Surprise signals in the supplementary eye field: rectified prediction errors drive exploration-exploitation transitions

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Kawaguchi N, Sakamoto K, Saito N, Furusawa Y, Tanji J, Aoki M, Mushiake H. Surprise signals in the supplementary eye field: rectified prediction errors drive exploration-exploitation transitions. J Neurophysiol 113: 1001–1014, 2015. First published November 19, 2014; doi:10.1152/jn.00128.2014.—Visual search is coordinated adaptively by monitoring and predicting the environment. The supplementary eye field (SEF) plays a role in oculomotor control and outcome evaluation. However, it is not clear whether the SEF is involved in adjusting behavioral modes based on preceding feedback. We hypothesized that the SEF drives exploration-exploitation transitions by generating “surprise signals” or rectified prediction errors, which reflect differences between predicted and actual outcomes. To test this hypothesis, we introduced an oculomotor two-target search task in which monkeys were required to find two valid targets among four identical stimuli. After they detected the valid targets, they exploited their knowledge of target locations to obtain a reward by choosing the two valid targets alternately. Behavioral analysis revealed two distinct types of oculomotor search patterns: exploration and exploitation. We found that two types of SEF neurons represented the surprise signals. The error-surprise neurons showed enhanced activity when the monkey received the first error feedback after the target pair change, and this activity was followed by an exploratory oculomotor search pattern. The correct-surprise neurons showed enhanced activity when the monkey received the first correct feedback after an error trial, and this increased activity was followed by an exploitative, fixed-type search pattern. The correct-surprise neurons showed enhanced activity when the monkey received the first correct feedback after an error trial, and this increased activity was followed by an exploitative, fixed-type search pattern. Our findings suggest that error-surprise neurons are involved in the transition from exploitation to exploration and that correct-surprise neurons are involved in the transition from exploration to exploitation.

The supplementary eye field (SEF) plays a crucial role in the control of higher-order eye movements. The SEF, first identified as an oculomotor area in the dorsomedial frontal cortex (Schlag and Schlag-Rey 1987), is involved in the control of antisaccades (Schlag-Rey et al. 1997) and the temporal organization of multiple saccades (Berdyyeva and Olson 2010; Isoda and Tanji 2003; Lu et al. 2002). The SEF has recently been found to exert nonmotor supervisory functions in oculomotor control (Schall et al. 2002). Specifically, distinct groups of SEF neurons were activated after errors, after the successful withholding of a prepared eye movement, or in association with reinforcement in an oculomotor countermanding task (Stuphorn et al. 2000; Stuphorn and Schall 2002). In addition, the SEF is related to prediction and detection of reward (Amador et al. 2000) and to the evaluation of the amount of reward (Roesch and Olson 2003; Uchida et al. 2007). Furthermore, the SEF is suggested to have executive control over saccade generation by monitoring behavioral consequences (Schall and Boucher 2007; Stuphorn and Schall 2006). These studies show that the SEF is involved in both the motor and cognitive aspects of eye movement control. However, it remains unclear how the SEF contributes to adaptive oculomotor search based on performance monitoring. Thus we attempted to investigate how the error- and correct-outcome signals represented in the SEF are used to adjust subsequent searches. We hypothesized that the SEF controls transitions between exploration and exploitation by producing two types of surprise signals in response to unexpected erroneous and unexpected correct outcomes (Fig. 1). To test this hypothesis, we introduced an oculomotor two-target search task in which monkeys were required to explore valid targets with eye movements and to exploit memorized target locations to select the next valid target. To classify SEF neurons, we constructed a reinforcement learning model in which the predictions of correct and error feedback were updated via surprise signals, defined as the differences between prediction and outcomes. We found that two types of surprise neurons responded to unexpected correct and error feedback, respectively. Their postfeedback activities were related to the shift between oculomotor search patterns in the following trials, implying that the SEF plays a supervisory role in the exploration-exploitation transitions based on performance monitoring.

