CELLULAR NEUROSCIENCE

Indirect pathway from caudate tail mediates rejection of bad objects in periphery

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The essential everyday task of making appropriate choices is a process controlled mainly by the basal ganglia. To this end, subjects need not only to find "good" objects in their environment but also to reject "bad" objects. To reveal this rejection mechanism, we created a sequential saccade choice task for monkeys and studied the role of the indirect pathway from the CDt (tail of the caudate nucleus) mediated by cvGPe (caudal-ventral globus pallidus externus). Neurons in cvGPe were typically inhibited by the appearance of bad objects; however, this inhibition was reduced on trials when the monkeys made undesired saccades to the bad objects. Moreover, disrupting the inhibitory influence of CDt on cvGPe by local injection of bicuculline ($GABA_A$ receptor antagonist) impaired the monkeys' ability to suppress saccades to bad objects. Thus, the indirect pathway mediates the rejection of bad choices, a crucial component of goal-directed behavior.

INTRODUCTION

Experts as chess masters can rapidly and automatically perceive visual information and make decisions based on skilled memory (*1*, *2*). Previous studies suggest that the basal ganglia are involved in these skills in humans and monkeys (*3*–*6*), but their neuronal mechanisms are unclear. Basal ganglia dysfunction causes distinct cognitive and movement disorders (*7*, *8*), and various models have been proposed to explain the mechanism of these impairments (*9*–*17*).

A major theme of this work considers whether the two main basal ganglia circuits, namely, the direct and indirect pathways, function in a competitive or cooperative manner. Previous studies suggest that the direct pathway facilitates action while the indirect pathway suppresses action (*18*, *19*), consistent with a competitive interaction. However, more recent studies suggest that these pathways work in a complementary manner for controlling actions (*20*–*23*). The posterior basal ganglia circuitry in monkeys has several advantageous features for experimentally probing this apparent discrepancy in the literature, which we took advantage of in the present study.

The posterior basal ganglia circuits originate from the CDt (tail of the caudate nucleus) and send signals to the superior colliculus (SC) either directly through the caudal-dorsal-lateral substantia nigra pars reticulata (cdlSNr) or indirectly via the cvGPe (caudal-ventral globus pallidus externus) (*24*–*26*). All areas within this circuit have two key features: (i) sensitivity to long-term stable value of objects and (ii) peripheral receptive fields. Many neurons within CDt, cvGPe, cdlSNr, and SC develop long-lasting value sensitivity to large numbers of objects associated with good versus bad outcomes and respond to peripheral (mostly contralateral) visual stimuli regardless of eccentricity (*24*, *25*, *27*–*29*). However, the role of these neurons in active choice is still unclear, as these properties were mainly revealed under passive viewing conditions. Here, we assessed the specific contributions of the direct and indirect pathways in the circuits arising from CDt in the context of an active choice task requiring value-based action.

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RESULTS

We first examined neurons in cvGPe and cdlSNr, which previous studies showed coding for the value of objects (*24*, *25*), using an object-reward association learning task (Fig. 1A) and a passive viewing task (Fig. 1B). Most neurons in cvGPe and cdlSNr responded differently to good and bad objects (examples shown in Fig. 1, C and D), consistent with previous studies. Bad objects inhibited cvGPe neurons (Fig. 1C) but excited cdlSNr neurons (Fig. 1D); good objects caused opposite responses. This pattern of opposite sign of responses in cvGPe and cdlSNr (especially to bad objects) can be explained by sequential inhibitory connections (Fig. 1E): (i) from CDt to cvGPe, (ii) from cvGPe to cdlSNr, and (iii) from cdlSNr to SC (i.e., indirect pathway). These results suggest that saccades are suppressed by the indirect pathway (Fig. 1E).

We then tested the above hypothesis by using a new procedure called the "sequential saccade choice task" (Fig. 2A and movies S1 and S2). In each block of trials, eight fractal objects (four good and four bad) appeared in random sequence at peripheral positions, until the subject chose one object. In the example trial shown (Fig. 2A and movie S1), the subject first rejected two bad objects (first object: no saccade, second object: saccade to object, immediately followed by another saccade back to the center) and then accepted a good object (saccade to object, followed by maintained gaze), which led to a reward. On trials when the subject accepted a bad object by maintaining gaze, no reward was given. Both subjects experienced multiple sets of objects used in this task (four sets for ZB and four sets for SP). In the first learning session (when all objects were new), the subject made a saccade to most good as well as bad objects (Fig. 2B, left). Across the subsequent sessions, saccade rate to bad objects gradually decreased (i.e., rejection of bad objects increased) (Fig. 2B). Bad objects were also rejected, sometimes by a returning saccade (e.g., response to the second object in Fig. 2A and movie S1). Acceptance of good objects remained nearly 100% (red curves in Fig. 2B). The good-bad discrimination was completely maintained more than 1 month after the final learning session (Fig. 2B, right).

