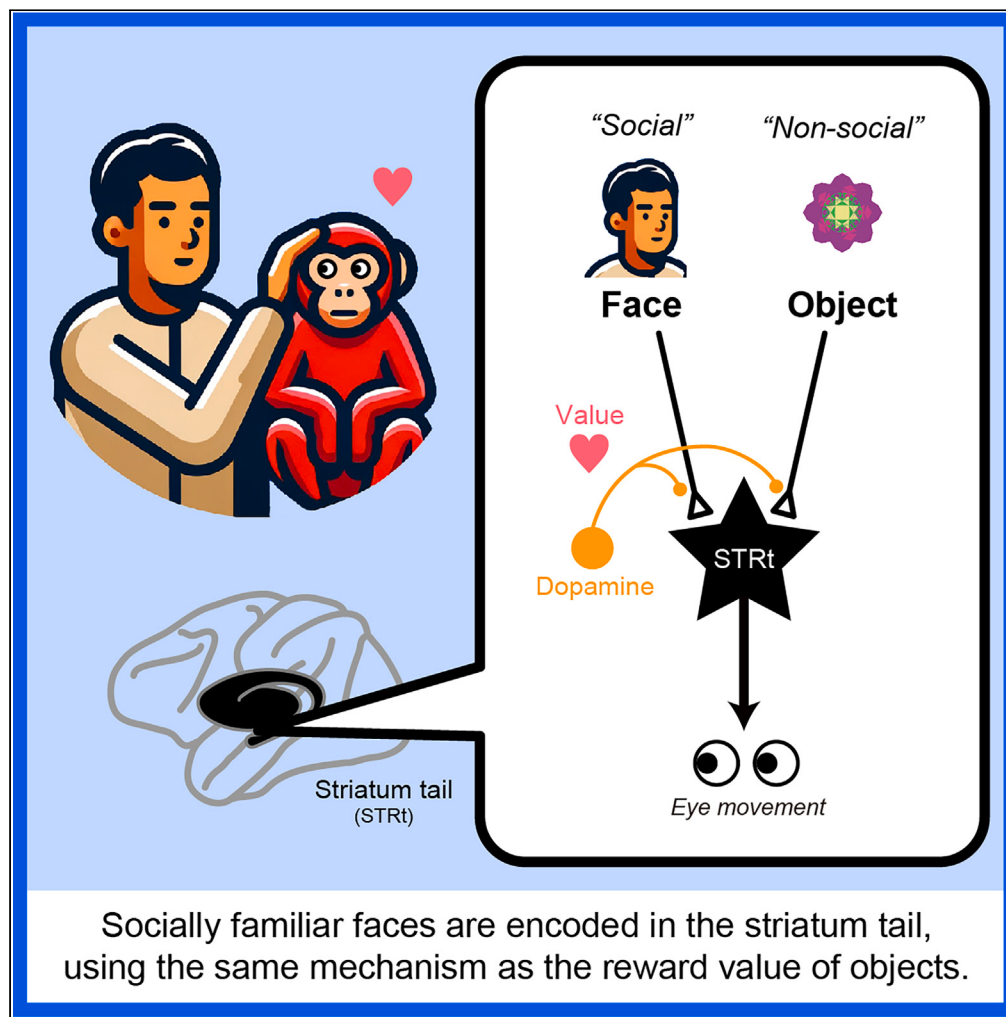


Article

Neuronal response of the primate striatum tail to face of socially familiar persons



Jun Kunimatsu,
Hidetoshi Amita,
Okihide Hikosaka

jkunimatsu@md.tsukuba.ac.jp

Highlights

Neurons in the striatum tail strongly respond to socially familiar faces

The face-responsive neurons in the striatum tail encode long-term object value

Strength of social familiarity and object value coding are positively correlated

Social familiarity and object value information may be mediated by a common mechanism

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Article

Neuronal response of the primate striatum tail to face of socially familiar persons

Jun Kunitatsu,^{1,2,3,5,*} Hidetoshi Amita,^{1,4} and Okihide Hikosaka¹

SUMMARY

Recent studies have suggested that the basal ganglia, the center of stimulus-reward associative learning, are involved in social behavior. However, the role of the basal ganglia in social information processing remains unclear. Here, we demonstrate that the striatum tail (STRt) in macaque monkeys, which is sensitive to visual objects with long-term reward history (i.e., stable object value), is also sensitive to socially familiar persons. Many STRt neurons responded to face images of persons, especially those who took daily care of the subject monkeys. These face-responsive neurons also encoded stable object value. The strength of the neuronal modulation of social familiarity and stable object value biases were positively correlated. These results suggest that both social familiarity and stable object value information are mediated by a common neuronal mechanism. Thus, the representation of social information is linked to reward information in the STRt, not in the dedicated social information circuit.

