

Article

Functional Roles of Saccades for a Hand Movement

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Abstract: An eye saccade provides appropriate visual information for motor control. The present study was aimed to reveal the role of saccades in hand movements. Two types of movements, i.e., hitting and circle-drawing movements, were adopted, and saccades during the movements were classified as either a leading saccade (LS) or catching saccade (CS) depending on the relative gaze position of the saccade to the hand position. The ratio of types of the saccades during the movements was heavily dependent on the skillfulness of the subjects. In the late phase of the movements in a less skillful subject, CS tended to occur in less precise movements, and precision of the movement tended to be improved in the subsequent movement in the hitting. While LS directing gaze to a target point was observed in both types of the movements regardless of skillfulness of the subjects, LS in between a start point and a target point, which led gaze to a local minimum variance point on a hand movement trajectory, was exclusively found in the drawing in a less skillful subject. These results suggest that LS and some types of CS may provide positional information of via-points in addition to a target point and visual information to improve precision of a feedforward controller in the brain, respectively.

Keywords: eye movements; reaching arm movements; eye-hand coordination; visual information; movement precision; movement segment; forward model; control model of the brain

1. Introduction

Complex movement is considered to have consecutive segments of movement [1,2]. A connecting point of each segment can be called a via-point [3]. Thus, previous studies have focused on hitting or reaching movements with the hand as an elemental movement or a movement segment to reveal behavioral characteristics [4,5] and to investigate neuronal activity patterns [6,7]. Such studies often include a drawing movement [8]. Investigation of generation mechanism of the via-point may lead to understanding a complex movement.

In daily life, movements depend heavily on visual information, which is used for feedforward and feedback controls. For example, goal-directed movements of the hand are usually accompanied by an eye saccade that precisely directs an individual's gaze to an observed target location in case of stationary target [9–13] or a predicted target location in case of moving target [14,15] before the hand starts to move. This type of saccades has been thought to provide visual information about the observed or predicted target location to guide a hand movement. Feedback control of the reaching movements also relies substantially on visual information [16–19]. Additionally, another type of saccade was identified during the performance of a simple line-drawing movement in which a sequence of small eye saccades closely followed the trajectory of a pencil [20]. The author of this study suggested that this type of saccade contributed to feedback control. Therefore, at least two types of saccades may be associated with hand movement: a saccade that directs an individual's gaze to a target position, which has been observed during a reaching movement, and a saccade that directs an individual's gaze to a hand position, which has been observed during the drawing of a simple line.

The goal of the present study was to reveal the relationship between the two types of saccades and hand movements, especially its feedforward control, and to get an insight into the role of visual information acquired by the saccades on movement control of the hand. We adopted hitting and circle-drawing movements as discrete and continuous movements, respectively. These two types of movements were selected instead of reaching and circle-tracking movements to increase the relative contribution of feedforward control to feedback control. Saccades during the movements were quantitatively classified as either a leading saccade (LS) or catching saccade (CS) depending on the relative gaze position of the saccade to a cursor position that represented the hand position: LS and CS directed the gaze to the cursor position in the direction of the cursor movement and to around the current cursor position, respectively. Precision of the hand movements was analyzed in relation to the saccades.

2. Materials and Methods

Two Japanese monkeys (*Macaca fuscata*; male: Monkey H, 6.7 kg, female: Monkey U, 6.6 kg) were used in the present study. Using a robotic arm manipulandum, the monkeys were trained to execute hitting and drawing tasks. During the tasks, hand and gaze positions of the monkey were recorded. All experimental procedures were performed in accordance with the Guidelines for Proper Conduct of Animal Experiments of Science Council of Japan and approved by the Committee for Animal Experiment at Tokyo Institute of Technology.

2.1. Subjects and Apparatus

To fixate the head position during the tasks, a head holder was installed on each monkey. Induced by ketamine (10 mg/kg, intramuscular injection (i.m.)) and xylazine (2 mg/kg, i.m.), the monkey was deeply anesthetized with pentobarbital (25 mg/kg for an initial dose and 12.5 mg/kg for a supplementary dose when required by intravenous injection), a surgical operation was performed under aseptic conditions while monitoring heart rate and blood saturated oxygen concentration. The head holder was installed on the monkey skull and fixed with dental cement after cortical screws were implanted into the skull.

After an appropriate recovery period from the surgical operation, the monkeys were well trained to perform behavioral tasks (Figure 1). The monkey sat comfortably in a primate chair with its head fixated. RANARM, a robotic arm manipulandum for normal and altered reaching movements [21], was used to control the tasks and record the hand position of the monkeys, and a 19-inch computer monitor was set 61 cm away from the monkeys' eyes. A cursor on the monitor provided visual feedback regarding the current spatial location of a gripper of RANARM that the monkey held in its hand. Gaze position was estimated by measuring the position and shape of the pupil at a sampling rate of 1000 Hz with EyeLink (SR Research, Ottawa, ON, Canada).