After long-term learning (10 sessions), we recorded the activity of cvGPe and cdlSNr neurons. In response to bad objects, cvGPe neurons were significantly inhibited (Fig. 2C), whereas cdlSNr neurons were significantly excited (Fig. 2D). Similar results were obtained

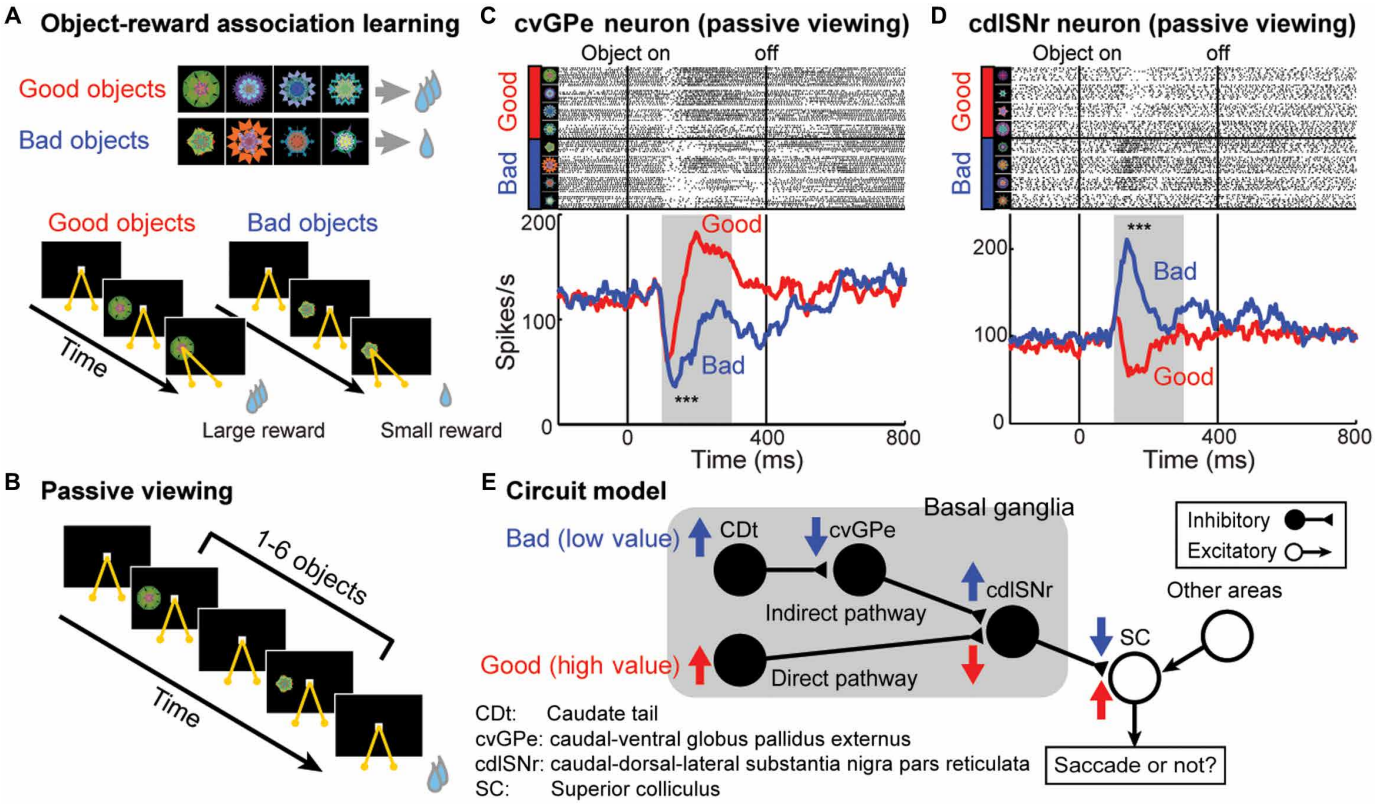

Fig. 1. Value-coding circuits in the basal ganglia. (**A**) Object-reward association learning task. (**B**) Passive viewing task. (**C**) Representative cvGPe neuron inhibited by bad objects during passive viewing task ($n = 33$ trials; $t_{32} = 5.17$; ***$P < 0.001$, paired t test). Its activity, which is shown by raster plots (above) and spike density functions (below), is aligned on object onset and offset. Responses are shown separately for all eight objects (above) and as the averaged responses to good and bad objects (below). (**D**) Representative cdlSNr neuron excited by bad objects ($n = 34$ trials; $t_{33} = -8.38$; ***$P < 0.001$, paired t test). (**E**) Neuronal circuit model for value-based saccades. Value signals for bad objects (blue) are sent through the indirect pathway (CDt-cvGPe-cdlSNr), while value signals for good objects (red) are sent through the direct pathway (CDt-cdlSNr), both within the basal ganglia (gray region). Upward and downward arrows indicate excitation and inhibition, respectively.

