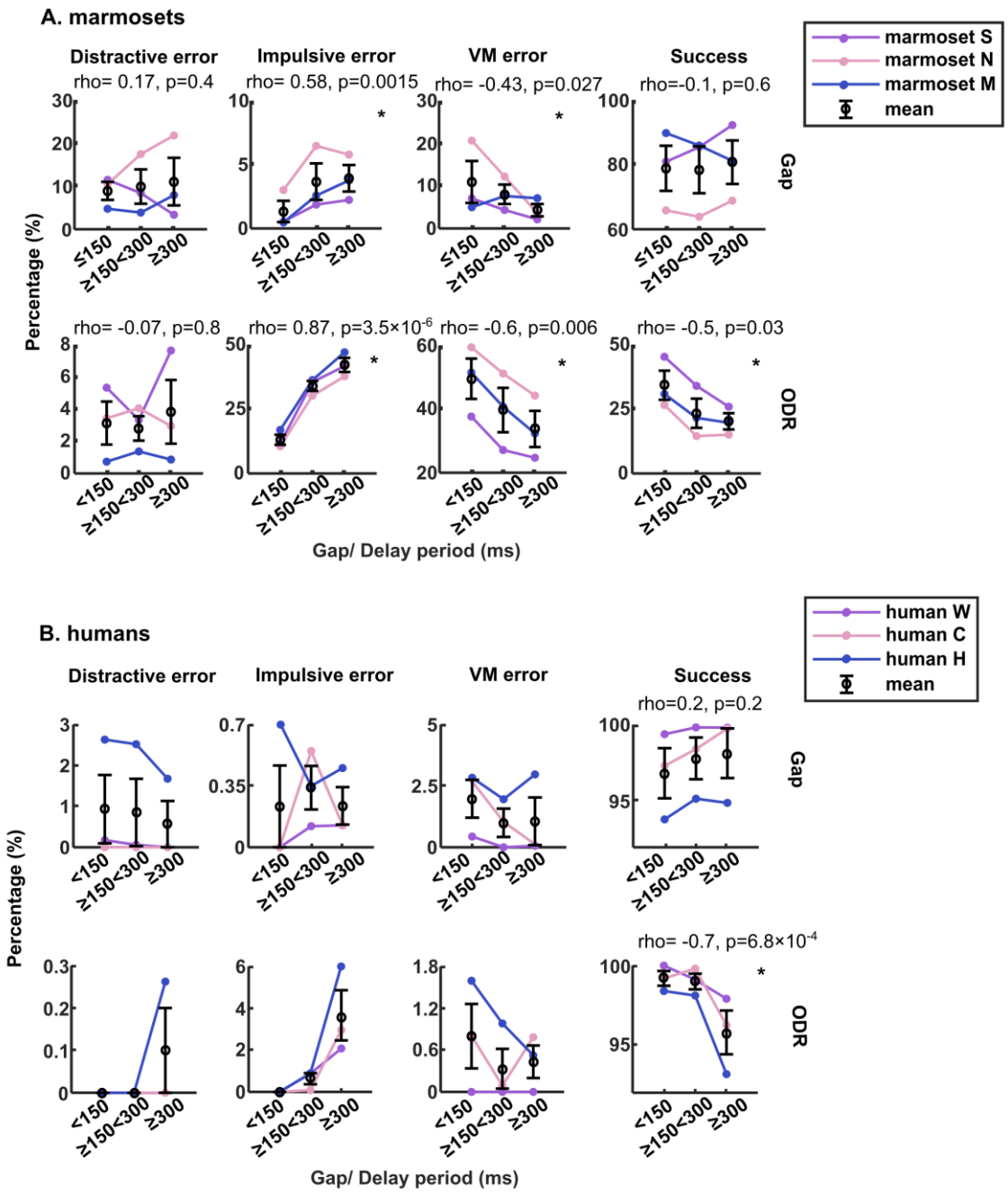
A. marmosets
Distractive error
Impulsive error
VM error
Success
rho= 0.17, p=0.4
rho= 0.58, p=0.0015
rho= -0.43, p=0.027
rho=-0.1, p=0.6
rho= -0.07, p=0.8
rho= 0.87, p=3.5×10-6
rho= -0.6, p=0.006
rho= -0.5, p=0.03
marmoset S
marmoset N
marmoset M
mean
Gap
ODR
Percentage (%)
≤150
≥150<300
≥300
<150
Gap/ Delay period (ms)
B. humans
Distractive error
Impulsive error
VM error
Success
rho=0.2, p=0.2
rho= -0.7, p=6.8×10-4
human W
human C
human H
mean
Gap
ODR
Percentage (%)
<150
≥150<300
≥300
Gap/ Delay period (ms)