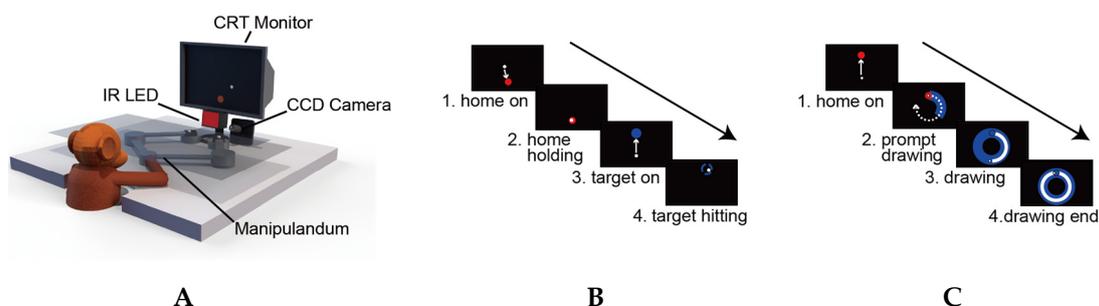


Figure 1. Experimental setup and time consequence of the tasks are illustrated. (A) A monkey directs a cursor on a monitor by manipulating a robotic arm with its right hand on a horizontal plane. The hand position and its eye position are recorded during the tasks. (B) Hitting task: monkeys are required to move the cursor from the bottom red home point to the top blue target point within a designated amount of time.

(C) Circle drawing task: a prompt shows the required direction (blue: clockwise, green: counter-clockwise (not shown)) of drawing while the monkey holds the cursor within the start point. Eight evenly spaced start points are used. The monkey can begin drawing at any time and without any time restrictions on movement time.

2.2. Behavioral Tasks

Two tasks were executed by each monkey with the right hand: a hitting task and a circle-drawing task.

In the hitting task, a red home point appeared 0.100 m below the center of the monitor at the start of each trial. The monkey was required to move the cursor to the home point and then hold it there for a random period of time that ranged from 0.50 to 1.00 s. Next, a blue target point appeared 0.075 m above the center of the monitor, and the monkey was required to move the cursor to the target point within a designated amount of time. If the monkey hit the target point in the allotted time, the target point disappeared, and the monkey received a drop of water as a reward. If the monkey did not hit the target in time, the trial was considered a failure. To ensure quick and precise hand movements, the size of the home and target points, and the required task time (reaction time plus movement time) were regulated so that the ratio of successful trials to failure trials was equal to approximately 1.

In the circle-drawing task, a red start point (radius: 0.030 m) appeared at one of eight predetermined positions located at 45° intervals around a circle (radius: 0.100 m) in the center of the monitor. The monkey was required to move the cursor (radius: 0.010 m) into the start point and to hold the cursor there for 1 sec. Then, a prompt consisting of a circle was quickly drawn beginning from the start point and using different colors to identify the direction of movement (blue: clockwise, green: counterclockwise). During this period, the monkey was required to hold the cursor within the start point and was then able to begin its drawing movement at any time after the prompt drawing was completed. There were no time restrictions on the movement, and the trajectory of the cursor during hand movement was recorded. Three indices were used to determine a successful trial: 1) the drawing direction of the monkey was the same as that of the prompt drawing; 2) the center of cursor passed within 0.070 m of the center of the prompt trajectory; and 3) the cursor returned to the start point. The monkey got a drop of water as a reward after a successful trial.

2.3. Data Recording and Analysis

Gaze and hand positional data were outputted to a home-made data recording system using LabView (National Instruments, Austin, TX, USA) through a 16-bit analog to digital converter and saved as a binary file. Data were analyzed using MATLAB (The MathWorks, Natick, MA, USA).

2.3.1. Saccade

The eye saccades were detected from the gaze positional data that were filtered with a fourth-order Butterworth low-pass filter at 50 Hz. The onset and offset of the saccades were determined using the following criteria: the gaze speed exceeded a threshold criterion of $61^\circ/\text{s}$ or it was lower than a threshold criterion of $3^\circ/\text{s}$ after the saccade onset. We classified the saccades into two types depending on the relative gaze position at offset of the saccade to the hand position: a leading saccade (LS) and a catching saccade (CS). LS and CS directed the gaze to the cursor position in the direction of the cursor movement and to around the current cursor position, respectively. We analyzed CS in the hitting task and both LS and CS in the circle-drawing task from a viewpoint of relationships between saccades and precision of the hand movement.

2.3.2. Hand Movement

The cursor positional data that corresponded to the hand position were obtained using RANARM and were filtered with a fourth-order Butterworth low-pass filter at 10 Hz. Precision of the hand movement was evaluated.

In the hitting task, it was evaluated at three different points during the movement where the hand acceleration was maximum, its velocity was maximum, and its acceleration was minimum, each of which represents the initial, middle, and terminal phases of the movement. Movement precision was defined based on the positional variance of the cursor's x -coordinate. At the acceleration maximum point, another index, which was the directional variance of tangential movement direction (D_m) of the cursor, was adopted. We expected that D_m was more robust to variation of the start position of the cursor and was a more appropriate index for a very early phase of the movement.