during the passive viewing task (Fig. 1, C and D). Notably, the inhibition of cvGPe neurons by bad object was stronger when no saccade was made to the bad object (blue) than when a saccade was made (cyan) (Fig. 2C). Correspondingly, cdlSNr neurons were more strongly excited when no saccade was made (blue) than when a saccade was made (cyan) (Fig. 2D). The analysis window was set at 100 to 200 ms after object onset, because more than 80% of all trials showed saccade latency within 100 to 200 ms after object onset in both subjects (fig. S1A, ZB: 83.1%; fig. S1B, SP: 88.5%). Equivalent data are shown in more detailed (for example, eye trajectory) (fig. S2A) example neuronal data in cvGPe (fig. S2B) and cdlSNr (fig. S2C). These results suggest that the inhibition of cvGPe neurons by a bad object leads to excitation of cdlSNr neurons through disinhibition, which then suppresses the saccade to the bad object if the activity of cdlSNr neurons reaches a threshold (blue in Fig. 2E).

The results so far suggest that the cvGPe-cdlSNr pathway can suppress saccades based on object values. To test this hypothesis, we experimentally manipulated the cvGPe-cdlSNr pathway by injecting bicuculline [γ-aminobutyric acid type A ($GABA_A$) receptor antagonist] locally into cvGPe (Fig. 3, A and B). We chose bicuculline because cvGPe neurons receive massive GABAergic inputs mainly from CDt (Fig. 1E) (*26*). We also recorded the activity of single cdlSNr neuron continuously before and after the injection (Fig. 3A), while the subject continued to perform the sequential saccade choice task (Fig. 2A). We found that bicuculline injection changed both saccade behavior (Fig. 3C and movie S3) and cdlSNr neuronal activity (Fig. 3D) during the sequential saccade choice task. The probability of saccades to bad objects increased significantly from about 25% to almost 95% (blue bars in Fig. 3C). That is, the subjects were no longer able to suppress saccades to bad objects when GABAergic inputs to cvGPe neurons were blocked. This occurred for bad objects located only contralateral to the bicuculline injection side (fig. S3A). Injection of saline in cvGPe led to no notable change (fig. S3B and movie S4). Moreover, the excitatory response of the cdlSNr neuron to bad objects decreased significantly (Fig. 3D, also see Fig. 2D as control data). These data support the schematic model we proposed (Fig. 3E compared with Fig. 2E). In the current experiment, we have shown that the experimental manipulation of neuronal activity (by bicuculline) changed saccade behavior, as the model predicts. According to the model (Fig. 3E), bicuculline suppressed the inhibitory response of cvGPe neurons to bad objects, which led to the suppression of the excitatory response of cdlSNr neurons (blue dotted line shown in Fig. 3D). The subject was then unable to suppress saccades to bad objects because the inhibition of SC saccadic neurons by cdlSNr neurons was too weak (i.e., below threshold). Notably, the probability of saccades to good objects remained 100% (red bars in Fig. 3C), and the inhibition