INTRODUCTION

We feel close to those who take care of us or provide daily necessities such as food and water. Especially for children and companion animals, it is crucial for survival to remember the faces of those familiar individuals.^{1,2} Facial information, which is processed through specific visual circuits, should be integrated into complex social information in the brain.

The basal ganglia play pivotal roles in associative learning based on experience.^{3,4} Patients with Parkinson's and Huntington's diseases, whose brains have distinct neuronal loss in the striatum and its connected regions,^{5,6} show deficits not only in associative learning but also in face recognition and discrimination.^{7–12} Human imaging studies also suggest that the striatum is related to social behaviors such as face recognition.¹³ Additionally, face-selective areas in the inferior temporal cortex, which encode facial identity, are functionally connected to the striatum.^{14–16} However, the specific role that the striatum plays in face processing remains unclear.

One possible role of the striatum in face processing is to associate familiar faces with rewards based on social context, similar to how objects are associated with rewards. Face-selective areas in the inferior temporal cortex encode face familiarity,^{17,18} and these areas preferentially project to the striatum tail (STRt), which is the caudal part of the striatum.^{19–22} Thus, the STRt may receive face familiarity information from these areas. Each STRt neuron selectively responds to specific visual objects, discriminates between familiar and novel objects, and distinguishes objects previously associated with a large reward from other objects for months and years.^{23–27} Therefore, similar to the long-term value of objects, STRt neurons may encode the long-term value of faces based on reward experiences in a social context. To test this hypothesis, we recorded the activity of STRt neurons in monkey subjects during the presentation of face images of individuals who took care of them daily.

RESULTS

This study examined neuronal responses when a monkey viewed face images under two conditions: social familiarity condition and object value condition (Figure 1). In the social-familiar condition, total 12 images were used from three categories: (a) face images of socially familiar persons who had provided daily care of the subject monkeys for >1 year [social familiarity (+)], (b) face images of socially unfamiliar persons [social familiarity (–)], and (c) fractal objects associated with no reward (Figure 1B). We used category (c) as a control to identify the neurons' properties. In the object-value condition, eight fractal objects were used (Figure 1C). The monkeys learned the values of these objects using a previously described stable object value task (Figures S1A and S1B).^{23–25,27–29} In each trial of the stable object value task (Figure S1C), one fractal object was randomly selected from a set of eight objects and presented as a target. The monkey made a saccade to the target followed by reward delivery. Each object was associated with a fixed amount of reward (small or large) across trials and sessions. Four of the eight objects were always associated with a large reward [high-valued objects, object value (+)]; the other four objects were always associated with a

¹Laboratory of Sensorimotor Research, National Eye Institute, National Institutes of Health, Bethesda, MD 20892, USA²Division of Biomedical Science, Institute of Medicine, University of Tsukuba, Tsukuba, Ibaraki 305-8577, Japan³Transborder Medical Research Center, University of Tsukuba, Tsukuba 305-8577, Japan⁴Systems Neuroscience Section, Center for the Evolutionary Origins of Human Behavior, Kyoto University, Inuyama, Aichi 484-8506, Japan⁵Lead contact

*Correspondence: jkunitatsu@md.tsukuba.ac.jp

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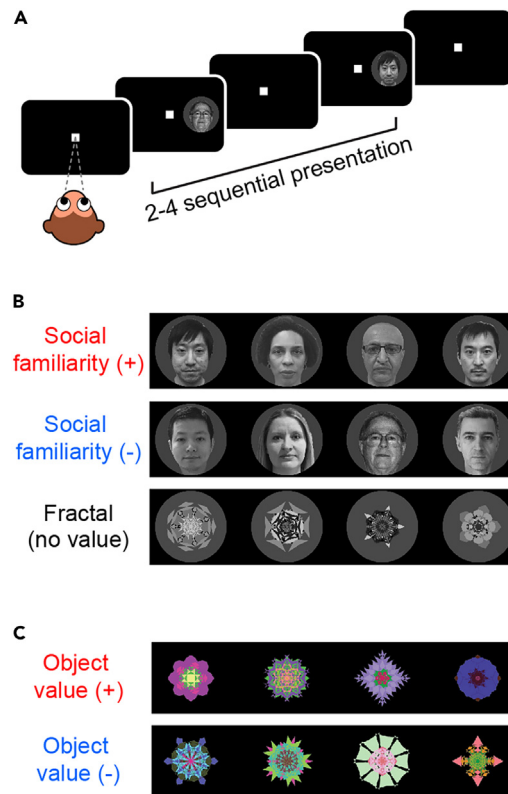