In the circle-drawing task, the position of the cursor was expressed in polar coordinates, and precision of the hand movement was defined as the positional variance of the cursor in the radial direction at a given phase. As another index of the precision, we also adopted curvature of the hand movement, which was calculated as follows: $|\dot{x}\ddot{y} - \ddot{x}y|(\dot{x}^2 + \dot{y}^2)^{-3/2}$, where x and y are the cursor's coordinates of its position in Cartesian coordinates with the horizontal direction and the center of the monitor as its x -axis and origin, respectively.

3. Results

3.1. Hitting Task

Monkeys had to control its hand quickly and precisely to execute the task. For *Monkey H*, the radii of the home and target points were set at 0.012 and 0.014 m, respectively, and the task time was designated at 0.75 s. This subject completed a total of 780 trials, of which 401 (52%) were successful. For *Monkey U*, the radii of the home and target points were both set at 0.006 m, and the task time was designated at 0.54 s. This subject completed a total of 560 trials, of which 403 (58%) were successful.

Although success ratio of the task was more or less the same in the two monkeys, movement characteristics of the hand in the hitting task varied depending on the monkey. *Monkey U* showed better performance than *Monkey H* with smaller target diameter, shorter movement time (0.47 ± 0.04 s vs 0.33 ± 0.03 s) (mean \pm standard deviation [SD]), higher peak hand velocity (0.54 ± 0.05 m/s vs 0.90 ± 0.07 m/s) (mean \pm SD), all of which indicate more precise feedforward control of the hand.

In the following analysis, trials that did not reach 0.125 m in y -coordinate within the designated task time were excluded; 762 trials in Monkey H and 556 trials in Monkey U were analyzed as a result. In almost all of the hitting task trials, both monkeys made a saccade directly to the target point upon its appearance and prior to the onset of hand movement. Subsequently, two different types of gaze control were observed. In one type, the monkey kept its gaze on the target point until the cursor hit it (Figure 2A), and in the other type, the monkey returned its gaze from the target to the cursor and made a couple of saccades around the cursor while following its movement (Figure 2B). LS and CS that execute these two types of gaze control were analyzed. We defined LS and CS as follows: LS was a saccade that directed the gaze in the range from 0.135 to 0.200 m in y -coordinate; CS was one that was not LS and difference of gaze position directed by that and the cursor position was within ± 0.050 m in y -coordinate.

The LS was observed in both monkeys in more than 90% of the trials. Inversely correlated with the performance of the task, interestingly, the number of the CS in Monkey H was prominently higher than that in Monkey U (Table 1). Therefore, the CS in Monkey H was analyzed in the following analysis. In the trial with the CS in Monkey H, the subject executed the CS along the hand trajectory (Figure 3A). The gaze points following the CS in Monkey H seemed bimodally distributed in the direction of cursor movement with a border point at 0.11 m from the center of the start point (Figure 3B), which roughly corresponded to the cursor velocity maximum point. We tentatively classified the CS into two types; the CS in hand acceleration phase (CSa) and the CS in hand deceleration phase (CSd).

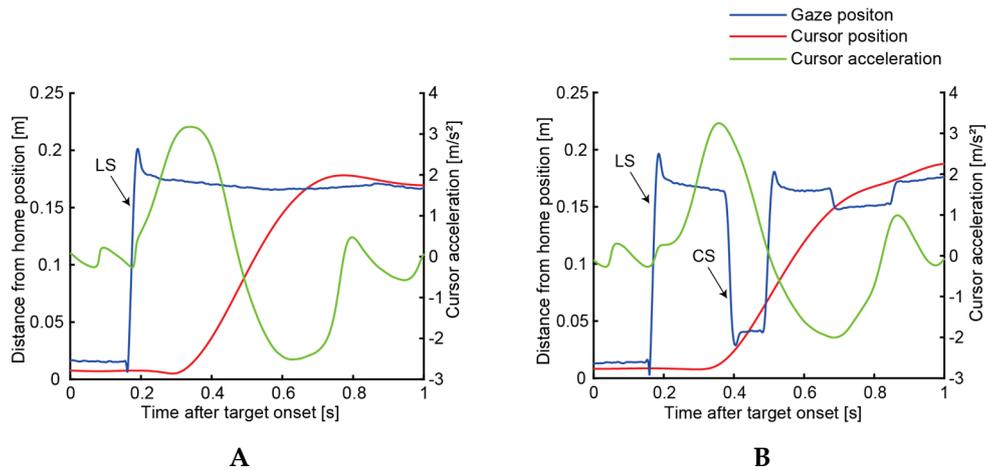


Figure 2. Two types of saccades during the hitting task are depicted. (A) leading saccade (LS) occurs almost simultaneously at the onset of acceleration of the cursor. (B) catching saccade (CS) follows LS in this trial.