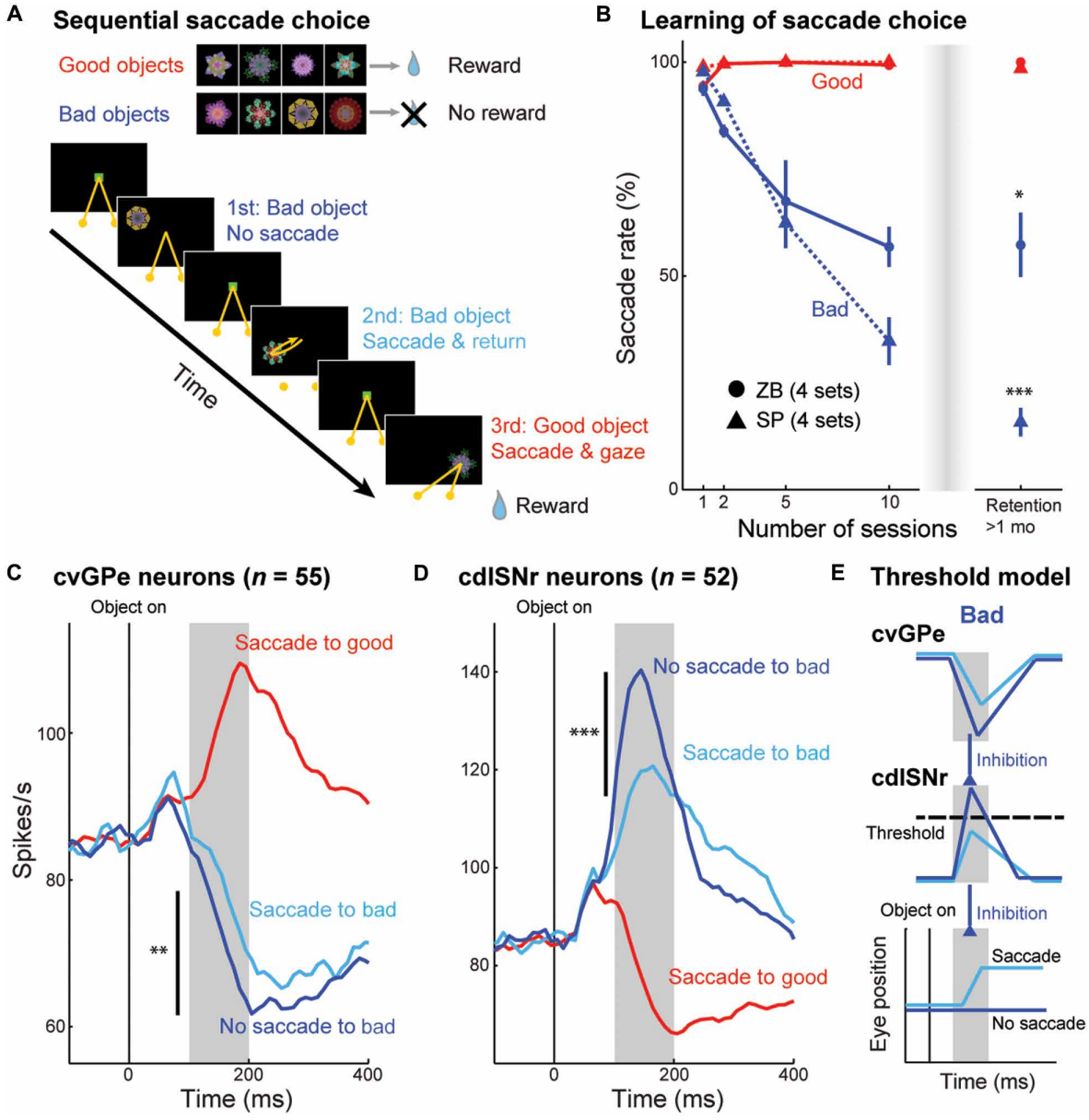

Fig. 2. Neuronal activity for rejecting bad object. (**A**) Sequential saccade choice task. (**B**) Learning of saccade choice for each object set, averaged across four sets (32 objects) in each monkey (ZB and SP). Red and blue symbols indicate averaged saccade rate (%) to good and bad objects, respectively, across learning sessions. Error bars indicate SEM. The same task was also tested long after the last learning was completed (retention, >1 month) (ZB: $t_3 = -3.87$; $^*P = 0.030$, paired *t* test; SP: $t_3 = -19.4$; $^{***}P < 0.001$, paired *t* test). (**C**) Averaged activity of cvGPe neurons ($n = 55$ neurons) in response to good (red) and bad objects (cyan and blue). The inhibition by bad objects ($t_{54} = 3.77$; $^{***}P < 0.001$, paired *t* test) was stronger when no saccade occurred (blue) than when saccades occurred (cyan) (gray period; $t_{54} = -2.94$; $^{**}P = 0.0047$, paired *t* test). (**D**) Averaged activity of cdlSNr neurons ($n = 52$ neurons), shown in the same format. The excitation by bad objects ($t_{51} = -7.12$; $^{***}P < 0.001$, paired *t* test) was stronger when no saccade occurred (blue) than when saccade occurred (cyan) (gray period; $t_{51} = 4.65$; $^{***}P < 0.001$, paired *t* test). (**E**) Hypothetical role of cvGPe-cdlSNr pathway to control responses to bad objects. Blue and cyan indicate no saccade and saccade conditions, respectively. Black dashed line indicates a threshold level for suppressing a saccade.

of cdlSNr neurons in response to good objects did not significantly change after the bicuculline injection (red dotted line in Fig. 3D).

We also examined the effect of bicuculline in cvGPe on the choice of objects using a simultaneous saccade choice task (Fig. 4A), instead of the sequential saccade choice task (Fig. 2A). In the simultaneous saccade choice task, a pair of good and bad objects was presented in either the contralateral or ipsilateral hemifield randomly. During each saccade, the objects were replaced by white dots. The outcome (i.e., large or small reward) was based on the choice (Fig. 4A, below). The choice rate of bad objects significantly increased after the bicuculline injection (Fig. 4B). That is, the subject's choice of good objects decreased significantly. Injection of saline in cvGPe led to no notable change (fig. S4B). These data together indicate that the cvGPe-cdlSNr pathway suppresses saccades to bad objects, which enables the subject to choose good objects, whether they appear sequentially or simultaneously.