Figure 1. Neuronal tests for social familiarity and stable object value

(A) Face images or fractal objects were sequentially presented in the neuron's receptive field as the monkey was fixating on the center (passive-viewing task). (B) In the social-familiarity condition, face images were divided into the following three categories: (1) socially familiar human faces [social familiarity (+), top], (2) socially unfamiliar human faces [social familiarity (-), middle], and (3) fractal objects associated with no reward (bottom). Category (3) was used as a control to determine the neuron's property.

(C) In the stable object value condition, fractal images were divided into the following two groups: (1) fractal objects consistently associated with a large reward [object value (+), top] and (2) fractal objects consistently associated with a small reward [object value (-), bottom].

small reward [low-valued objects, object value (-)]. After several (>5) learning sessions, the monkeys tended to look at the high-valued object quickly among multiple objects (Figure S1D) even one month later.^{23,29} This behavior resembles the capability to identify familiar individuals among various faces.^{30–32}

We first tested STRt neuronal responses to face and fractal images using a passive-viewing task (Figure 1A). In this task, each object was presented at the neuron's receptive field while the monkey was fixating on the center. The object was randomly selected among 12 (in the social-familiarity condition) or 8 (in the stable object value condition, Figure 1B) images. A fixed amount of reward was delivered after two to four sequential presentations. Thus, the neuronal responses reflected long-term object-value memories rather than predicted rewards. We recorded the activity of putative medium spiny neurons (MSN) during the passive-viewing task (Figure 1A, 22 from monkey W, 27 from monkey S, and 19 from monkey Z) as a previous study reported the relationship of MSNs with value coding. Figure 2A shows the activity of a representative neuron in the STRt that responded to the face images. This neuron showed a stronger response to the social familiarity (+) faces (left) than to the social familiarity (-) faces (middle; $p < 0.05$, Fisher's test), although the responses to the social familiarity (+) faces varied. This neuron also showed a stronger response to the value (+) objects than to the value (-) objects (Figure 2B, $p = 0.01$, Wilcoxon rank-sum test). The responses to valued objects also widely varied. These results are consistent with those previously reported by us, wherein we demonstrated that STRt neurons encode stable object values but are sensitive to particular objects.^{27,33} The neuron with low visual selectivity also showed strong responses to the socially familiar faces and high-valued objects ($p < 0.05$, $p = 6.94 \times 10^{-4}$; Figure S2).

First, we analyzed the responses during the social-familiarity condition to examine the property of facial responses of STRt neurons. Among 68 recorded neurons, 52 (75%) showed a significant visual response (Figure 3A, $p < 0.05$ with Bonferroni correction, paired t-test). Further, 50% of neurons responded to the face images (face-responsive neurons; 14 from monkey S, 9 from monkey W, and 12 from monkey Z). Quantification of the strength of social-familiarity coding for each neuron (modulation index) revealed their distributions among all face-responsive neurons (Figure 3B and see also Figure S3A). A receiver operating characteristic (ROC) area of >0.5 indicated that the neurons showed a stronger response to social familiarity (+) faces than to social familiarity (-) faces. The index was often away from 0.5, indicating that many neurons encoded social familiarity for face images. Overall, the STRt neurons encoded socially familiar