Table 1. Occurrence probability of each type of saccades during the hitting task.

Subject	Number of Trials	Saccade [Times/Trial] (Number of Trials)				
		Total	LS	Total CS	CSa ¹	CSd ²
Monkey H	762	2.51 (762)	1.77 (762)	0.35 (242)	0.27 (199) ³	0.09 (67) ³
Monkey U	556	1.49 (556)	1.16 (540)	0.01 (8)	0.01(8)	0.00 (0)

¹ CSa: CS in cursor acceleration phase. ² CSd: CS in cursor deceleration phase. ³ Both CSa and CSd were observed in 24 trials.

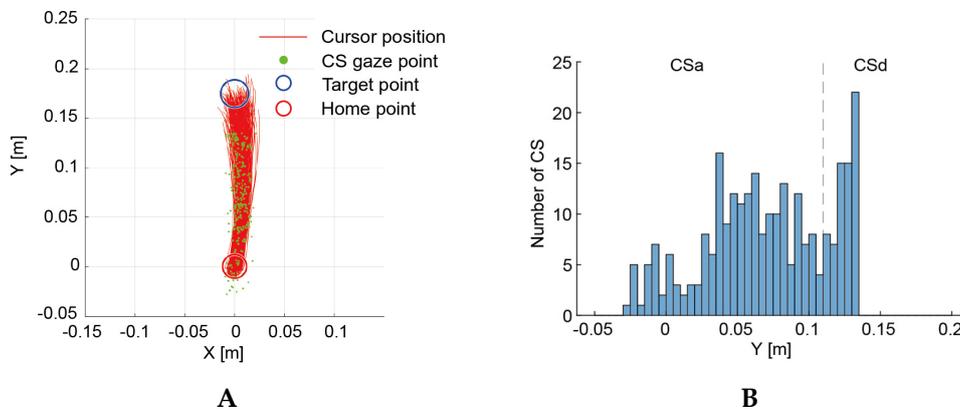


Figure 3. Cursor trajectories of trials with CS and distribution of gaze points directed by CS. (A) Cursor trajectories of the hitting trials with CS and gaze points directed by CS in *Monkey H*. (B) Distribution of gaze points directed by CS in y-coordinate. Broken line indicates the border point (0.11 m) of CS in hand acceleration phase (CSa) and CS in hand deceleration phase (CSd).

To analyze the relationship between the CS and precision of the hand movement, the hitting task trials were grouped into three; those without the CS, those with CSa, and those with CSd, and precision of the hand movement among the groups was compared. The trials with CSd showed a tendency towards larger variance of the movement than the other two groups from the middle phase of the movement and showed significantly larger variance than those without the CS both at the middle (F-test, $p = 0.0144$) and deceleration (F-test, $p = 0.0158$) phases of the movement (Figure 4A). Although there was no significant difference in the variance of Dm among the three groups, we found that only the subsequent trials to ones with CSd showed a tendency towards smaller variance than the current trials (Figure 4B). This was indicative of influence of CSd on improvement of precision of

the subsequent movement in its initial phase, i.e. feedforward control component. Like in the task performance indices, e.g. size of the target and peak hand velocity, precision of the movement by *Monkey U* was superior to that by *Monkey H* in all the movement phases.