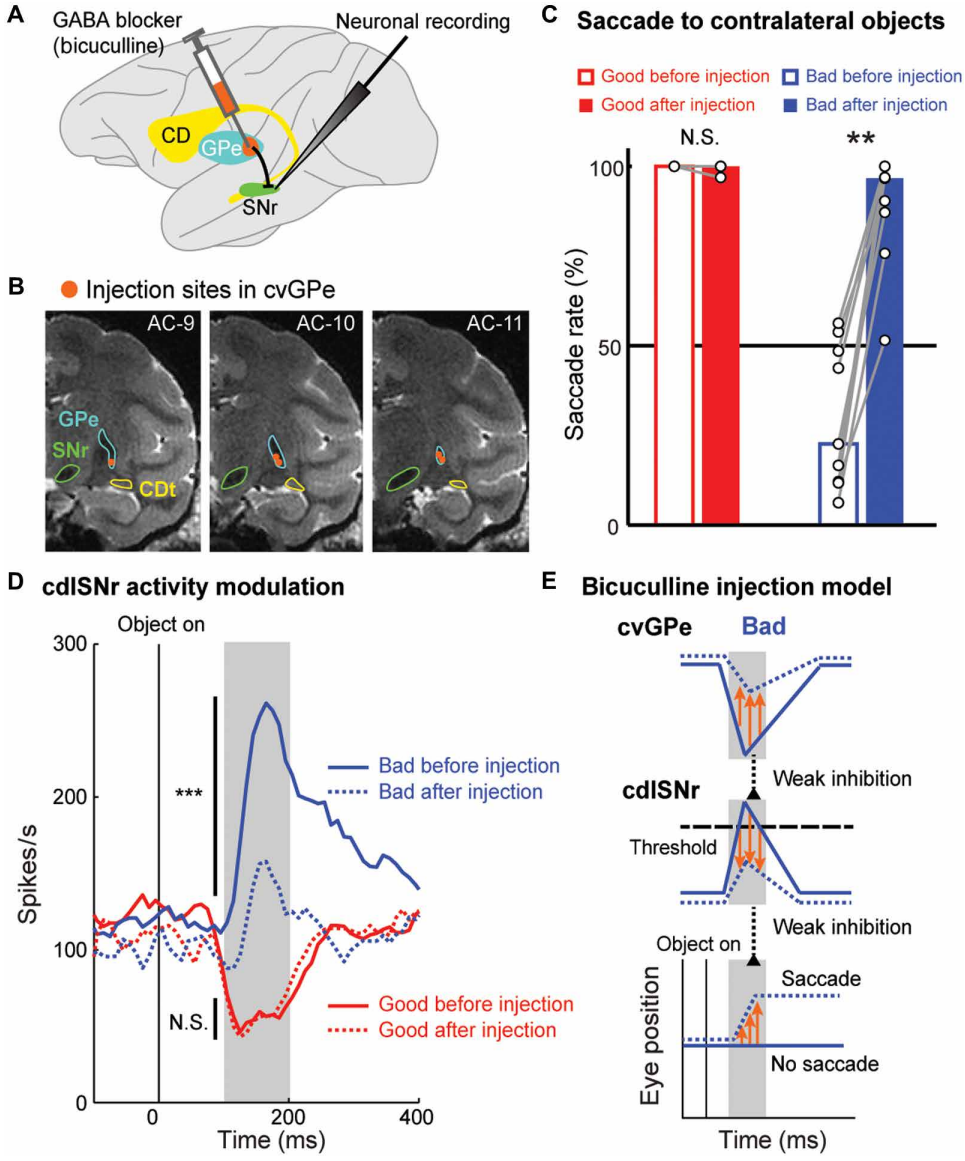

Fig. 3. Blocking of the indirect pathway impairs rejection of bad object during sequential saccade choice task. (**A**) Local injection of GABA blocker (bicuculline) in cvGPe, while neuronal activity in cdlSNr was recorded. (**B**) Magnetic resonance images showing five injection sites (orange) in cvGPe of monkey ZB that were located in three coronal sections (9, 10, and 11 mm posterior to the anterior commissure). (**C**) Comparison of saccade rates between before and after the bicuculline injection in response to contralateral good objects (red; $n = 9$ sessions; $P = 1.00$, Wilcoxon signed-rank test) and bad objects (blue; $n = 9$ sessions; $^{**}P = 0.0039$, Wilcoxon signed-rank test). Each bar indicates median of saccade rate to contralateral objects. Each pair of connected dots depicts a single injection session. N.S., not significant. (**D**) Comparison of one cdlSNr neuron's activity between before and after the bicuculline injection in response to good objects (red; $n = 64$ trials; $P = 0.99$, Mann-Whitney U test) and bad objects (blue; $n = 64$ trials; $^{***}P < 0.001$, Mann-Whitney U test). (**E**) Schematic model for explaining the neuronal and behavioral effects (orange arrows) of GABA blocker in cvGPe. Blue solid and dotted lines indicate responses to bad objects before and after the bicuculline injection.

DISCUSSION

These results are in harmony with the "competitive" scheme in which the direct pathway facilitates action (Go) and the indirect pathway suppresses action (No-go) (*18*, *19*), yet also consonant with evidence supporting the "complementary" scheme that actions activate both direct and indirect pathways (*20*–*23*). The logic of this reconciliatory view follows from the fact that, when one action needs to be chosen (by the direct pathway), alternative actions must necessarily be suppressed (by the indirect pathway) at the same time. By examining basal ganglia function within the framework of value-based choice and action, our findings support the model of the indirect pathway suppressing unnecessary competing actions (*13*, *14*, *16*). This "rejection" mechanism is important for visual search skill in humans and other animals (*30*, *31*). A recent study demonstrated that humans could quickly find a target object in visual search task when they were instructed to ignore the specific feature of a distractor (*30*). The current study sheds light on the crucial role of the indirect pathway for rapidly finding a good object by ignoring bad objects (distractors) in periphery.