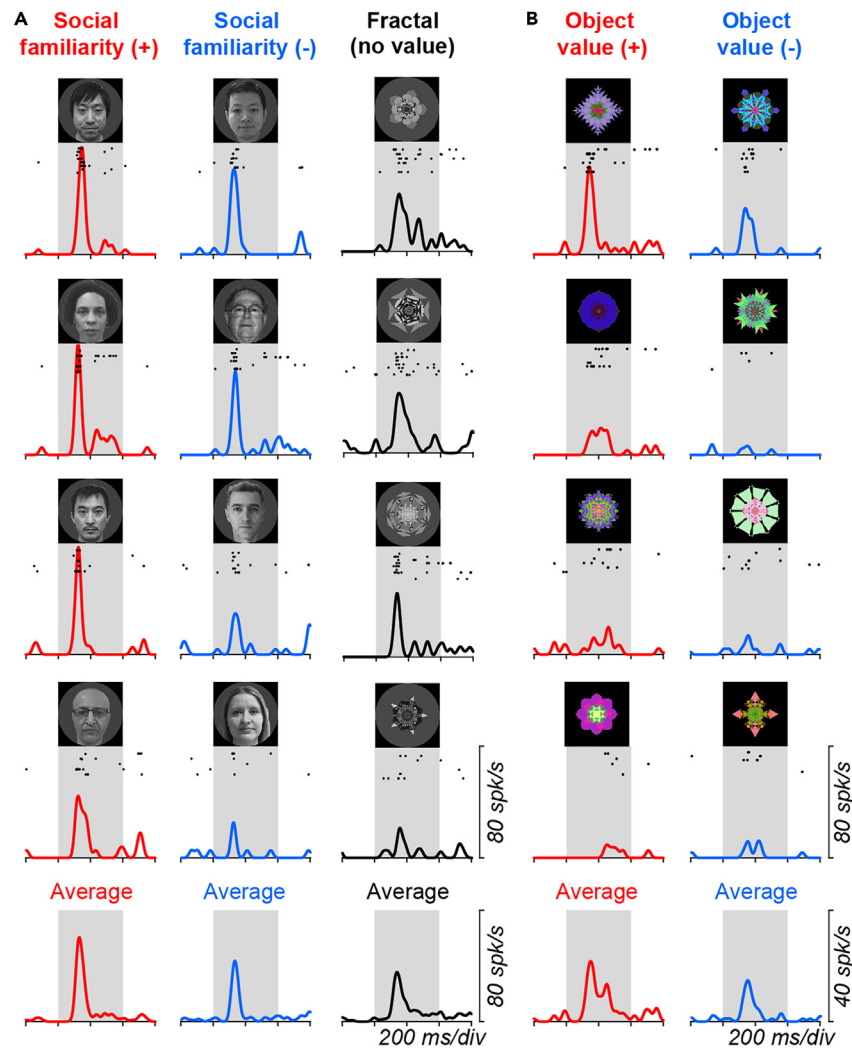


Figure 2. Representative face-responsive neuron in the striatum tail

(A) Neuronal response to the socially familiar (+) faces (left), socially familiar (–) faces (middle), and fractal objects (right) in the passive-viewing task. The averaged responses of the neuron to each category of visual stimuli (bottom).

(B) Neuronal response to the value (+) objects (left) and value (–) objects (right) in the same neuron as (A).

information, especially in the positive direction ($p = 0.0051$, unpaired t-test). Our previous study identified two groups of neurons in the STR; namely: a) positive-value and b) negative-value coding neurons.^{24,25,27} Accordingly, we analyzed the time course of population activity of these face-responsive neurons according to each face-coding type (positive or negative) (Figure 3C). Social-familiarity coding started approximately 50 ms after the appearance of the image in both groups. These results suggest that STRt neurons quickly detect socially familiar faces. The visual responses to each face image were different among monkeys (Figure S4). These results may reflect individual differences in relationship with each person. Neurons from all monkeys encoded the social familiar information in a positive direction ($p < 0.05$, unpaired t-test), except monkey S ($p = 0.82$). To examine whether these neurons also encode stable object values, we analyzed the activity of 33 face-responsive neurons in the STRt during the passive-viewing task with long-term reward-associated objects. Figure 3D shows the population activity of negative and positive-value coding neurons, in which the neuron types were defined by their responses to socially familiar and unfamiliar faces. The value modulation index of individual STRt neurons was biased toward 1.0 ($p = 0.023$, unpaired t-test), which indicates an absolute preference for positive-value objects (see also Figure S3B). Notably, the detection of social familiarity preceded that of stable object value in both coding types.

The above results demonstrate the encoding of two types of information—social familiarity and object value—in STRt neurons. We then asked whether these signals are encoded by different or the same neurons in the STRt. Figure 4 shows that the strengths of the social familiarity and object value biases were significantly correlated (Pearson's $r = 0.41$, $p = 0.02$). These results indicate that social information and value information are co-encoded in the STRt and that these signals are mediated by the same neuronal mechanism.