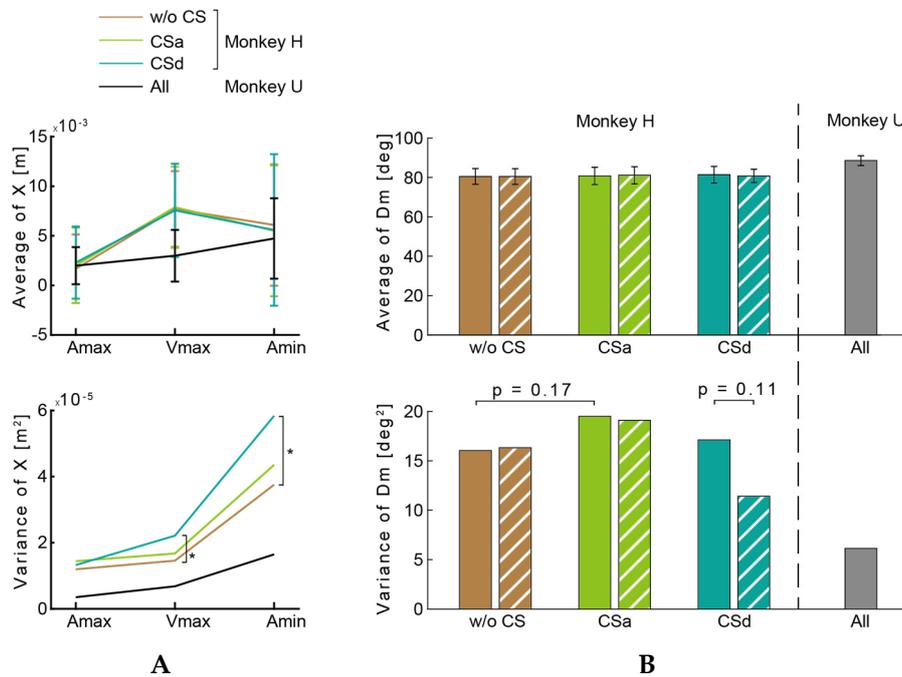


Figure 4. Effects of the CS on accuracy and precision of the hand movement in the hitting task are shown. Trials are grouped into three depending on the types of saccades during the trial in *Monkey H*; those without (w/o) CS (520 trials), with CSa (199 trials), and with CSd (67 trials). As a comparison, the result of all trials in *Monkey U* (556 trials) is also shown. **(A)** Top and bottom panels: average and variance of the cursor position in x-coordinate are shown, respectively ($* p < 0.05$). They are evaluated at cursor acceleration maximum (Amax), velocity maximum (Vmax), and acceleration minimum (Amin) point during the hand movement. **(B)** Top and bottom panels: average and variance of movement direction (Dm) are shown, respectively. The current and subsequent trials are shown as filled boxes and white oblique-lined boxes, respectively. An error bar represents a standard deviation in all panels.

3.2. Circle-Drawing Task

Following a training period, both monkeys were able to smoothly draw a circle from all eight start points in both directions of rotation at success rates up to around 90%. In total, 2,000 trials (two rotation directions \times eight start points \times 125 trials) were recorded from each monkey. All of the following analyses were applied to the successful trials in which cursor trajectory was within ± 2 SD range from the average and the saccades that directed the gaze within ± 3 SD range from the average trajectory of the cursor.

Monkey H performed the task with a movement time of 0.90 ± 0.14 s and 0.97 ± 0.11 s (mean \pm SD) in the counterclockwise and clockwise directions, respectively. *Monkey U* did it with a movement time of 0.77 ± 0.08 s and 0.71 ± 0.07 s (mean \pm SD) in the counterclockwise and clockwise directions, respectively.

Similar to the hitting task, both monkeys made several saccades throughout the drawing task (Figure 5A). We focused on the saccades that led the gaze on the way to the target. Therefore, we excluded the saccade within the final 45° range of the phase and plotted the distribution of phase difference of the saccade against the cursor (Figure 5B). In *Monkey H*, the distribution seemed to be bimodal with peaks around at 0° and -100° in both rotation directions. In contrast, in *Monkey U*, it seemed to be unimodal with a peak around at 0° in both rotation directions. We defined LS and CS in the drawing task as a saccade that had the phase difference smaller than -35° and within $\pm 35^\circ$, respectively. More than 40% of the saccades were the LS in *Monkey H* (46% in the counterclockwise

rotation direction, 44% in the clockwise rotation direction). In contrast, the CS dominated in Monkey U (45% in the counterclockwise rotation direction, 76% in the clockwise rotation direction) (Figure 5C) (Table 2).