Fig. 6

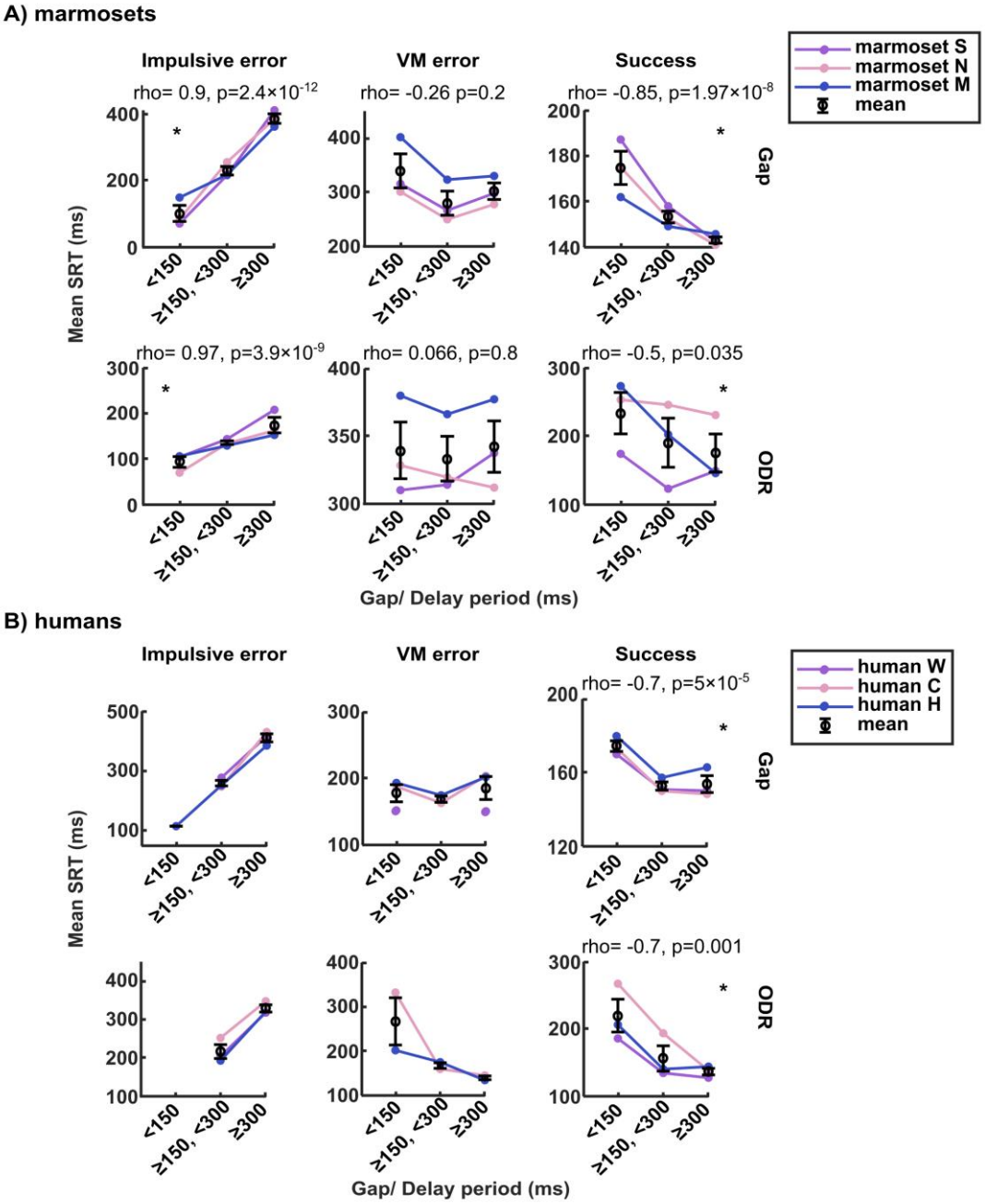
A) marmosets
Impulsive error
VM error
Success
rho= 0.9, p=2.4×10-12
rho= -0.26 p=0.2
rho= -0.85, p=1.97×10-8
rho= 0.97, p=3.9×10-9
rho= 0.066, p=0.8
rho= -0.5, p=0.035
marmoset S
marmoset N
marmoset M
mean
Gap
ODR
Mean SRT (ms)
<150
≥150, <300
≥300
Gap/ Delay period (ms)
B) humans
Impulsive error
VM error
Success
rho= -0.7, p=5×10-5
rho= -0.7, p=0.001
human W
human C
human H
mean
Gap
ODR
Mean SRT (ms)
<150
≥150, <300
≥300
Gap/ Delay period (ms)