Recent studies revealed that the activation of the indirect pathway causes switching of behavior (*32*, *33*). Because ongoing behavior

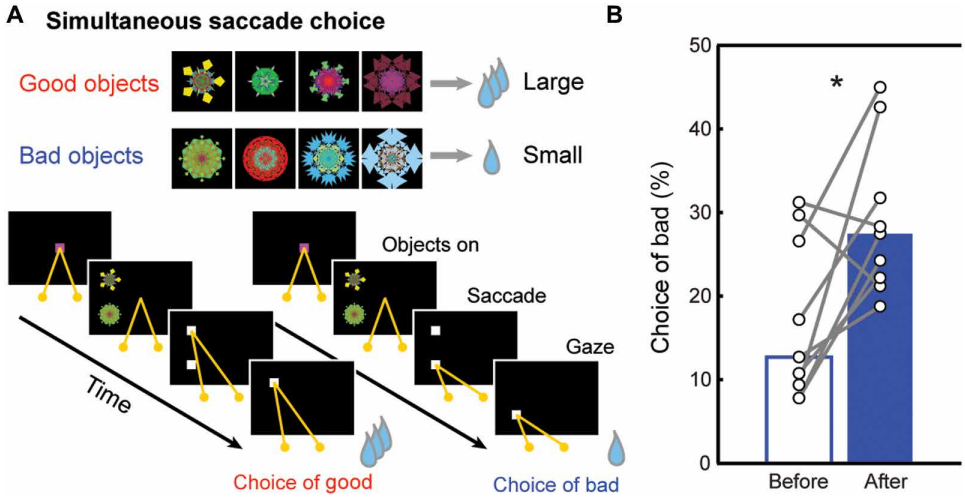

Fig. 4. Blocking of the indirect pathway impairs choice of good objects. (**A**) Simultaneous saccade choice task. (**B**) Comparison of bad object choice before versus after the bicuculline injection in cvGPe ($n = 9$ sessions; $^*P = 0.027$, Wilcoxon signed-rank test). Each bar indicates median of choice rate. Each pair of connected dots depicts a single injection session.

tends to be executed automatically and quickly, a critical aspect of switching is to halt ongoing behavior in a timely manner (*34*). The need for such a halting mechanism is common to both the sequential choice process we studied here (see Fig. 2A) and to the flexible reversal tasks used in previous rodent studies (*32*, *33*). However, evidence from primate studies revealed a dissociation between flexible behavior under rapidly changing conditions versus consistent behavior under long-term stable conditions, mediated by the caudate head and tail circuits, respectively (*35*). Thus, the interplay between the direct and indirect pathways is superimposed on the orthogonal organization of the basal ganglia along the rostrocaudal axis governing flexible versus stable behavior. According to our current hypothesis, many parallel circuits (i.e., caudal and rostral basal ganglia circuits and cortical areas) make decisions in different conditions or contexts (*35*). SC finally receives these variable decision signals for making an appropriate final action (saccade) in many conditions (*36*, *37*). Further study is necessary to test this hypothesis.

MATERIALS AND METHODS

Subjects

Two adult male rhesus monkeys (*Macaca mulatta*, monkeys ZB and SP) were used for behavioral experiments, neuronal recordings, and neuropharmacological experiments. All animal care and experimental procedures were approved by the National Eye Institute Animal Care and Use Committee and complied with the Public Health Service Policy on the Humane Care and Use of Laboratory Animals.

Surgeries

A plastic head holder, plastic recording chambers, and scleral search coils were implanted under anesthesia with ketamine, diazepam, and isoflurane gas throughout these surgeries. After 6 weeks of recovery period, we started training and recording. We routinely cleaned the implants by flushing with hydrogen peroxide or a mixture of betadine and saline solution at least three times a week for the health and well-being of subjects.

Behavioral procedures

Object-reward association learning task (Fig. 1A)

This task was to let the subject learn the association of object with reward. This task procedure followed previous studies from the laboratory (*24*, *25*, *28*). In each trial, one object (out of eight objects) was presented, to which the subject made a saccade. This saccade was followed by a large or small reward, depending on the object value (good or bad). The subject learned the values of many objects in this manner (a total of 80 in ZB and a total of 48 in SP).

Passive viewing task (Fig. 1B)

This task was used to investigate whether neurons encoded the values of individual objects more than 1 day after the object-reward association learning task. This task procedure also followed the previous studies (*24*, *25*, *28*). In each trial, several learned objects (one to six objects) were chosen pseudo-randomly and presented sequentially at a peripheral position (i.e., neuron's receptive field) while the subject was fixating at the center. The trial ended with a reward, which, however, was not congruent with the presented objects. This task focused on the effect of object-value learning on neuronal responses before any behavioral response occurred.

