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Modulation of saccadic eye movements by predicted reward outcome

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Abstract Reward is a primary goal of behavior and is crucial for survival of animals. To explore the mechanisms underlying such reward-oriented behavior, we devised a memory-guided saccade task in which only one fixed direction out of four was rewarded, which was called the one-direction-rewarded task (1DR). As the rewarded direction was changed in four blocks, saccades in a given direction were rewarded in one block (constituting reward-oriented behavior), but non-rewarded in the other blocks (non-reward-oriented behavior). As a control, an all-directions-rewarded task (ADR) was used. Using these tasks, we found that the parameters of saccades changed depending on whether or not the saccade was followed by reward. (1) The mean saccadic peak velocity was higher and the mean saccade latency was shorter in the rewarded condition than in the non-rewarded condition. (2) The mean saccade amplitude showed no difference in two out of three monkeys. (3) The variations of saccadic velocity, latency and amplitude were smaller in the rewarded condition. (4) Within a block of 1DR, the saccade velocity remained high in the rewarded condition, but decreased gradually in the non-rewarded condition; it decreased only slightly in ADR. The saccade latency showed the opposite pattern of change, but less clearly. (5) The saccades in the non-rewarded condition tended to have slower velocities and longer latencies in the trials shortly after a rewarded trial. (6) The ratio of error trials was much higher in the non-rewarded condition than the rewarded condition. (7) The errors, which

were due to premature or incorrect saccades, showed unique spatiotemporal patterns that would reflect the competition between the cognitive and motivational processes. These results provide important constraints to the neuronal mechanism underlying reward-oriented behavior because it must satisfy these rules.

Keywords Saccade parameters · Memory-guided saccade · Reward · Motivation · Monkey

Introduction

If an action is followed by an immediate reward, the action is more likely to be elicited (Thorndike 1911). The animal is thought to be more motivated (Konorski 1967). This type of behavior is often called reinforcement learning (Barto 1994). However, the neuronal mechanisms underlying reinforcement learning are still unclear, although recent studies have suggested that the basal ganglia may play an important role (Houk et al. 1995; Schultz 1998). This may partly be because we have no clear behavioral measure with which neuronal activities should be correlated. We propose in this paper that saccadic eye movement can be a suitable behavioral measure for studying reinforcement learning and motivation.

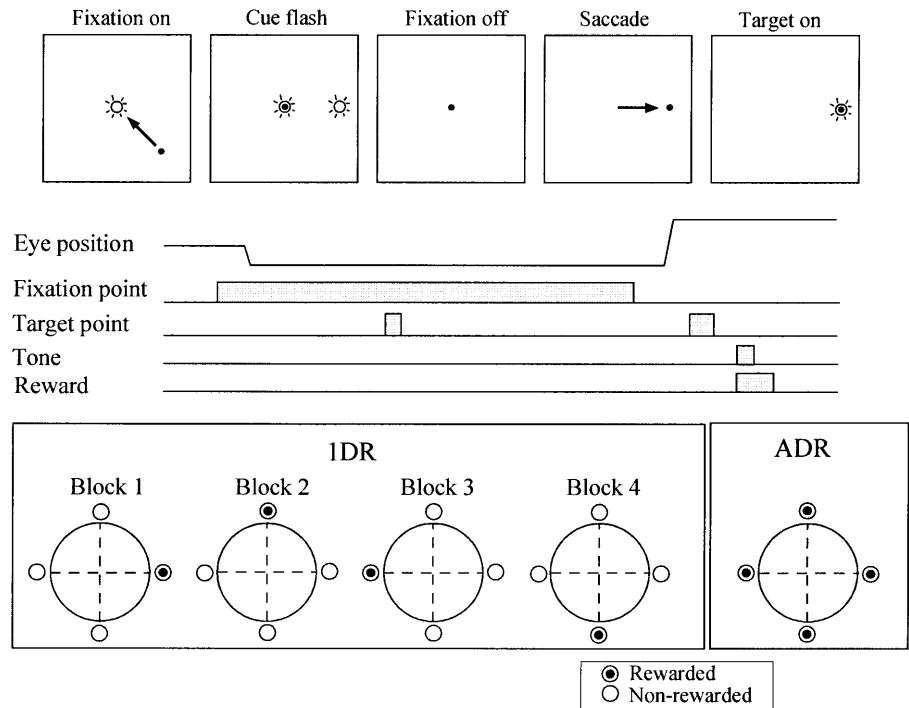
It is well known that the basal ganglia contribute to the control of saccadic eye movement (Hikosaka et al. 2000). Among basal ganglia nuclei involved in saccadic control, the caudate nucleus may play a pivotal role because it receives convergent inputs from cortical areas carrying visuospatial and saccadic signals (Stanton et al. 1988; Parthasarathy et al. 1992; Shook et al. 1991) and from midbrain dopaminergic neurons carrying reward-related signals (Smith and Bolam 1990; Schultz 1998). Many caudate neurons show visuosaccadic and cognitive activities (Hikosaka et al. 1989a, 1989b, 1989c). Furthermore, the visuospatial activities of caudate neurons are modulated profoundly by the presence or absence of reward after the saccade (Kawagoe et al. 1998). This was shown by asking the monkeys to perform a modified