Fig. 7

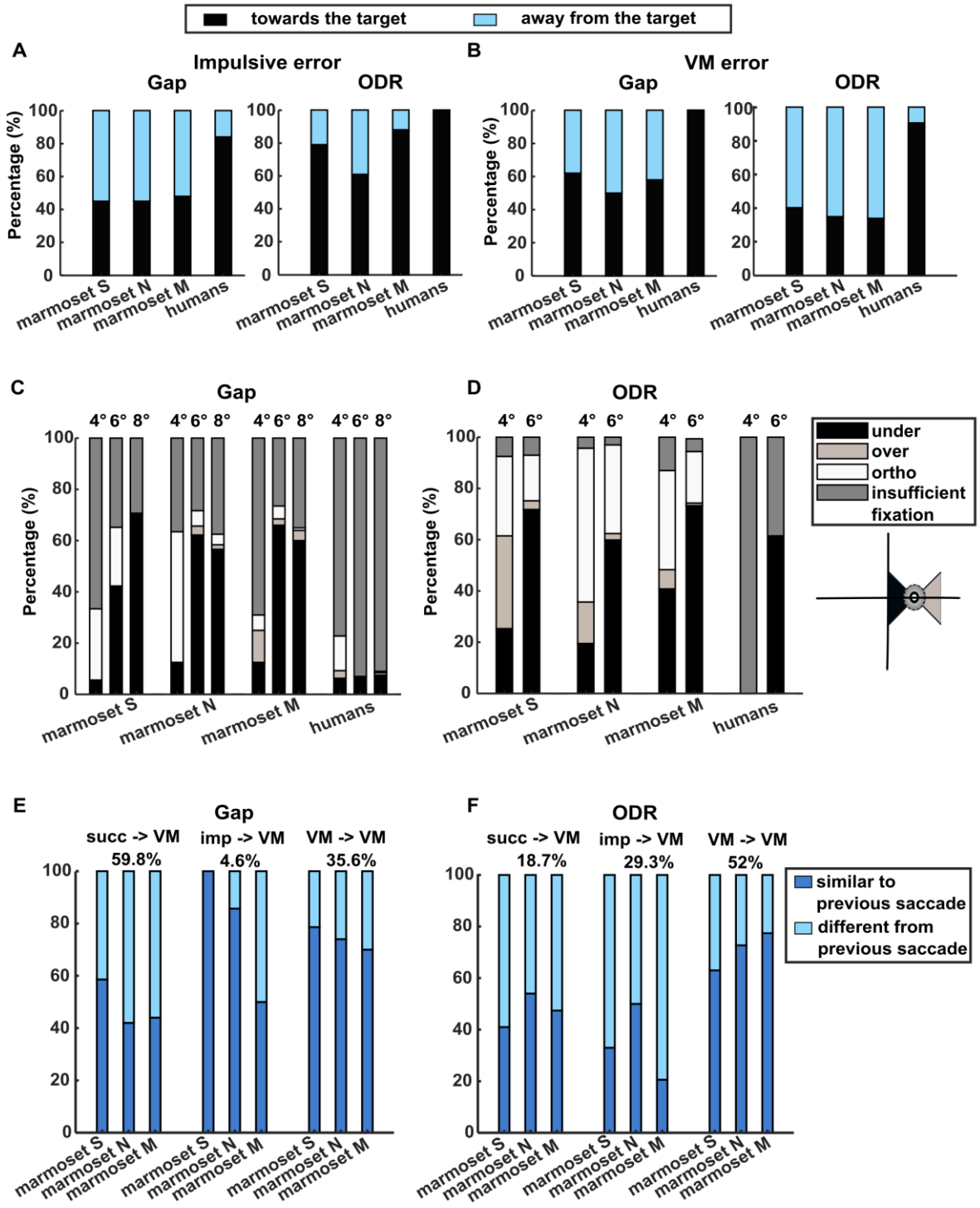
towards the target
away from the target
A
Impulsive error
Gap
ODR
B
VM error
Gap
ODR
Percentage (%)
marmoset S
marmoset N
marmoset M
humans
C
Gap
D
ODR
4° 6° 8°
under
over
ortho
insufficient fixation
E
Gap
succ -> VM
imp -> VM
VM -> VM
59.8%
4.6%
35.6%
F
ODR
18.7%
29.3%
52%
similar to previous saccade
different from previous saccade