Sequential saccade choice task (Fig. 2A and movies S1 and S2)

This task was used to investigate both neuronal and behavioral responses during and after object-value learning. A set of eight objects were used in one block of 128 trials: four objects were associated with a large reward (good objects), while the other four objects were associated with no reward (bad objects) (Fig. 2A). In each trial, these objects were presented in a random sequence until the subject chose one (see below in detail). Each object appeared pseudo-randomly at one of four positions (up-right, down-right, up-left, and down-left) at 15° eccentricity from the center. After the subject fixated at a center green square for 700 ms, the fixation cue disappeared, and one object appeared. If the subject did not make a saccade to the object within 400 ms (i.e., made no choice), another object appeared after the same fixating period (see the first object in Fig. 2A). No choice trials were also deemed to occur if

the monkey made a saccade to the presented object and then quickly (<400 ms) returned gaze to the center of the screen (see the second object in Fig. 2A). Conversely, a choice occurred if the subject made a saccade to the object within 400 ms and then gazed at it for 400 ms (i.e., choice), and the subjects received the outcome (reward or no reward) depending on the chosen object (good or bad) (see the third object in Fig. 2A). The next trial started after an intertrial interval of 1000 to 2000 ms. Overall, the subject learned to consistently reject bad objects before choosing a good object to get the reward.

Simultaneous saccade choice task (Fig. 4A)

This task was used to investigate whether the pharmacological manipulation modulated the learned choices between good and bad objects that appeared simultaneously at different positions. The subject learned several object sets (ZB: three sets and SP: two sets) under the object-reward association learning task (Fig. 4A, top) before testing on the simultaneous saccade choice task (Fig. 4A, bottom). Each trial started with gaze fixation (700 ms) at a center magenta square. Then, the fixation cue disappeared and two randomly chosen objects (one good object and one bad object) appeared simultaneously. Their positions (15° from the center) were chosen pseudo-randomly from four combinations (up-left and down-left, up-right and down-right, up-left and up-right, and down-left and down-right). When a saccade occurred to any of the two objects, these objects turned to white squares immediately (Fig. 4A, bottom). After gazing at either square for 600 ms, a large or small reward was delivered depending on the subject's choice (good or bad object). In each block of trials, one set of eight learned objects was used.

Neuronal recordings

Neuronal activity was recorded from two subjects (ZB and SP) in the cvGPe and the cdlSNr: 55 cvGPe neurons (ZB: 29 and SP: 26) and 52 cdlSNr neurons (ZB: 34 and SP: 18). The recording sites were determined with a 1-mm spacing grid system, and magnetic resonance images (4.7 T, Bruker) were obtained along the direction of the chamber. Single-unit recording was performed using epoxy-coated tungsten microelectrodes (FHC). The electrodes were inserted into the brain through a stainless steel guide tube and advanced by an oil-driven micromanipulator (MO-97A, Narishige). The electric signals from the electrode were amplified and bandpass-filtered (0.2 to 10 kHz; BAK). All behavioral tasks and recordings were controlled by custom-written visual C++ based software (Blip; www.robilis.com/blip/).

Neuropharmacological manipulations

To temporarily block GABAergic inputs to cvGPe neurons, we locally injected bicuculline ($GABA_A$ receptor antagonist) in cvGPe. The injection was done in the right cvGPe of each subject. We first recorded the neuronal activity encoding stable value to confirm that the site was localized within cvGPe (*25*) and then injected bicuculline. For this purpose, we used a custom-made injectrode consisting of a microelectrode (FHC) and a silica tube (Polymicro Technologies). Bicuculline methiodide (14343; Sigma-Aldrich) was dissolved in physiological saline. We injected 1 μl of bicuculline (1 μg/μl) in each site at a speed of 0.2 μl/min using a manual pump. The subjects performed behavioral tasks starting 5 min after the injection. We studied the behavioral effect of bicuculline using the sequential saccade choice task (Fig. 2A) and the simultaneous saccade choice task (Fig. 4A). Main analyses were based on the comparison of saccades to (and from) the presented object between the pre-injection sessions and the post-injection sessions (within 1 hour after the injection). We sometimes studied the neuronal effect of bicuculline in cdlSNr (that is, the target of cvGPe; Fig. 3, A and D). For control sessions, we injected 1 μl of physiological saline in each site in cvGPe at a speed of 0.2 μl/min. In total, nine sessions for bicuculline injections (ZB: five and SP: four) and eight sessions for saline injections (ZB: five and SP: three) were conducted.

Behavioral analysis

Saccade latency

Eye position was sampled at 1 kHz using a scleral search coil. Saccade latency was determined using software custom-written with MATLAB (MathWorks). The saccade latency was measured from the object onset to the saccade onset.