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Fig. 1 Memory-guided saccade task in one-direction-rewarded condition (1DR) and all-directions-rewarded condition (ADR). *Top* The sequence of the task events with light stimuli (open circles), eye positions (filled circles), and saccades (arrows). *Center* The durations of stimuli and other task-related events. *Bottom* Four blocks of 1DR and one block of ADR, as a minimum experimental set. In 1DR, only one direction was rewarded throughout a block of 60 trials. Different directions were rewarded in different blocks. See “Materials and methods” for details



version of the memory-guided saccade task in which reward was given for the saccade in one particular direction out of four, which we call the one-direction-rewarded task (1DR). Along with the changes in caudate neuronal activities, saccade velocities and latencies were modulated by the predicted presence or absence of reward. In the present study we decided to investigate the changes in saccade parameters more precisely because the results would allow us to study the neural-behavioral correlations in relation to the reinforcement learning mechanisms.

Materials and methods

General

We used three male Japanese monkeys (*Macaca fuscata*). The monkeys were kept in individual primate cages in an air-conditioned room where food was always available. The monkeys were given restricted amounts of fluid during periods of training and recording. Their body weight and appetite were checked daily. Supplementary water and fruit were provided daily after the experiment. All surgical and experimental protocols were approved by the Juntendo University Animal Care and Use Committee and are in accordance with the National Institutes of Health Guide for the Care and Use of Animals. The experiments were carried out while the monkey's head was fixed. For this purpose, a head holder and a scleral eye coil were implanted under surgical procedures.

Behavioral tasks

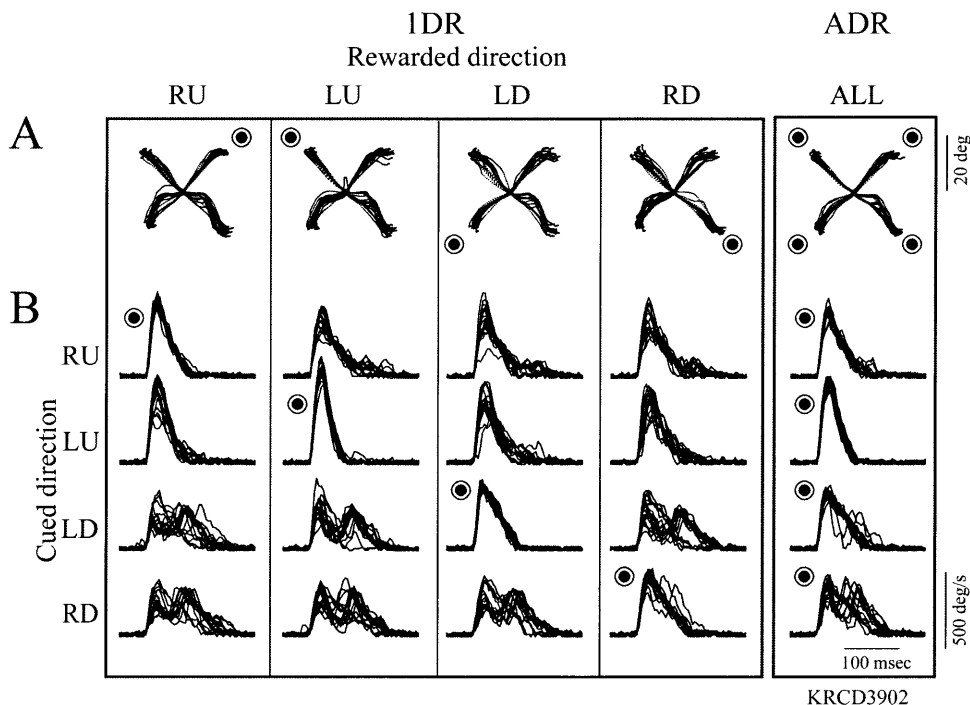
The monkey sat in a primate chair in a dimly lit and sound attenuated room with its head fixed. In front of it was a tangent screen (30 cm from its face) onto which small red spots of light (diameter: 0.2°) were backprojected using two LED projectors. The first projector was used for a fixation point, and the second for an instruction cue

stimulus. The position of the cue stimulus was controlled by reflecting the light via two orthogonal (horizontal and vertical) galvanomirrors.

The monkeys were first trained to perform memory-guided saccades (Hikosaka and Wurtz 1983) (Fig. 1). A task trial started with onset of a central fixation point on which the monkeys had to fixate. A cue stimulus (spot of light) came on 1 s after onset of the fixation point (duration: 100 ms), and the monkeys had to remember its location. After 1–1.5 s, the fixation point turned off, and the monkeys were required to make a saccade to the previously cued location. The target came on 400 ms later for 150 ms at the cued location. The saccade was judged to be correct if the eye position was within a window around the target (usually within $\pm 3^\circ$) when the target turned off. The correct saccade was indicated by a tone stimulus and reward (drop of water). The monkeys made the saccade before target onset based on memory, because, otherwise, the eyes could not reach the target window within the 150-ms target-on period; the target was presented only to give the monkeys accurate feedback information. The next trial started after an inter-trial interval of 3.5–4 s.