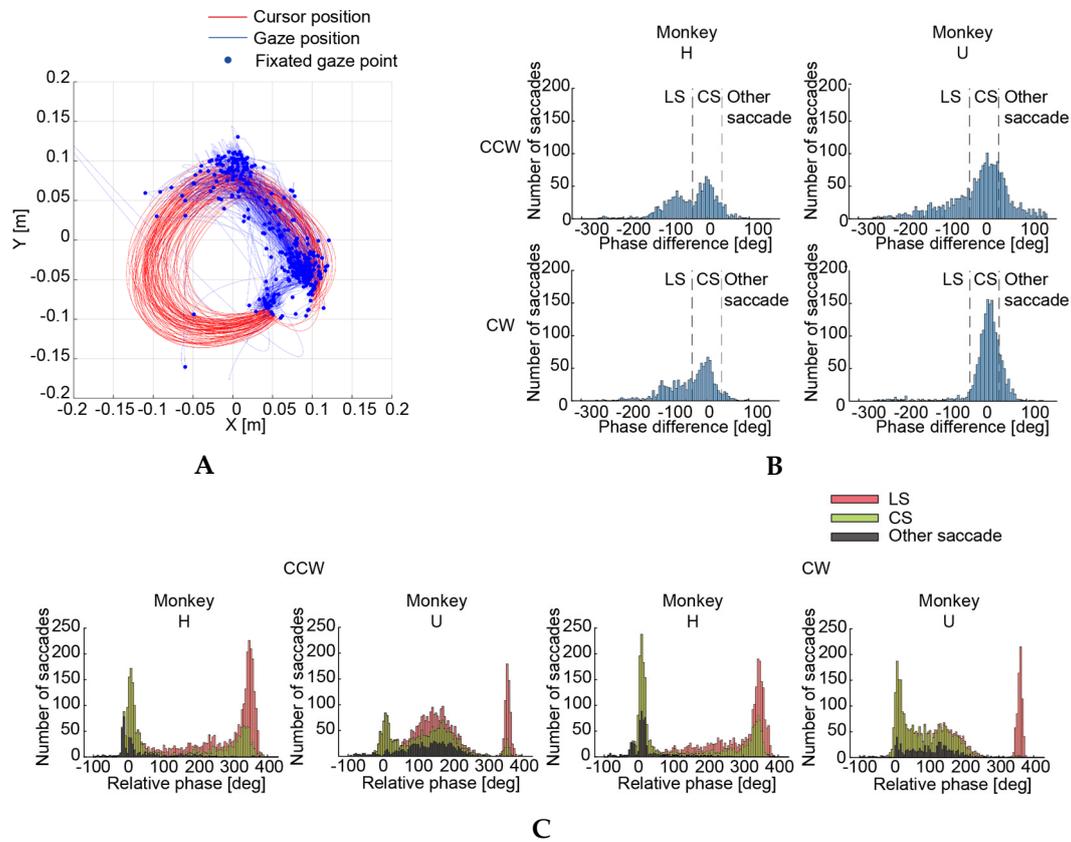


Figure 5. Two types of saccades during the circle-drawing task are depicted. (A) Example trials of the circle-drawing task from the 315° start point toward the clockwise direction in *Monkey H*. (B) Distributions of gaze points directed by saccades relative to the hand position are shown. Broken lines indicate the borders (−35° and 35°) of LS, CS, and other saccades. (C) Distributions of gaze points directed by LS, CS, and the other saccade are plotted in relation to a start point (a positive sign is assigned to the phase when the gaze point is in the cursor movement direction). Bin width is 5° in all the panels.

Table 2. Occurrence probability of each type of saccades during the circle-drawing task.

Subject	Direction ¹	Trial	Saccade [Times/Trial] (Number of Trials)		
			All/Midway ²		
			Total ³	LS	CS
Monkey H	CCW	743	5.22 (741)/ 1.81 (723)	2.33 (735)/ 0.83 (457)	2.27 (694)/ 0.86 (447)
	CW	751	4.77 (751)/ 1.72 (648)	1.78 (714)/ 0.75 (439)	2.22 (668)/ 0.88 (441)
Monkey U	CCW	749	4.70 (749)/ 3.04 (749)	1.70 (691)/ 0.89 (531)	1.80 (638)/ 1.35 (624)
	CW	769	4.60 (769)/ 2.29 (769)	1.10 (679)/ 0.16 (110)	2.60 (744)/ 1.73 (729)

¹ CCW: counterclockwise, CW: clockwise. ² Midway: saccades except the final 45° range of the phase. ³ Total = LS + CS + Other saccades.

We then analyzed the relationship of these saccades and precision of the hand movement. In Monkey H, variance of the movement tended to be small at a specific phase around 30°–60° irrespective of the eight different start points and two different rotation directions, toward which point the LS tended to be directed (Figure 6A). When the LS was aligned at the local minimum phase of the variance in the range of 0°–100°, it clearly showed that the LS directed the gaze 0° (counterclockwise rotation direction) and –30° (clockwise rotation direction) in advance to the local minimum point of the variance (Figure 6B). In Monkey U, the number of the LS was relatively small (29% in the counterclockwise rotation direction, 7% in the clockwise rotation direction), and no obvious relationship of the LS and precision of the hand movement was found.