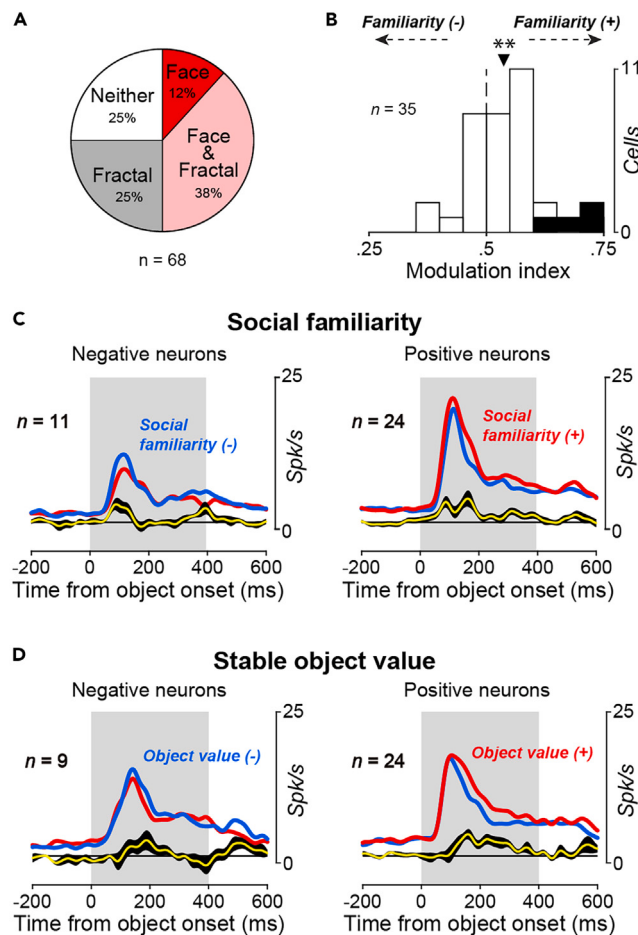


Figure 3. Face-responsive neurons encode social familiarity

(A) Proportions of visual neurons in the striatum tail categorized by the passive-viewing task.

(B) Social familiarity modulation index of individual face responsive neurons in the striatum tail during the passive-viewing task. The filled bars indicate neurons significantly modulated by social familiarity ($p < 0.05$, Fisher's exact test). A value modulation index score of 1.0 signifies that the neuronal response to familiar faces is always stronger than that to unfamiliar faces; 0.0 signifies the opposite response pattern. The triangle indicates the population average of the modulation index. The asterisks indicate a significant difference from 0.5 (** $p < 0.01$, paired t-test).

(C) Population neuronal activity in the social-familiarity condition; negative social-familiarity coding neurons (negative neurons, left) and positive social-familiarity coding neurons (positive neurons, right). The red and blue lines indicate the averaged neuronal responses to socially familiar faces and unfamiliar faces, respectively. The yellow line indicates the difference in response to the socially familiar faces and unfamiliar faces (mean $\pm$ SEM).

(D) Population neuronal activity in the stable object value condition; negative-value coding neurons (negative neurons, left) and positive-value coding neurons (positive neurons, right). The red and blue lines indicate the averaged neuronal responses to value (+) and (-) objects, respectively. The yellow line indicates the difference in response to value (+) and (-) objects (mean $\pm$ standard error of the mean).

DISCUSSION

Role of STRt in the detection of familiar faces

The STRt neurons receive inputs from the inferior temporal (IT) cortex,^{34,35} which encodes personally familiar faces.^{17,18,36} We note that the socially familiar faces are personally familiar faces associate with positive experience.^{37,38} The STRt neurons also receive inputs from dopamine neurons, which convey sustained reward signals based on experience.³⁹ Therefore, the personal familiarity information from the IT cortex may be modulated by reward experience in the STRt through dopamine signals. This processing may be involved in not only face recognition but also gaze shift toward faces. Humans can find familiar faces more quickly and accurately than unfamiliar ones.^{30–32} Furthermore, a previous study showed that monkeys looked more at human faces associated with large reward than faces associated with small reward from 150 ms after face image presentation.⁴⁰ Our recent studies showed that the visual responses in STRt neurons lead to the automatic detection of individual high-valued objects.²⁴ The STRt neurons modulate saccadic eye movements based on long-term value memory through the direct and indirect pathways.^{26,41} The superior colliculus (SC) neurons are excited by high-valued object-dominant signal through the direct pathway from the STRt for facilitating saccades toward high-valued objects.^{42,43} While the SC neurons are suppressed by low-valued object-dominant