The monkeys were then trained to perform a modified version of the memory-guided saccade task called 1DR (one-direction-rewarded task) (Kawagoe et al. 1998) (Fig. 1). In 1DR, only one particular direction was rewarded while the other three directions were either not rewarded (exclusive 1DR) or rewarded with a smaller amount (about 1/5) (relative 1DR). We used the exclusive 1DR for two out of three monkeys; the third monkey had difficulty in performing the exclusive 1DR so that we used the relative 1DR. The highly rewarded direction was fixed in a block of 60 trials. Even for the non-rewarded or less-rewarded direction, the monkeys had to make a correct saccade, because otherwise the same trial was repeated. The correct saccade was indicated by the tone stimulus. For comparison, the traditional memory-guided saccade task was examined in which every correct saccade was rewarded with the liquid reward together with the tone stimulus; this was called ADR (all-directions-rewarded task). The amount of reward per trial was set approximately the same between 1DR and ADR. The cue was chosen pseudo-randomly such that the four directions were randomized in every subblock of four trials; thus, one block (60 trials) contained 15 trials for each direction. Other than the actual reward, no indication was given to the monkeys as to which

Fig. 2 Reward-contingent modulation of saccade trajectories (A) and velocities (B). The data were obtained from monkey K in one experiment, which consisted of four blocks of IDR (with different rewarded directions) and ADR. The rewarded direction is indicated by a bull's eye mark. Tangential eye velocities aligned on saccade onsets are shown separately for four cue (and saccade) directions. The double peaks of velocity for left- and right-downward saccades reflect their curved nature (horizontally and then downward) as seen in the saccade trajectories. Target eccentricity was 20 deg



direction was currently rewarded. IDR was performed in four blocks, in each of which a different direction was rewarded highly. The order of the rewarded direction in four blocks of IDR was randomized.

Recording procedures

Eye movements were recorded using the search coil method (Enzanshi Kogyo MEL-20U) (Robinson 1963; Matsumura et al. 1992). Eye positions were digitized at 500 Hz and stored into a file continuously during each block of trials.

Data analysis

We used the following procedure to determine the time of saccade. We judged that an eye movement (candidate of a saccade) occurred if velocity and acceleration exceeded threshold values (30°/s and 90°/s², respectively). Since velocity and acceleration are actually two-dimensional vectors, we calculated the absolute values of these vectors at each sampling time and checked if they satisfied the above and following criteria for saccade detection. The eye movement was accepted as a saccade based on its velocity and duration. After the onset, the velocity must exceed 45°/s and this suprathreshold velocity must be maintained for at least 10 ms. The total duration must be longer than 25 ms. The end of the eye movement was determined if the velocity became lower than 40°/s. These threshold values were determined empirically by applying them to sample saccades. For each saccade thus determined, we obtained several parameters: latency, amplitude, peak velocity, duration, and eye position at the beginning and end of the saccade.

To examine whether the characteristics of memory-guided saccades depended on the reward condition, we statistically compared the saccade parameters (mainly velocity, latency, and amplitude) between the rewarded and non-rewarded conditions of IDR. For each experiment, we obtained the mean values of saccade parameters for each saccade direction, separately for the rewarded condition (about 15 trials) and the non-rewarded condition (about 45 trials) of IDR. We then performed a statistical comparison (paired *t*-test) between the rewarded and non-rewarded conditions for the means

of each parameter and its variation (coefficient of variation), for each saccade direction in each monkey.

A task trial was aborted in one of three cases: (1) when the monkey failed to fixate the fixation point (no-fixation), (2) when the monkey broke fixation after cue onset before the fixation point went off (fixation-break), or (3) when the monkey failed to make a saccade correctly to the remembered cue location (incorrect-saccade). To compare the performance among different reward conditions, we defined cases 2 and 3 as error trials and calculated their rate of occurrence for each reward condition in each experiment. Case 1 was not counted since the reward condition in the given trial was unknown when the failure occurred.

Results

Saccadic eye movement is affected by reward outcome

Figure 2 shows, as an example, the trajectories and velocities of saccades for four blocks of IDR and one block of ADR. In this case, we used an oblique set of four targets with the eccentricity of 20 deg. The bull's eye mark indicates the rewarded direction. In ADR, the upward saccades were nearly straight, while the downward saccades were sometimes curved upward (right column in Fig. 2A). In IDR, the saccade trajectories changed slightly, but consistently (left four columns in Fig. 2A). The right-up saccades, for example, were more straight in the block when the right-up direction was rewarded (column: RU) than when this direction was not rewarded (columns: LU, LD, RD). The same tendency was true for the saccades in the other directions.