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Subjects and Apparatus

Our animal research was performed in accordance with National Institutes of Health guidelines and the guidelines of Tohoku University. All experimental protocols were approved by the Animal Care and Use Committee, Tohoku University (Permit No. ido-74). Two Japanese monkeys (Macaca fuscata; monkey K: 6.5 kg, monkey M: 6.1 kg) were trained to perform the task in this study. The monkeys were kept in individual primate cages in an air-conditioned room with food available ad libitum. During the experiments, the monkeys sat in a primate chair with their heads restrained and faced a screen on which visual stimuli were presented. Eye position was monitored with an infrared corneal reflection system sampling at 250 Hz.

Behavioral Task

We introduced an oculomotor search task in which the monkeys were required to find two valid targets among four identical targets and to make saccades alternately to the two targets (Fig. 2A). Because the positions of the valid targets were not shown explicitly, the monkeys had to search for the targets by trial and error. After a predetermined number of correct trials, the valid-target pair was changed without instruction; thus the monkeys had to change their search strategy (i.e., exploration and exploitation) after receiving error feedback. The events in a trial are shown in Fig. 2A. Monkeys were allowed to choose one target in each trial. First, the monkeys were required to fixate on a central fixation point for 500–700 ms. The onset of fixation was signaled when the color of the central fixation point changed from white to red. When the monkeys fixated on the point for 500–700 ms successfully, the color was changed from red to green; this was followed by the appearance of four identical visual targets: 2 × 2° white points presented 8.5° from the central fixation point. If the monkeys maintained fixation on the central fixation point for an additional 500–700 ms, the fixation point disappeared (Go signal) and the monkeys were allowed to make a saccade to one of the four peripheral targets. When the monkeys fixated on a target, the color of the selected target turned from white to red, signaling the start of fixation. The monkeys had to maintain fixation for 700 ms to receive feedback, which indicated whether the selected target was valid. There were two types of visual feedback. When the monkey fixated on an invalid target, the four dots disappeared (error feedback). When the monkeys fixated on the valid target, the color of the selected stimulus turned from red to green (correct feedback) and the four stimuli turned off 500 ms after the color change. The reward was then provided 500 ms after the disappearance of the four stimuli. After an interval of 2,000–2,500 ms, the next trial began. After the monkeys selected the valid target, the currently valid target was shifted to the other one within the currently valid pair (Fig. 2A, see the changes between “Bottom-Right” and “Bottom-Left”). If the fixation was interrupted before the feedback, the four peripheral targets were turned off, and the next trial began without reward (fixation-break trial). The fixation-break trials were excluded from our analyses.

We defined four types of valid pairs, each of which consisted of two adjacent targets among the four presented (Fig. 2B). The valid pair was changed in a pseudorandom manner after a predetermined number of consecutive correct choices (6–10 trials) or the total number of correct choices (10–20 correct trials) after each pair change. Because the current valid pair was shifted without instruction, the monkeys had to search the valid paired targets based on behavioral outcomes.

We classified the oculomotor search pattern into three types: “adjacent,” “diagonal,” and “repeat” (Fig. 2C). These patterns were defined by the relative location of the target chosen in the current trial (n) compared with that of the target chosen in the previous trial (n – 1). For example, if the subject selected a target that was adjacent to the previously selected one, the search was classified as an adjacent search pattern. The adjacent search patterns were further divided into two types based on whether the target selected in the current trial was included in the current valid pair or not. “Diagonal” patterns were defined as searches in which the subject selected the target diagonal to the previously selected one. “Repeat” patterns were defined as searches in which the same target selected in the previous trial was selected again.

We distinguished two phases of search behavior: exploration and exploitation. We defined the exploration phase as the trials from the first error trial after a valid-pair change to the first correct trial in which the monkey found the first valid target. The exploitation phase was defined as the consecutive correct trials after the trial in which the monkey found both targets of the current valid pair. If the subject made an error during the consecutive correct trials, the trials after the error were not categorized into the exploitation phase. On the basis of these definitions, we inferred the internal behavioral mode of the monkeys from their oculomotor search patterns and determined the timing of the behavioral transitions. Examples of behaviors and feedback are presented in Fig. 2D. After the valid targets were changed without instruction, the monkeys made errors and began to search for new valid targets.

Computational Model: General Characteristics

To categorize the task-related neurons, we developed a model for an evaluation system to monitor behavioral outcomes, predict forthcoming feedback, and generate “surprise signals.” The following two general assumptions underpinned this model.