Fig. 8

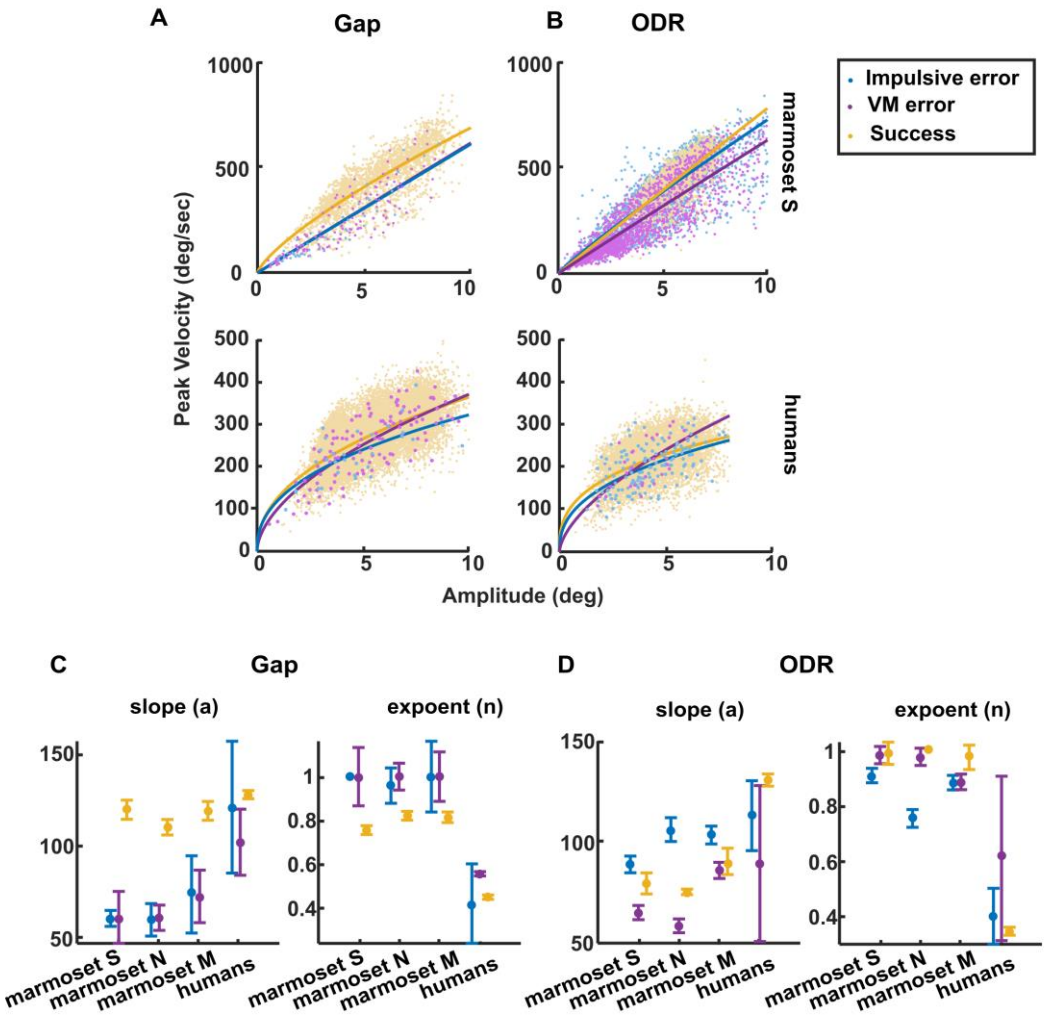
A
Gap
B
ODR
Impulsive error
VM error
Success
marmoset S
humans
Peak Velocity (deg/sec)
Amplitude (deg)
C
Gap
D
ODR
slope (a)
expoent (n)
marmoset S
marmoset N
marmoset M
humans

Fig. 9

Table 1

	Gap				ODR	
Impulsive	**VM**	**Success**		**Impulsive**	**VM**	**Success**
46	136	2402	**marmoset S**	3363	1793	2236
165	503	1852	**marmoset N**	1371	1921	549
64	147	1780	**marmoset M**	2338	1542	1092
4	3	4312	**human W**	34	0	2561
10	19	4176	**human C**	35	11	2296
17	96	3442	**human H**	79	19	2219

Table 1