In Fig. 2B, the velocities of these saccades are shown aligned on the saccade onset and are shown separately for different cue directions in a block (shown in a column). The saccade velocities were different among

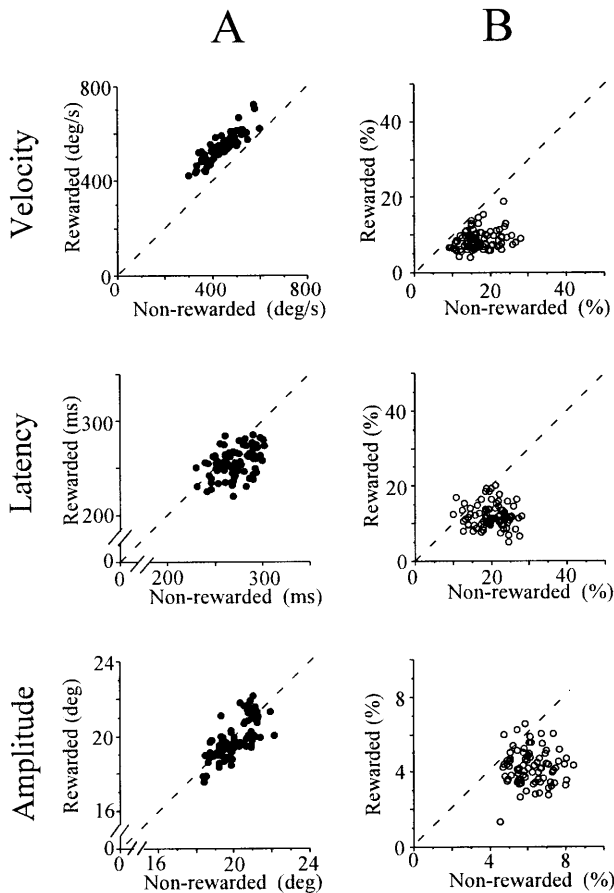


Fig. 3A, B Reward-contingent modulation of saccade parameters: peak velocity, latency, and amplitude. *Each dot* is based on a single experiment, its coordinates indicating the mean (**A**) and the coefficient of variation (**B**) in the rewarded (*ordinate*) and non-rewarded (*abscissa*) trials for a particular direction. The data were obtained from monkey H based on 21 experiments in which the oblique set of targets (20 deg eccentricity) was used

the four directions even in ADR (right column in Fig. 2B), the left-up direction being the fastest (LU) and the right-down direction being the slowest (RD). In IDR, the saccade velocities changed depending on the reward conditions. For example, the saccade velocities for the right-up saccades were higher in the block when this direction was rewarded than when it was non-rewarded (row RU). The same tendency was true for the other directions, which is evident as higher velocities aligned on

Table 1 Reward-contingent modulation of saccade parameters in three monkeys. The means of a parameter value for individual directions were averaged across experiments. The statistical com-

Monkey	Number of experiments (trials)	Velocity (deg/s)			Latency (ms)			Amplitude (deg)		
		IDR(+)	IDR(-)	ADR	IDR(+)	IDR(-)	ADR	IDR(+)	IDR(-)	ADR
H	21 (5025)	548.6*	444.6	510.5***	255.4*	270.3	266.5**	19.9	20.1	20.1**
K	19 (4635)	481.9*	364.6	431.5***	192.3*	227.1	205.3***	19.1*	18.7	19.2***
G	16 (3055)	629.1*	544.1	537.8**	222.0*	231.4	234.1**	19.8	19.7	19.2***

* $P < 0.001$ IDR(+) vs IDR(-), ** $P < 0.001$ ADR vs IDR(+), *** $P < 0.001$ ADR vs IDR(-)

the diagonal line. The saccade velocities for the downward directions were particularly low in the non-rewarded condition, partly because there were two peaks for the downward saccades. The two peaks corresponded to the two regions in the curved trajectory (initially more horizontal and later more vertical), not separate saccades.

Effects of reward outcome on saccade parameters

The differences in saccade parameters between the IDR rewarded condition and the IDR non-rewarded condition are shown graphically in Fig. 3 for monkey H. In the rewarded condition (*ordinate*) compared with the non-rewarded condition (*abscissa*), the saccade velocities for each direction tended to be higher (A) and their variations smaller (B), as all data points in these graphs were above and below the 45-deg line respectively. The saccade latencies for each direction tended to be shorter (A) and their variations tended to be smaller (B). These tendencies for the saccade latency and velocity were also true for the other monkeys. In contrast, the saccade amplitudes were not significantly different between the rewarded and non-rewarded condition in two of the three monkeys (A); however, their variations were smaller (B) and therefore the saccades were more accurate in the rewarded condition.

The differences in two IDR conditions observed in monkey H generally applied to monkey K and G (Table 1). Table 1 further shows that, in ADR compared with the IDR rewarded condition, the saccade velocities were lower and latencies were longer in all monkeys. The comparison between the IDR non-rewarded condition and ADR gave mixed results. The differences between the three reward conditions for the saccade amplitude were inconsistent among the three monkeys.

Evolution of reward effects on saccade parameters

The reward-contingent differences in the saccade parameters were absent at the start of each block of trials when the rewarded direction was unknown to the monkey, and became apparent gradually within the block (Fig. 4A–C). The saccade velocities became lower evidently for the IDR non-rewarded condition and less evidently for ADR, whereas those for the IDR rewarded

comparisons were made using the values for individual experiments. Included are only the data from experiments using a 20-deg target set