1) We assumed that the evaluation system detects changes in the environment by calculating the differences between predictions and actual outcomes. The products of such comparisons were so-called “prediction errors,” which can be represented as either signed or unsigned values. A signed prediction error was calculated by subtracting the prediction value from the actual outcome. Thus a prediction error was either positive or negative, depending on the two values. Dopamine neurons are well-known examples of signed prediction errors (Schultz 1997, 2006). In our analysis, signed prediction errors were rectified, and only the positive components were used as surprise signals that encoded the occurrence of an unexpected event or the nonoccurrence of an expected event (Alexander and Brown 2011).
Specifically, when an event occurred unexpectedly the surprise signal was calculated as a rectified prediction error by subtracting the prediction value from the actual outcome value. Based on Alexander’s original model, we hypothesized two types of rectified prediction error signals: correct and error. The correct type responded to correct feedback with an increasing firing rate, and the error type responded to error feedback with an increasing firing rate. Although the two types of rectified prediction errors are two aspects of the signed prediction error, this issue of whether the surprise signals are encoded in the brain as single or multiple prediction errors is not trivial, because the rectified prediction errors could lead to different behaviors.

We assumed that the evaluation system would be able to predict future events such as the occurrences of correct and error feedback. Furthermore, the two signals were followed by different behavioral adjustments as shown by the results of the behavioral analyses. It is plausible that two separate representations of correct and error outcomes enable flexible behavioral adjustments by facilitating the prompt switch to the next search.

On the basis of these assumptions, we defined two types of prediction errors: surprise signals for correct and error feedback. The mathematical details are presented in the Appendix.
and Olson 2007). Neuronal activity was recorded with glass-insulated Elgiloy electrodes (impedance of 0.8–1.0 MΩ) and Parylene-insulated tungsten microelectrodes (impedance of 1.0–1.8 MΩ). An electrode was inserted through the dura with a hydraulic microdrive (Narisige, Tokyo, Japan). Neuronal activity was amplified and bandpass filtered (1–6 kHz), and single-unit potentials were discriminated with a template-matching algorithm (MCP-Plus and MSD; Alpha Omega Engineering, Nazareth, Israel). Data were stored in a microcomputer for off-line analysis.

Analysis of Single-Unit Activity

**Task-related neurons.** If neuronal activity changed during the feedback or saccade period, the neurons were judged to be task related. Specifically, if neuronal activity during a prefeedback (0–300 ms before feedback) or postfeedback (0–300 ms after feedback) period differed significantly from that during the control period (200–500 ms after onset of fixation to the central fixation point, Mann-Whitney, \( P < 0.05 \)), the neuron was judged to be feedback related (Fujii et al. 2002). If the activity during a saccade period (0–300 ms after the Go signal) differed significantly from that during the control period (Mann-Whitney, \( P < 0.05 \)), the neuron was judged to be “eye movement related.”

**Regression analysis.** We hypothesized that SEF neurons would play evaluative roles in the oculomotor search task. Therefore, we tested whether the neurons represented the variables in the evaluation system described above. To classify the neurons, we performed regression analyses containing a variable representing each value in the aforementioned model. We determined the value that fits best for each neuron by comparing the coefficients of determinants. We performed regression analyses on a trial-by-trial basis as

\[
\text{Firing rate} = \alpha_1 \text{Value}_i + \epsilon (i = 1, \ldots, 10)
\]

where Value, denotes the explanatory variables that were the values described above (\( O_e \), \( V_c \), \( SS_e \), signed \( PE_e \), \( O_c \), \( V_e \), \( SS_c \), signed \( PE_c \)) and by the feedback in the current and correct trials. \( \alpha \) are regression coefficients, and \( \epsilon \) are intercepts for the explanatory variables. We calculated the coefficient of determination (\( R^2 \)) for each model for each neuron. We defined a neuron as feedback related when the \( R^2 \) was > 0.1. On the basis of this analysis, we selected the model with the higher \( R^2 \) as the best to characterize neuronal activity.