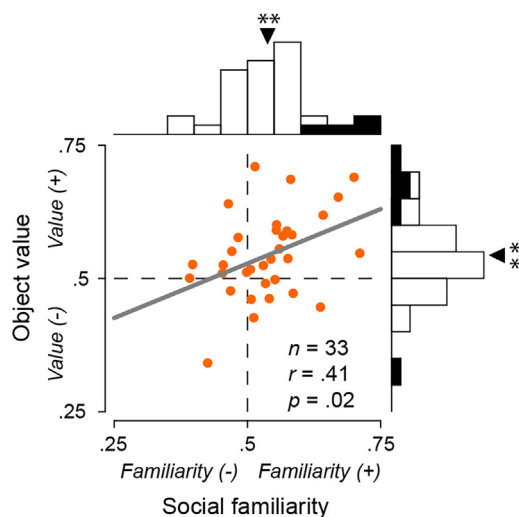


Figure 4. Correlation between social familiarity and stable object value

The correlation between modulation indices of social familiarity and stable object value. The numbers indicate the Pearson's correlation coefficients and *p* value. The strength of the object value coding is significantly correlated with that of social-familiarity coding.

signal through the indirect pathway from the STRt for suppressing saccades toward low-valued objects.^{26,43} We observed a positive correlation between social familiarity and stable object value modulations in the present study (Figure 4). The activity of STRt neurons may allow to make saccadic eye movements toward socially familiar faces similar to valued objects.

Encoding the face of socially familiar person

We showed that the STRt neurons encoded not only objects with stable value but also faces with social familiarity. The finding that neurons encode both social information and object value, has also been validated in the amygdala, which encodes faces with social status as well as objects with reward value.⁴⁴ In this study, we used images of the faces of individuals who had been caring for the monkeys daily for over a year. The monkeys gradually became familiar with these individuals through experiences encountered in their daily routines. Therefore, the current study suggests that STRt neurons retain long-term memories of face images associated with daily reward experience in social contexts. On the other hand, the social environment is complex and influenced by various factors: e.g., behavioral context, emotional state, and social rank. In our study, we employed a simple method of presenting gray-scale face pictures within experimental booths to limit these factors. Consequently, the effect size was small, making the results less robust, however, the significant differences observed indicate the value attributed to faces (Figure 3).

The STRt neurons exhibited a high selectivity for face images, akin to the high object selectivity observed in previous studies.^{25,27,33} In the present study, we used only four face images as socially familiar faces, because these four persons frequently provided daily necessities to the monkey subjects. The difference in STRt responses to these four face images (social familiarity (+)) from the other four face images (social familiarity (-)) may be attributed to facial features. While our results do not exclude this possibility, selectivity for face images alone cannot explain the findings that the modulation index score for social familiarity was significant (Figure 3B) and comparable to the modulation index score for object value (Figure 4).²⁷ Further study is necessary to examine how STRt neurons respond to more familiar face images and how each STRt neuron develops its response to faces through daily social interactions.

Social information in the basal ganglia

Previous studies have reported impaired familiar and unfamiliar face detection,^{8,9} but not facial expression,⁴⁵ in patients with Parkinson's disease. In Parkinson's disease, DA neurons tend to disappear in the lateral part of SN, which tends to project to the STRt.⁶ Moreover, patients with early-stage Huntington's disease, which includes degeneration of CDT neurons,⁵ show deficits in face recognition and discrimination.⁷ These reports are consistent with our findings of the involvement of the STRt in face representation. Notably, people with autism, who have impaired social communication abilities,⁴⁶ show no deficits in the recognition of familiar faces.⁴⁷ This report supports our conclusions that the same mechanism is responsible for encoding socially familiar faces and stable object values in the STRt, independent of the circuit for social communication. Thus, the basic reward value systems in the caudal basal ganglia circuit contribute to encoding familiar faces in the social context.