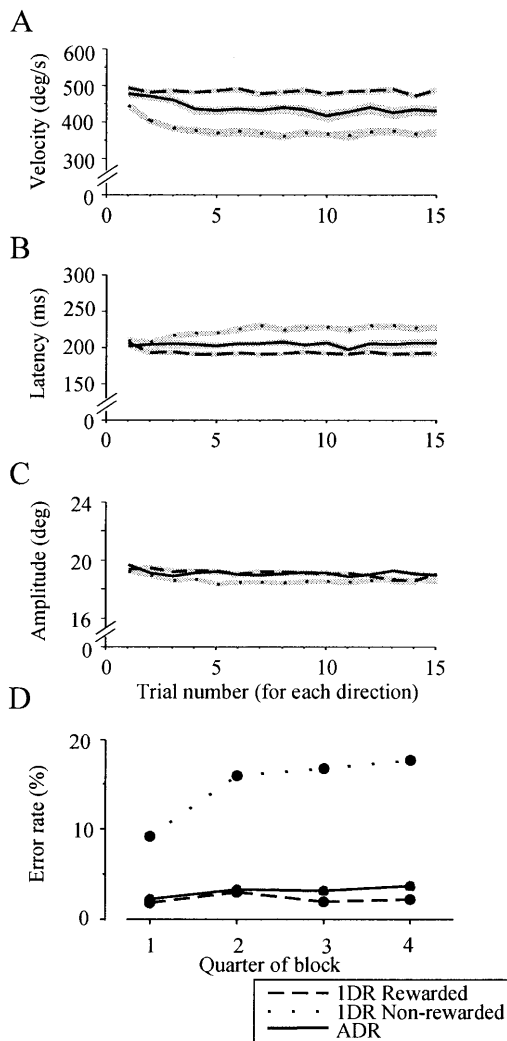


Fig. 4 Within-block changes in saccade parameters: velocity (A), latency (B), amplitude (C), and the ratio of error trials (D). The data are shown separately for three conditions: 1DR-rewarded, 1DR-non-rewarded, and ADR. Shown in A–C are the mean data (the SE range shown by *shade*) plotted against the trial number for each direction (maximum: 15). For the data in D, a block was divided into four quarters, each consisting of 15 successful trials. The data in A–C are based on all experiments using the target set of 20 deg in monkey K. The data in D are based on 5824 error trials among 43,430 trials of 1DR (13.4%) and 321 error trials among 9715 trials of ADR (3.3%) in three monkeys

condition remained high (Fig. 4A). The saccade latencies became longer for the 1DR non-rewarded condition, whereas those for ADR and more so for the 1DR rewarded condition remained short (Fig. 4B). The saccade amplitudes became slightly smaller, especially for the 1DR non-rewarded condition (Fig. 4C).

We also found that the saccade parameters in the non-rewarded trials changed in a shorter time scale depending on how many non-rewarded trials preceded the rewarded trial in question, which will be called “the post-reward order effect” (Fig. 5A–C). The saccade velocities tended to be lowest immediately after a rewarded trial, and became higher gradually with the number of

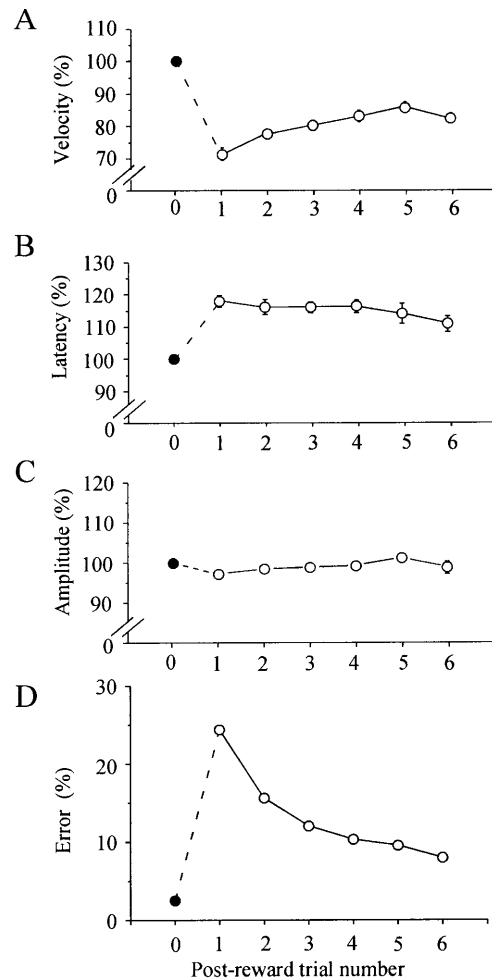


Fig. 5 Post-reward order effects of saccade parameters: velocity (A), latency (B), amplitude (C), and the ratio of error trials (D). The data are plotted against the number of non-rewarded trials after the last rewarded trial; all rewarded trials are shown at 0. The ordinate in A–C indicates the percentage magnitude of each saccade parameter relative to the mean value of the rewarded trials for each cued direction. The data in D include two kinds of errors: fixation-break saccades and incorrect saccades. The data in A–C are based on ten experiments using the target set of 20 deg in monkey K. The data in D are based on all experiments in three monkeys as in Fig. 4D

non-rewarded trials (Fig. 5A). The latencies showed a reverse pattern, though not so clearly as the peak velocities (Fig. 5B). The amplitudes showed little changes (Fig. 5C).