To eliminate the simple visual-stimuli-responsive neurons from the feedback-related neurons, we compared the neuronal activity following the visual stimuli that signaled a correct or an error outcome to those that signaled only task phases. If the neuron did not show a significant change in activity after the outcome signals (\( P < 0.05 \)), we excluded that neuron from further analyses. Specifically, to eliminate a neuron that responded to the change from red to green, we compared the activities during the periods after fixation onsets with those after correct feedback (both stimuli consisted of a change in the color of the fixed target from red to green). We excluded the neuron if it did not exhibit significantly different activities during the two periods. Additionally, to exclude neurons related to the absence of stimuli and those related to eye movements, we compared the activities during the periods in the error and correct trials in which stimuli were disappeared. We excluded the neuron if it did not show a significant difference between the activities in error and correct trials.

**Directional selectivity.** To examine whether task-related neurons were modulated by saccade direction, we performed regression analyses using the following equation:

\[
\text{Firing rate} = \alpha_3 H + \alpha_2 V + \epsilon
\]

where \( H \) denotes the horizontal location of the selected target, left (0) or right (1), \( V \) denotes the vertical location, bottom (0) or top (1), \( \alpha_1 \) and \( \alpha_2 \) are coefficients, and \( \epsilon \) is an intercept. If the effect of either \( H \) or \( V \) was significant (\( P < 0.05 \)) during the saccade period (0–300 ms after Go signal), the neuron was classified as having directional selectivity.

**Normalized firing rate.** The firing rate for each neuron was normalized in a 20-ms window by constructing a z score of activity for each neuron in each bin. The z score was computed across all correct and error trials by normalizing by the standard deviation in the mean activity of each neuron (Buschman and Miller 2009).

**Statistical analyses of neuronal activity and behavior.** To investigate the activity pattern of the surprise neurons, we examined the changes in activity during the postfeedback period during trials that were crucial to oculomotor target selection. Specifically, we calculated the firing rates for the following four types of trials: the first error trial after the change in the valid-target pair (1st E), the first correct trial after the pair change (1st C), the second correct trial after the pair change (2nd C), and the correct trials after more than two consecutive correct trials (CC). We calculated the averaged firing rates of the surprise neurons in these index trials. We used ANOVA with Tukey’s honestly significant difference (HSD) correction (factor: trial types, \( P < 0.05 \)) to assess the differences in neuronal activity between the activities in these trial types. For other statistical tests, we used paired or simple t-tests for comparisons of two values. To investigate the relationship between the activity and oculomotor search patterns, we categorized trials by the oculomotor search pattern in the following trials (diagonal or adjacent) and calculated the mean postfeedback activity in the trials. In this analysis, the exploration phase was analyzed for the error-surprise and error-outcome neurons, and the exploitation phase was analyzed for the correct-surprise and correct-outcome neurons.

**Choice probability.** To determine the extent to which the activity of a neuron predicted the oculomotor search pattern (adjacent or diagonal), we calculated the change probability of task-related neurons (Britten et al. 1996). In this situation, the choice probability was an estimate of the probability that an observer correctly predicted whether the monkey would engage in the adjacent or diagonal search pattern in the subsequent trial. To compute the choice probability, a receiver operating characteristic curve was computed from the distributions of neuronal activities for each of the two search patterns of the animal. The area under the curve was integrated to produce the choice probability (Yang and Heinen 2014).

**RESULTS**

**Behavioral Results**

After training, the accuracy of the two monkeys reached ~90% in the exploitation phase (monkey K: 91 ± 3%, monkey M: 88 ± 4%; mean ± SD). After a valid-pair change, they began to explore new targets and found two targets in a new pair within an average of 4.2 trials (K: 4.2 ± 1.2, M: 4.3 ± 1.3). We first examined the monkeys’ oculomotor search patterns in the exploration and exploitation phases in terms of the three search patterns described in METHODS: diagonal, adjacent, and repeat. During the exploitation phase, the adjacent search pattern was dominant (K: 97 ± 2%, M: 96 ± 2%) and the diagonal search was observed only rarely (K: 1 ± 1%, M: 1 ± 1%) (Fig. 3A). In contrast, during the exploration phase the probability of the diagonal search increased (K: 54 ± 5%, M: 48 ± 5%) and the probability of the adjacent search decreased (K: 39 ± 5%, M: 47 ± 4%). This increase in the probability of the diagonal search during the exploration phase compared with the exploitation phase was statistically significant (paired t-test; \( P < 0.001 \)). In the exploitation phase, 4.2 trials were required to find the current pair of targets after a pair change. However, this raised the question of whether the 4.2 trials were optimal. To answer this, we performed the following analyses.
patterns and saccade directions (ANOVA, factor: direction of stimuli, $P = 0.17$). These results suggest that distinct search strategies operated during the exploration and exploitation phases.