Sequential saccade choice task

The main question of this task was whether a saccade followed by gaze occurred in response to the onset of an object. Saccade detection was triggered when the eye position left a central window (10° square) within 400 ms of object onset, whereas a no-saccade was registered when the eye position stayed within the central window. A saccade response was judged as the acceptance of the object if the eye position stayed within the peripheral window (13° square around the object) for 400 ms, which was followed by an outcome (reward or no reward). Otherwise, the behavior was judged as the rejection of the object, as explained in the "Behavioral procedures" section. The saccade rate (%) was calculated by (the number of trials in saccade to object)/(the total number of trials) × 100 (Figs. 2B and 3C and fig. S3).

Simultaneous saccade choice task

This task examined which object was chosen by the first saccade after two objects (one good and one bad) appeared simultaneously at different positions. The choice rate of bad object (%) was calculated by (the number of trials in first saccade to bad object)/(the total number of trials) × 100 (Fig. 4B and fig. S4).

Statistical analysis

Passive viewing task

To investigate whether cvGPe and cdlSNr neurons responded to bad objects, we applied a paired *t* test (two-tailed) to neuronal spike counts. These responses to bad objects (from 100 to 300 ms after bad object onset) were compared with baseline activities (from 200 to 0 ms before bad object onset) in the same trials (Fig. 1, C and D).

Sequential saccade choice task

To investigate the difference in behavioral (saccade) response to good and bad objects, we used a Mann-Whitney *U* test (two-tailed) for saccade latency (fig. S1) and for saccade choice more than a month after the last session of the task (Fig. 2B). To investigate the neuronal data, we used a paired *t* test (two-tailed) (Fig. 2, C and D). A total of 55 cvGPe neurons and 52 cdlSNr neurons were used for this analysis, respectively. To investigate whether these cvGPe and cdlSNr neurons responded to bad objects, we compared responses to bad objects (from 100 to 300 ms after bad object onset) with baseline activities (from 200 to 0 ms before bad object onset) in the same trials. To investigate whether these cvGPe and cdlSNr neurons showed different response depending on action choice to bad objects (saccade or not), we compared their activity between saccade (+) trials and saccade (−) trials in the same spike count window (from 100 to 200 ms after bad object onset).

Neuropharmacological experiments

To investigate whether the bicuculline injection affected cdlSNr activity in the sequential saccade choice task, we applied a Mann-Whitney *U* test (two-tailed) to compare the activity of the same cdlSNr neuron between before and after the injection, separately for good or bad objects (Fig. 3D). To investigate whether the bicuculline injection modulated saccade rate to good or bad objects in the sequential saccade choice task, we applied a Wilcoxon signed-rank test (two-tailed) to compare the saccade rates between before and after bicuculline injection (Fig. 3C and fig. S3A) and saline injection (fig. S3B). To investigate whether the injection modulated the saccade choice rate to bad objects in the simultaneous saccade choice task, we applied a Wilcoxon signed-rank test (two-tailed) to compare the saccade choice rates of bad objects between before and after bicuculline injection (Fig. 4B and fig. S4A) and saline injection (fig. S4B).

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at http://advances.sciencemag.org/cgi/content/full/5/8/eaaw9297/DC1

Fig. S1. Latency of saccade to good and bad objects in sequential saccade choice task.
Fig. S2. Saccades and neuronal activities during sequential saccade choice task.
Fig. S3. Selective change in saccade rate by cvGPe manipulation during sequential saccade choice task.
Fig. S4. Change in choice rate by cvGPe manipulation during simultaneous saccade choice task.
Movie S1. Monkey's eye movement with the sequential saccade choice task in slow motion at 1/3× speed.
Movie S2. Monkey's eye movement with the sequential saccade choice task at normal speed.
Movie S3. Monkey's eye movement with the sequential saccade choice task after the bicuculline injection in right cvGPe.
Movie S4. Monkey's eye movement with the sequential saccade choice task after the saline injection in right cvGPe.

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Acknowledgments: We thank M. Smith for creating injectrodes; A. M. Nichols for creating chambers; D. Parker for help with animal care and surgery; A. Ghazizadeh, H. F. Kim, M. Isoda, and Y. Tachibana for technical advice; and J. Kunimatsu, K. Maeda, D. McMahon, G. Atul, G. Costello, H. Lee, A. Yoshida, J. P. Herman, and B. Amarender for comments. **Funding:** This work was supported by the Intramural Research Program at the NIH National Eye Institute. **Author contributions:** H.A. and O.H. conceived and designed experiments. H.A. performed all experiments. H.A. and O.H. formed the conceptual model. H.A. analyzed the data and made all figures. H.A. and O.H. wrote the paper. **Competing interests:** The authors declare that they have no competing interests. **Data and materials availability:** All data needed to evaluate the conclusions in the paper are present in the paper and/or the Supplementary Materials. Additional data related to this paper may be requested from the authors.

Submitted 6 February 2019
Accepted 27 June 2019
Published 7 August 2019
10.1126/sciadv.aaw9297

Citation: H. Amita, O. Hikosaka, Indirect pathway from caudate tail mediates rejection of bad objects in periphery. *Sci. Adv.* **5**, eaaw9297 (2019).