Effects of reward outcome on task performance

The monkeys made more errors in the 1DR non-rewarded condition than in the 1DR rewarded condition; the ratio of errors in ADR was similar to the 1DR rewarded condition (Table 2). Figure 4D shows that the likelihood of errors changed within a block, similarly to saccade parameters (Fig. 4A–C). The ratio of error trials in the 1DR non-rewarded condition increased toward the end

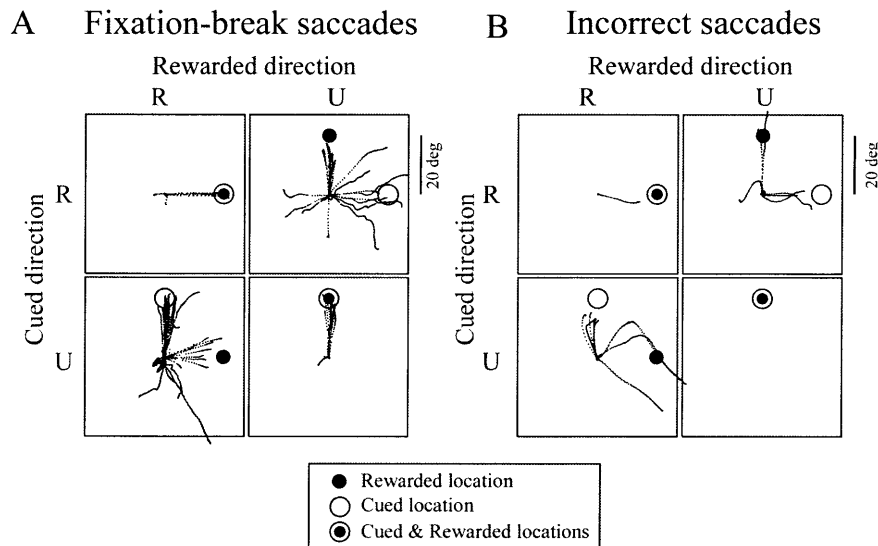


Fig. 6A, B Superimposed saccade trajectories in error trials, shown separately for two kinds of saccade errors. **A** Fixation-break saccades: premature saccades that occurred after cue onset and before fixation point offset. **B** Incorrect saccades: saccades that occurred after fixation point offset but were not judged to be correct. Selected data are shown for the 2×2 combination of the right (*R*) and up (*U*) targets ($n=2$) and the rewarded and non-rewarded conditions ($n=2$). For the non-rewarded conditions (*RU* and *UR*), the cued location is indicated by an open circle, the rewarded location by a filled circle. For the rewarded conditions (*RR* and *UU*), the cued and rewarded location is indicated by a bull's eye mark. Data were based on 30 experiments on monkey H (**A**) and 18 experiments on monkey G (**B**). Note that the erroneous saccades occurred either to the cued locations or to the rewarded locations

of a block, whereas those in the 1DR rewarded condition and ADR trials remained at low levels.

The ratio of errors also showed the post-reward order effect (Fig. 5D), similarly to the saccade parameters (Fig. 5A–C). The error ratio was maximum in the trial following a rewarded trial and decreased gradually as non-rewarded trials were repeated.

There were two types of saccade errors: fixation-break saccades (saccades that occurred after cue onset during the fixation period) and incorrect saccades (saccades that occurred after the fixation period but were directed to the non-target regions). Figure 6A illustrates the trajectories of the fixation-break saccades in 1DR. The data are shown partially, for two cued directions (*R* and *U*) in two blocks (rewarded direction: *R* and *U*).

Trials were rewarded when the cued and rewarded directions were the same, as shown by bull's eye marks (*RR* and *UU*); the other two conditions (*RU* and *UR*) were non-rewarded. In the rewarded condition, the fixation-break saccades were almost always directed to the cue stimulus which indicated the upcoming reward (cued and rewarded direction). In the non-rewarded condition, the fixation-break saccades occurred largely in two groups: one group to the cued direction and the other to the rewarded direction in the block. The latter group of saccades is interesting because there was no stimulus in the rewarded direction to trigger the saccades.

Figure 6B shows the trajectories of the incorrect saccades. In the non-rewarded condition, the incorrect saccades were directed to the cued direction or to the rewarded direction, as for the fixation-break saccades. Interestingly, some of the saccades were curved such that the eyes started moving toward the cued direction and then were re-directed to the rewarded direction.

Discussion

Saccadic eye movement is not stereotyped

It has been shown that the predicted presence of reward facilitates the preceding behavior (Robbins and Everitt 1996; Schultz et al. 1992; Bowman et al. 1996; Shidara et al. 1998; Tremblay and Schultz 2000). Typically, the

Table 2 Reward-contingent modulation of errors in three monkeys. The means of the ratio of error trials in individual experiments were averaged across experiments. The statistical comparisons were made using the values for individual experiments

Monkey	Number of experiments (trials)	Fixation-break saccade (%)			Incorrect saccade (%)		
		1DR(+)	1DR(-)	ADR	1DR(+)	1DR(-)	ADR
H	85 (28,708)	2.8*	11.3	2.8***	0.9*	7.0	1.1***
K	37 (11,918)	0.4*	7.4	2.0	0.4*	4.3	0.5***
G	46 (13,401)	0.9*	9.5	1.1***	0.3*	2.4	1.3***