**Neuronal Database**

We recorded 295 neurons in two monkeys (monkey $K$: 268, monkey $M$: 27). Of these SEF neurons, 200 cells ($K$: 184, $M$: 16) were found to be feedback related and 212 cells ($K$: 197, $M$: 15) were eye movement related. Among the 212 eye movement-related neurons, 105 ($K$: 100, $M$: 5) showed significant directional selectivity ($P < 0.05$) during the saccade period. We present the various types of neurons in Table 1.

In the following section, we initially discuss outcome neurons that responded to correct or error feedback. We next address the surprise neurons that showed enhanced activity when the feedback was unexpected. Finally, we investigate the relationship between neuronal activities and behavioral patterns and present data showing that the enhanced activity of the surprise neurons was related to shifts between oculomotor search patterns.

**Outcome Neurons**

We identified SEF neurons showing elevated activity in response to error or correct feedback. The error-outcome neurons responded to error feedback in the current ($n$) trial, irrespective of the outcomes of previous trials (Fig. 4, A and B). The error-outcome neurons were categorized in terms of encoding the outcome values of error feedback ($OV_e$). We identified 47 error-outcome neurons. On the other hand, the correct-outcome neurons were divided into two types. The first type of neuron showed elevated activity in response to correct feedback, irrespective of the outcomes of previous trials (Fig. 4C). The second type of neuron showed distinctly decreasing activity in response to error feedback (Fig. 4D). We categorized 29 cells in the correct-outcome neurons, 21 of which were categorized as the first type of neuron and the remaining 8 of which were categorized as the second type. These correct-outcome neurons were viewed as encoding the outcome values of correct feedback ($OV_c$). Population-level activity was observed to increase slightly in the correct trials and to decrease slightly in the error trials (Fig. 4E). These neurons were not classified as prediction-error neurons but as outcome neurons, because they responded differentially depending on outcome history.

**Surprise Neurons**

The surprise neurons showed enhanced activity when the unpredicted-outcome signals were fed back. There were two types of surprise neurons. First, error-surprise neurons in-

### Table 1. Categorized neurons

<table>
<thead>
<tr>
<th>Neuron Type</th>
<th>Error</th>
<th>Correct</th>
</tr>
</thead>
<tbody>
<tr>
<td>Outcome neuron</td>
<td>47 (44 + 3)</td>
<td>29 (28 + 1)</td>
</tr>
<tr>
<td>Surprise neuron</td>
<td>15 (13 + 2)</td>
<td>14 (13 + 1)</td>
</tr>
<tr>
<td>Prediction-error neuron</td>
<td>3 (2 + 1)</td>
<td>8 (8 + 0)</td>
</tr>
<tr>
<td>Prediction neuron</td>
<td>20 (20 + 0)</td>
<td>10 (8 + 2)</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td>85 (79 + 6)</td>
<td>61 (57 + 4)</td>
</tr>
</tbody>
</table>

Values in parentheses are values for monkey $K$ + monkey $M$.  

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**Fig. 3. Behavioral results.** A: oculomotor search patterns depended on exploration and exploitation phases. The relative incidences of the specific search patterns of 2 monkeys were plotted for each phase. The adjacent search pattern was dominant during the exploitation phase. The diagonal search pattern was common during the exploration phase. B: the search patterns in subsequent trials ($n + 1$) depended on the combination of the outcomes in the current ($n$) and previous ($n - 1$) trials. The diagonal search pattern was frequent after an error was fed back in the current ($n$) trial, especially after feedback to a correct target (Fig. 3B). The adjacent search pattern was dominant after feedback to a correct response was given in the current ($n$) trial, irrespective of the outcomes in the previous ($n - 1$) trials (correct $\rightarrow$ correct and error $\rightarrow$ correct). The adjacent search pattern was divided into groups according to whether the selected target was included in the current pair (other pair).