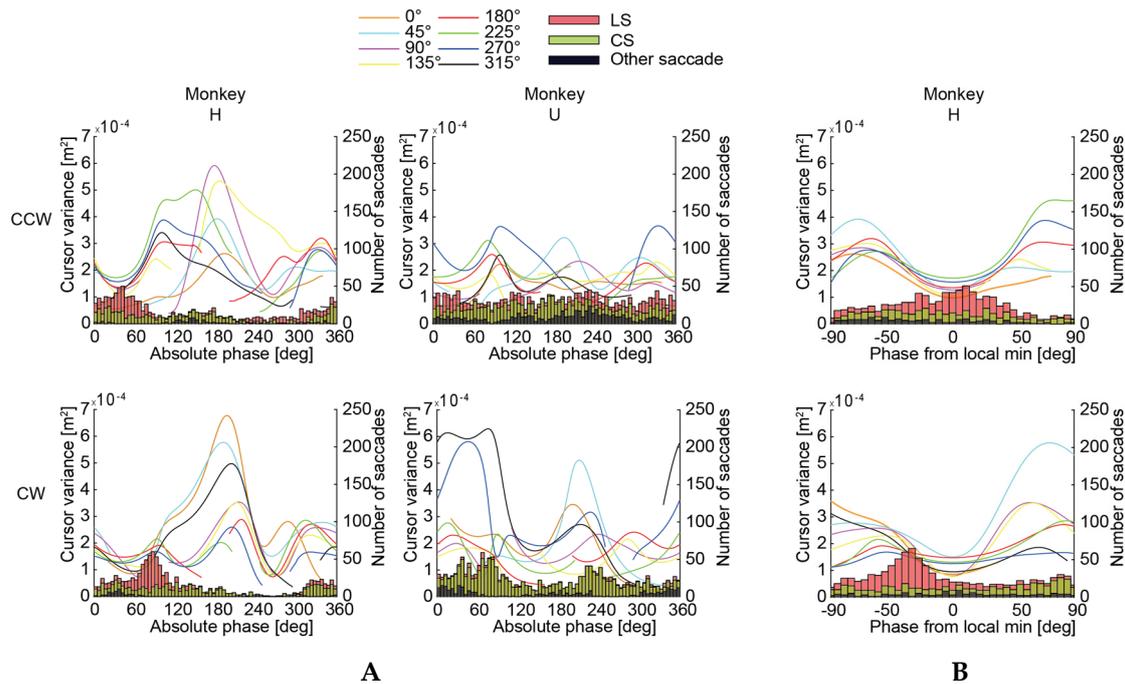


Figure 6. Relationships of the cursor positional variance and gaze points directed by saccades in between (within 45°–315° phase range relative to the start point) the start and target points in the circle-drawing task are shown. (A) The relationships are plotted in absolute phase (phase in polar coordinates with its origin at the center of the monitor). Cursor variance and number of each saccade are indicated by the solid lines and bars, respectively. Note that the cursor variance gets local minimum at the phase of around 30°–60° for almost all starting point regardless of the rotational directions in *Monkey H*. (B) Gaze points directed by saccades are plotted against the local minimum phase of the cursor variance in *Monkey H* (a negative sign is assigned to the phase when the gaze leads the cursor movement). Bin width is 5° in all the panels.

Finally, the CS was analyzed in terms of precision of the drawing movement. We applied the same method as in the hitting task; precision of the movement was compared between trials with CSd within the phase range of 60° to the final target (CSt) and ones without it. As an index of the movement precision, curvature of the cursor was evaluated at the local minimum of the acceleration of the cursor. In *Monkey H*, the trials with CSt showed significantly higher variance of the curvature than those without CSt in the counterclockwise (F-test, $p = 1.6 \times 10^{-7}$) and clockwise (F-test, $p = 3.1 \times 10^{-3}$) rotation directions, respectively (Figure 7). The analysis was not applied to *Monkey U* because there were a few CSt found in both rotation directions.

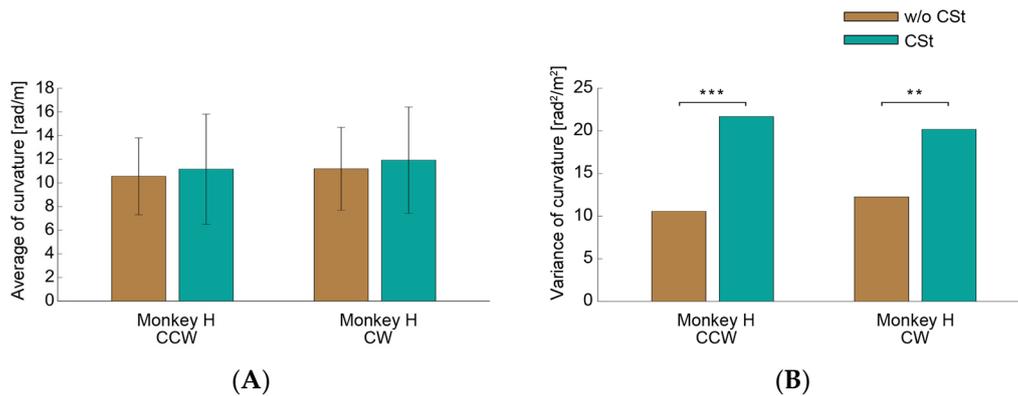


Figure 7. Effects of CS close to the target (CSt) on the cursor movement accuracy and precision during the circle-drawing task Monkey H are shown. They are evaluated at the cursor acceleration minimum point close to the target (A) Average of curvature of the cursor trajectory. An error bar represents a standard deviation. (B) Variance of the curvature. ** $p < 0.01$. *** $p < 0.001$.

4. Discussion

The relationship between saccades and hand movement has been studied using both pointing and drawing movements. For example, goal-directed pointing tasks were used to assess the type of saccades that preceded the onset of hand movement [9–15]. This type of saccades has been thought to provide visual information about the observed or predicted target location to guide a hand movement. Additionally, a simple line-drawing task was used to identify another type of saccade in which the gaze closely followed a pencil trajectory with a sequence of small saccades [20]. This type of saccade may be related to the feedback control of hand movement.

In the present study, saccades during the movements were quantitatively classified as either a leading saccade (LS) or catching saccade (CS) depending on the relative gaze position of the saccade to a cursor position that represented the hand position, and relationships between the saccades and feedforward control component of hand movements were analyzed.

4.1. Functional Roles of the Saccades

We found CS during the hitting task in addition to the circle-drawing task. Although CS during the circle-drawing task was predictable considering that a similar type of saccade was observed in a previous study using a line-drawing task [20], CS during the hitting task was a novel finding.