* $P < 0.001$ 1DR(+) vs 1DR(-), ** $P < 0.001$ ADR vs 1DR(+), *** $P < 0.001$ ADR vs 1DR(-)

manual reaction times tended to be shorter when reward was expected immediately after the trial. However, it was unclear whether individual movements changed their characteristics, such as speed or accuracy. Our results clearly showed that saccade performance changed depending on the presence or absence of reward after the saccade. In the rewarded trials, the number of errors was smaller, the peak velocities were higher, the latencies were shorter, the trajectories were more straight, and the goal positions were less variable. On the other hand, we found no systematic difference in saccade amplitudes. The last point is important because saccade parameters are correlated with each other. According to a traditional view, the peak velocity or the duration is a unique function of the amplitude in a species-specific manner. However, recent studies have shown that these functions vary with different types of saccades: for example, for a particular saccade amplitude, the peak velocity is lower for memory-guided saccades than for visually guided saccades (Hikosaka and Wurtz 1985; Smit et al. 1987; Takikawa et al. 1998). Our results now demonstrate that the functions vary even among memory-guided saccades.

Speed-accuracy covariation, not trade-off

We found that saccades were more variable in the non-rewarded than rewarded trials of IDR. This was true for all saccade parameters examined, including the amplitude and the final position. The results are interesting in relation to the well-known theory of “speed-accuracy trade-off” (Fitts 1954; Harris and Wolpert 1998). According to the theory, if a movement is made early or quickly, it will be inaccurate; if the movement is made slowly, it will be accurate.

Our results do not follow the speed-accuracy trade-off theory: the saccades in the rewarded trials were earlier, quicker, and more accurate. The speed-accuracy trade-off theory was based on the experiments in which subjects (usually human subjects) were, supposedly, fully motivated and fully alert. In contrast, in our experiments, especially IDR, motivation or alertness was apparently not stable across trials. When subjects are motivated and alert, their saccades would be early (short latency), quick (higher velocity), and accurate (less variation).

Gradual changes in saccade performance

At the beginning of IDR block, it was unknown which direction was to be rewarded, so that the saccade parameters were undifferentiated. The reward-predictive changes in saccade performance became clear gradually within the IDR block (which we called the “within-block change”). The saccade velocity, for example, remained high for the rewarded condition, while it decreased continuously in the non-rewarded condition.

These changes in saccade parameters were remarkably similar to the within-block changes in caudate neu-

ronal activities (Kawagoe et al. 1998). For most caudate neurons, the visual responses to the reward-indicating cue stimulus became stronger promptly and reached a plateau level whereas the responses to the non-reward-indicating cue became weaker continuously. These results are consistent with the idea that the caudate is involved in the reward-contingent modulation of saccades.

Another type of change in saccade parameters occurred after each rewarded trial (which we called the “post-reward order effect”). The performance was worst (e.g., velocity lowest) in the trial immediately after a rewarded one, but became better as the non-rewarded trials were repeated. There are at least three ways to interpret the data. First, the monkey might be more sated and therefore less motivated after the reward acquisition, as suggested by the decrease in saccade velocity. Second, the monkey may be least motivated in the trial immediately after a rewarded one because the probability that the next trial was rewarded was lowest (because of the pseudo-random schedule; see “Materials and methods”) (Shidara et al. 1998). Third, the monkey may have the memory, either explicit or implicit, of the association between the saccade and reward in the preceding trial so that attention was partly directed to the rewarded direction immediately after a rewarded trial (Maljkovic and Nakayama 1996).

Conflict between cognitive and motivational demands

An interesting aspect of the IDR task was that it created a conflict between cognitive and motivational demands in the non-rewarded trial. For example, if the cue came on in the up direction in a right-rewarded IDR block, the cognitive demand would be “go up” while the motivational demand would be “go right.” The observation of “error” trials indeed supports the dual process hypothesis. The monkeys occasionally made errors by making a premature saccade during the fixation period (Fig. 6A) or a wrong saccade after the end of the fixation period (Fig. 6B). Such erroneous saccades occurred frequently in the non-rewarded trials of IDR and, importantly, most of them were directed either to the instructed location (based on the cognitive demand) or to the rewarded direction (based on the motivational demand) (Fig. 6). Such a saccade often started toward the instructed location and then curved toward the rewarded location, or vice versa. Even a correct saccade could be deviated initially toward the rewarded location.

It has recently been reported that a curved saccade can be induced by attentional or sensory bias (Sheliga et al. 1995). In a typical paradigm in which two visual targets were presented simultaneously or with some temporal asynchrony, the induced saccade could be curved between the two target directions (McPeck and Keller 2000; Port and Wurtz 2000). A feasible mechanism for this phenomenon is that two sensorimotor processes go on simultaneously, say, in the superior colliculus.

We speculate that a similar explanation applies to our curved saccades. Unlike the previous studies using two

similar sensory inputs, our task is based on two different kinds of information, one sensory (or externally triggered) and the other motivational (or internally triggered). More specifically, we hypothesize that the cognitive demand and the motivational demand are processed in two separate neural mechanisms and then are integrated in some areas to produce an action. A major goal of our research project is to identify the brain areas contributing to the dual mechanisms and to characterize the neural mechanisms underlying the possible integration or competition of the cognitive and motivational demands.