Our results provide evidence of the neuronal mechanisms that underlie close interactions, akin to those observed between humans and monkeys in this study, which are commonly encountered in owner-companion animal relationships.⁴⁸ Though humans and social animals identify individuals by not only faces but also physical-characteristics, voices, and odor cues in the natural environment,^{49–51} several studies support that poor-quality face images such as grayscale face images are sufficient for face identification and discrimination.^{17,40} It is known that these abstract face images are rapidly processed by the subcortical visual pathway (SC-pulvinar-amygdala) with short latency.^{52,53} Because the neurons in the amygdala project to the STRt,⁵⁴ the signals through the subcortical pathway may be conveyed to the STRt for integration of the abstract face images with memory information. Furthermore, the STRt neurons may encode multi-sensory signals with faces

like the other brain regions including the amygdala.^{55,56} We found that the interneurons in STRt also responded to auditory stimuli (unpublished data). Further studies are required to clarify this point in the future.

Limitations of the study

Our research has some limitations, although we revealed that the STRt activity encodes both social familiarity and stable object value. First, it is not yet certain whether the STRt activity in response to familiar face images affects social behaviors including face-looking behavior. Second, it remains to be determined which aspects of social interaction modulate the STRt activity due to a lack of rigorous control over daily interactions such as greeting, feeding, training, and caring in this study. Further studies are therefore required to resolve these questions.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

- KEY RESOURCES TABLE
- RESOURCE AVAILABILITY
 - Lead contact
 - Materials availability
 - Data and code availability
- EXPERIMENTAL MODEL AND SUBJECT DETAILS
 - General procedures
 - Behavioral procedure
 - Passive-viewing task (social-familiarity coding test)
 - Stable object value task
 - Free-viewing task
 - Passive-viewing task (stable object value-coding test)
 - Recording procedure
- QUANTIFICATION AND STATISTICAL ANALYSIS

SUPPLEMENTAL INFORMATION

Supplemental information can be found online at <https://doi.org/10.1016/j.isci.2024.110043>.

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AUTHOR CONTRIBUTIONS

J.K. and O.H. designed this research, J.K. and H.A. performed the experiments, and J.K. analyzed the data; all authors wrote the manuscript.

DECLARATION OF INTERESTS

The authors declare no competing financial interests.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Experimental models: Organisms/strains		
<i>Macaca mulatta</i>	NIH	N/A
Software and algorithms		
MATLAB	MathWorks	http://www.mathworks.com RRID:SCR_001622
Blip	NIH, Simon Hong	http://www.robilis.com/blip/

RESOURCE AVAILABILITY

Lead contact

Further information and requests for resources and reagents should be directed to and will be fulfilled by the Lead Contact, Jun Kunimatsu (jkunimatsu@md.tsukuba.ac.jp).

Materials availability

This study did not generate any new unique reagents.

Data and code availability

Data: Original behavioral and neuronal data reported in this paper will be shared by the [lead contact](#) upon request.

Code: This paper does not report original code.

Additional information: Any additional information required to reanalyze the data reported in this paper is available from the [lead contact](#) upon request.

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Three adult male rhesus monkeys (*Macaca mulatta*, 8–11 kg, 6–8 years old) were used for all experiments. All procedures for animal care and experimentation were approved by the Animal Care and Use Committee of the National Eye Institute (proposal number: NEI-622) and complied with the Public Health Service Policy on the humane care and use of laboratory animals.

General procedures

We implanted a plastic head holder, eye coil, and plastic recording chamber under general anesthesia and sterile surgical conditions. After the monkeys fully recovered from surgery, we started training them in the oculomotor tasks. Several procedures, including the surgery, behavioral task, and statistical analysis, were identical between this and our previous studies.^{27,57}

Behavioral procedure

The behavioral procedure was controlled by a C++ based real-time experimentation data acquisition system (Blip: available at <http://www.robilis.com/blip/>). The monkey sat in a primate chair, facing a frontoparallel screen in a sound-attenuated and electrically shielded room. Visual stimuli generated by an active matrix liquid crystal display projector (PJ550, ViewSonic) were rear projected on the screen. Face images (10° × 10°) were provided by a member of the laboratory. Four persons [experimenters and animal caretakers, social familiarity (+)] were involved in monkey daily care and were familiar with each monkey. The other four persons [social familiarity (-)] had not met the subjects. We created the fractal objects (~10° × 10°) using fractal geometry.³³

Passive-viewing task (social-familiarity coding test)

The purpose of this task was to examine the response property of the striatal neurons to face images. We used grayscale images of faces (socially familiar and unfamiliar persons' faces) and of fractal objects (no value association) to test the neuronal response to face images (Figure 1A). In this task, two to four face images (face images or fractal objects) were sequentially presented in the receptive field (presentation time, 400 ms; interval, 400 ms) while the monkey fixated on a central white dot (Figure 1D). A fixed liquid reward (0.2 ml) was delivered 300 ms after the last presentation. The reward was thus not contingently associated with any face image. Each image was presented at least seven times in each session.