CS during the hitting task was exclusively observed in the monkey that showed lower precision of the movement than the other. While CS was found both in the hand acceleration phase and in the hand deceleration phase (CSd), precision of the middle and late phases of the movement in the trials with CSd was significantly lower than that in the trials without CSd. Since the subject had to heavily rely on feedforward control to accomplish the task because of its designated short movement time, the observed precision is considered to largely reflect that of the feedforward control component. Taking the following two results into account, therefore, we assume that CSd during the hitting task may arise from the imprecision of the feedforward control component to improve its precision. Firstly, the trials with CSd were significantly less precise than those without CSd at the middle and deceleration phases of the movement. Secondly, the initial movement direction, which represents the feedforward control component, in the subsequent trial tended to be more precise than that in the current trial with CSd, while no significant difference of the precision was found between trials without CSd. This assumption may support the previous study that showed a faster adaptation rate in a novel task in a trial with continuous visual feedback of the cursor position than in a trial with post-trial knowledge of task performance [22]. Although we could not detect any evidence suggesting contribution of CS to online error correction but find those suggesting contribution of CSd on offline error correction (“error” is used in terms of not systematic error but accidental error), it should be further carefully

investigated which saccade, i.e. LS or CS, provides visual information for the online feedback error correction [17,23,24].

In the drawing task, two types of CS were also observed like in the hitting task; one occurred in early phase of the movement (CSe) and the other in late phase of the movement, especially within a phase close to the target (CSt). While the monkey that showed higher precision in the hitting task had not CSt but exclusively CSe, the one that showed lower precision had both CSt and CSe. Like CSd in the hitting task, CSt in the circle-drawing task was observed exclusively in the monkey that showed lower precision in the hitting task. Furthermore, precision at the deceleration local minimum phase of the movement close to the target (curvature was used as an index) in the trials with CSt was significantly lower than that in the trials without CSt, which coincides with the finding in the hitting task. Taking this analogy between CSd and CSt into account, we assume that CSt during the circle-drawing task may also arise from the imprecision of the feedforward controller to improve its precision. As for CSe, we presume that CSe may have a role on precise control of the hand movement because CSe was predominantly observed in the monkey that executed more precise control of the hitting task although we could not find any valuable index to evaluate the function of CSe.

The present study also found LS during the circle-drawing task that directed the gaze to a point in between the start and target points although there was no explicit presentation of a via-point. This type of gaze control has been reported in walking in natural terrain [25], in which a saccade directed the gaze to a future point of foot placement about 1.5 ms in advance. In the present study, the LS (LSm) was always followed by a fixated gaze until the cursor passed the area and the gaze points of LSm were concentrated at a point with 40° or 0° phase lead depending on the rotation direction where the positional variance of the cursor reached a local minimum. These findings suggest that the gaze point by LSm is directed to close to an internally set via-point. These points were set in working coordinates, i.e. external coordinates because the local minimum points of the variance of the cursor were more or less consistent irrespective to the start point of the drawing movement. LSm was observed in the monkey that executed less precise control of the hitting task, suggesting that the skillful monkey regarded the circle-drawing movement as single segment of movement and the less skillful monkey divided the movement into multiple segments setting via-points.

4.2. The Saccades and the Control Model of an Arm Movement

An optimal feedback control model was proposed as one for pointing or reaching arm movements [26] and has successfully explained various characteristics of those behaviors [27–30]. According to the model, an optimal controller produces a control input to muscles based on the estimated state of an arm, i.e., a predicted online state that may be corrected by observed information. Furthermore, a forward model generates the predicted state using the control input. Thus, the optimal controller is able to serve as a controller for a segmental movement, and to control an object even without feedback information if the forward model is accurate and precise enough.

Based on the minimum intervention principle of the model, it predicts that variance of trajectories of movement becomes minimum at an aimed point, i.e. a via-point in multiple segmental movement. Therefore, the local minimum points of the variance of the cursor in the circle-drawing task can be reasonably regarded as a via-point. In the case of movements that are more complicated than the circle-drawing, it is possible that the brain internally sets via-points [3] toward which LS directs an individual's gaze and, in turn, sequentially feeds information to some type of neurological optimal controller.

The model does not inherently implement a mechanism that adaptively changes the forward model depending on a change of a control object. Since there has been accumulated evidence suggesting that the brain can adaptively change its feedforward control signal depending on a change of an environment [31–34], the forward model in the brain must adaptively changes. For the adaptive change of the forward model, some types of CS, e.g., CSd in the hitting task and CSt in the circle-drawing task may provide visual information.

Finally, a higher-level mechanism that governs the way of adaptation or learning has been proposed as meta-learning, which is mainly investigated in the framework of reinforcement learning [35,36]. An apparent different strategy to the drawing task found in two subjects in the present study might be a resultant outcome of a kind of meta-learning because the subjects had acquired the skill to perform the task through a reward-based training process. If this is the case, we suggest that precision or reliability of the forward model should be considered as an important factor to determine a strategy in the meta-learning. In other words, a more reliable forward model may lead to a strategy to perform a complex movement with a smaller number of moment segments.

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