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References

- Barto AG (1994) Reinforcement learning control. *Curr Opin Neurobiol* 4:888–893
- Bowman EM, Aigner TG, Richmond BJ (1996) Neural signals in the monkey ventral striatum related to motivation for juice and cocaine rewards. *J Neurophysiol* 75:1061–1073
- Fitts PM (1954) The information capacity of the human motor system in controlling the amplitude of movements. *J Exp Psychol* 47:381–391
- Harris CM, Wolpert DM (1998) Signal-dependent noise determines motor planning. *Nature* 394:780–784
- Hikosaka O, Wurtz RH (1983) Visual and oculomotor functions of monkey substantia nigra pars reticulata. III. Memory-contingent visual and saccade responses. *J Neurophysiol* 49:1268–1284
- Hikosaka O, Wurtz RH (1985) Modification of saccadic eye movements by GABA-related substances. I. Effect of muscimol and bicuculline in the monkey superior colliculus. *J Neurophysiol* 53:266–291
- Hikosaka O, Sakamoto M, Usui S (1989a) Functional properties of monkey caudate neurons. I. Activities related to saccadic eye movements. *J Neurophysiol* 61:780–798
- Hikosaka O, Sakamoto M, Usui S (1989b) Functional properties of monkey caudate neurons. II. Visual and auditory responses. *J Neurophysiol* 61:799–813
- Hikosaka O, Sakamoto M, Usui S (1989c) Functional properties of monkey caudate neurons. III. Activities related to expectation of target and reward. *J Neurophysiol* 61:814–832
- Hikosaka O, Takikawa Y, Kawagoe R (2000) Role of the basal ganglia in the control of purposive saccadic eye movements. *Physiol Rev* 80:953–978
- Houk JC, Adams JL, Barto A (1995) A model of how the basal ganglia generate and use neural signals that predict reinforcement. In: Houk JC, Davis JL, Beiser DG (eds) *Models of information processing in the basal ganglia*. MIT Press, Cambridge, MA, pp 249–270
- Kawagoe R, Takikawa Y, Hikosaka O (1998) Expectation of reward modulates cognitive signals in the basal ganglia. *Nat Neurosci* 1:411–416
- Konorski J (1967) *Integrative activity of the brain*. University of Chicago Press, Chicago
- Maljkovic V, Nakayama K (1996) Priming of pop-out: II. The role of position. *Percept Psychophys* 58:977–991
- Matsumura M, Kojima J, Gardiner TW, Hikosaka O (1992) Visual and oculomotor functions of monkey subthalamic nucleus. *J Neurophysiol* 67:1615–1632
- McPeck RM, Keller EL (2000) Competition between saccade goals in the superior colliculus or frontal eye fields results in curved saccades. *Soc Neurosci Abstr* 26:291 (109.1)
- Parthasarathy HB, Schall JD, Graybiel AM (1992) Distributed but convergent ordering of corticostriatal projections: analysis of the frontal eye field and the supplementary eye field in the macaque monkey. *J Neurosci* 12:4468–4488
- Port NL, Wurtz RH (2000) Two electrode recordings in monkey superior colliculus during curved saccades. *Soc Neurosci Abstr* 26:291 (109.2)
- Robbins TW, Everitt BJ (1996) Neurobehavioural mechanisms of reward and motivation. *Curr Opin Neurobiol* 6:228–236
- Robinson DA (1963) A method of measuring eye movement using a scleral search coil in a magnetic field. *IEEE Trans Biomed Eng* 10:137–145
- Schultz W (1998) Predictive reward signal of dopamine neurons. *J Neurophysiol* 80:1–27
- Schultz W, Apicella P, Scarnati E, Ljungberg T (1992) Neuronal activity in monkey ventral striatum related to the expectation of reward. *J Neurosci* 12:4595–4610
- Sheliga BM, Riggio L, Craighero L, Rizzolatti G (1995) Spatial attention-determined modifications in saccade trajectories. *Neuroreport* 6:585–588
- Shidara M, Aigner TG, Richmond BJ (1998) Neuronal signals in the monkey ventral striatum related to progress through a predictable series of trials. *J Neurosci* 18:2613–2625
- Shook BL, Schlag-Rey M, Schlag J (1991) Primate supplementary eye field. II. Comparative aspects of connections with the thalamus, corpus striatum, and related forebrain nuclei. *J Comp Neurol* 307:562–583
- Smit AC, Van Gisbergen JAM, Cools AR (1987) A parametric analysis of human saccades in different experimental paradigms. *Vision Res* 27:1745–1762
- Smith AD, Bolam JP (1990) The neural network of the basal ganglia as revealed by the study of synaptic connections of identified neurones. *Trends Neurosci* 13:259–265
- Stanton GB, Goldberg ME, Bruce CJ (1988) Frontal eye field efferents in the macaque monkey: I. Subcortical pathways and topography of striatal and thalamic terminal fields. *J Comp Neurol* 271:473–492
- Takikawa Y, Kawagoe R, Miyashita N, Hikosaka O (1998) Presaccadic omnidirectional burst activity in the basal interstitial nucleus in the monkey cerebellum. *Exp Brain Res* 121:442–450
- Thorndike (1911) *Animal intelligence*. Macmillan, New York
- Tremblay L, Schultz W (2000) Reward-related neuronal activity during go-nogo task performance in primate orbitofrontal cortex. *J Neurophysiol* 83:1864–1876