Stable object value task

We used the stable object value procedure to examine the long-term effect of object value learning.^{23,27} Eight fractal objects were divided into four high-valued objects [object value (+)] associated with a large reward (0.3 ml) and four low-valued ones [object value (-)] associated with a small reward (0.1 ml) (Figure 1B). The monkey learned each object value by making a saccade to each object followed by large or small reward delivery (Figure S1C). One learning session consisted of 80 trials. The monkey was trained for each set of objects with one learning session each day. The same sets of objects were repeatedly used across at least five learning sessions.

Free-viewing task

The free-viewing task was used as a behavioral test to examine monkey preference for value (+) or value (-) objects.^{23,27} After the monkey fixated on a central white dot for 300 ms, four objects were simultaneously presented in four symmetric positions (15° from center) (Figure 1C). The four objects were pseudo-randomly selected from eight objects used in the stable object value task. The monkey was free to look at the objects for 2 s without a reward outcome. After a blank period (500 ms), another white dot was presented at one of eight positions. When the monkey made a saccade to it, a fixed reward was delivered (0.2 ml). Each object was presented at least 10 times in each session.

Passive-viewing task (stable object value-coding test)

Once the monkey showed significant behavioral preference for value (+) objects in the free-viewing task, we tested neuronal responses to the objects with the passive-viewing task.^{23,27} This was the same as the passive-viewing task for the social-familiarity coding test except for the presented images. Two to four objects used in the stable object value task were sequentially presented in the receptive field while the monkey fixated on a central white dot. A fixed liquid reward (0.2 ml) was delivered after the last presentation. Therefore, each object was no longer associated with a large or small reward in this task. We usually used two to three sets of well learned objects.

The behavioral test (free-viewing task) and the neuronal test (passive-viewing task) were conducted on different days. To remind the monkey of the object value memory, we conducted the stable object value task at least once per 60 days after the initial learning.

Recording procedure

Based on a stereotaxic atlas, a recording chamber was placed over the parietal cortex, tilted laterally by 25° (monkey W and Z) or 0° (monkey S) and aimed at the STRt. Magnetic resonance images (4.7 T; Bruker) were then obtained along the direction of the recording chamber, which was visualized by filling a recording grid with gadolinium.

For single-neuron recording, a tungsten electrode (Alpha Omega Engineering or FHC) was lowered into the striatum through a guide tube using a micromanipulator (MO-97S; Narishige). The recording site was determined using a grid system, which allowed electrode penetrations at every 1 mm. We amplified and filtered (0.3–10 kHz; Model 1800, A-M Systems; Model MDA-4I, BAK) the signals obtained from the electrodes and collected at 1 kHz. Single neurons were isolated online using custom voltage–time window discriminator software (Blip).

QUANTIFICATION AND STATISTICAL ANALYSIS

We defined the putamen tail as the region 0–3.5 mm from the ventral edge of the putamen and the cdPUT as the region above it.^{27,57} As the putamen tail and CDt share the same anatomical pathway^{20,41} and showed similar long-term value coding,²⁷ we combined the neurons in these areas as STRt neurons. The offline analyses were performed using MATLAB (MathWorks). Using waveform and firing-rate criteria, we characterized the electrophysiological properties of recorded neurons. Putative MSNs exhibited a peak–trough distance >800 μ s (or 480 μ s) and a baseline firing rate <10 Hz.^{57,58} We defined visual neurons as neurons showing a significant difference in activity between the baseline period (400 ms before object onset) and visual period (50–350 ms after object onset; paired t test, $p < 0.05$ with Bonferroni correction). We considered “face-responsive” and “object-responsive” neurons showing a significant response to the faces and fractal objects, respectively. The time course of neuronal activity for each condition is shown after smoothing with a Gaussian kernel ($\sigma = 15$ ms). We only used the data in correct trials for the behavioral and neuronal analyses.

To examine neuronal discrimination, we measured the magnitude of the response to each visual stimulus by counting the numbers of spikes fired (on single trials) within a test window (50–350 ms after visual stimulus onset). A value modulation index was defined as the area under the ROC curve based on the response magnitude of the neuron to face images [social familiarity (+) vs. (-)] or fractal objects [object value (+) vs. (-)].