To investigate whether the subsequent oculomotor search pattern was dependent on behavioral history, we analyzed the search patterns in the next trials ($n + 1$) based on the outcomes in the current ($n$) and previous ($n - 1$) trials. The results showed that the frequency of diagonal search increased after the monkey made errors, especially when the error occurred after correct trials (Fig. 3B). However, adjacent searches were dominant when correct feedback occurred in the current trial ($n$), irrespective of the outcomes in the previous trial ($n - 1$). We observed that the monkeys chose the diagonal target in the specific situation in which the subject made an error after selecting the target that was adjacent to the previous correct target. This pattern was included in correct $\rightarrow$ error in Fig. 3B.

Next, we analyzed the dependence of the monkeys’ behavior on the history of the outcomes of the two preceding trials. Specifically, we compared the probability of a diagonal search occurring between the trials in which the two preceding trials ($n - 2$) were correct and erroneous, respectively. The outcome of the two preceding trials ($n - 2$) did not have a significant effect on the search patterns in the next trials ($n + 1$) (paired t-test, $P > 0.001$). Importantly, this suggests that the monkeys chose the search pattern based on the outcomes of the current ($n$) and previous ($n - 1$) trials and did not use the information provided before the previous trial. This result implied that the monkeys showed suboptimal behavior during our task. On the basis of the finding that the monkeys used a combination of information from the current and previous trials, we categorized the neurons by the outcomes of the current and previous trials.

In addition, to examine whether the search pattern was affected by the direction of the chosen target, we analyzed the relationship between the position of the target selected in the current trial and the search patterns in the subsequent trials. The results revealed no significant relationship between search
neurons were viewed as encoding the surprise signal as error feedback (SS). A total of 15 SEF neurons were placed in this group. Population-level analysis showed the highest activity when the error feedback was received in the current (n) trial after correct feedback had been received in the previous (n−1) trial (Fig. 5B, correct→error). There was no response when the correct feedback was received in the current (n) trial (correct→correct and error→correct). The second example was a correct-surprise neuron, which exhibited elevated activity when correct feedback was given in the current (n) trial after error feedback was received in the previous (n−1) trial (Fig. 5C, error→correct). The postfeedback activity decreased when correct trials occurred successively and were predicted (correct→correct). Because the outcome of the current trial differed from that of the previous trial, the current correct outcome was surprising, and we refer to these neurons as “correct-surprise neurons.” These neurons were viewed as encoding the surprise signal for correct feedback (SS). A total of 14 neurons were placed in this group. Population-level analysis showed similar activity when correct feedback was received in the current (n) trial following error trials (Fig. 5D, error→correct). Notably, these error- and correct-surprise neurons increased in activity in response to the error feedback after a correct trial. Second, correct-surprise neurons increased in activity in response to the correct feedback after an error trial. Afterwards, we investigated how these neurons were related to the behavioral transitions between exploration and exploitation.

The first example was an error-surprise neuron, which showed elevated activity in response to the error feedback in the current (n) trial when correct feedback was received in the previous (n−1) trial (Fig. 5A, correct→error). However, the activity was moderate when the error feedback occurred repeatedly and was predicted (Fig. 5A, error→error). Because the outcome of the current trial differed from that of the previous trial, the current-error outcome was surprising, and we refer to these neurons as “error-surprise neurons.”

Fig. 4. Outcome neurons. A: example of an error-outcome neuron in the SEF. This neuron responded to error feedback (FB), regardless of the outcome of the preceding trial. This neuron did not respond to correct feedback. B: population-level activity of the error-outcome neurons. C: example of a correct-outcome neuron. This neuron showed increasing activity in response to correct feedback, irrespective of the outcomes in the previous trials. D: second example of correct-outcome neuron. This neuron showed reduced activity in response to error feedback. E: population-level activity of the correct-outcome neurons. All firing rates were normalized, and the average z scores were aligned to error or correct feedback (gray dashed lines), respectively. Colored dashed lines in B and E indicate SE of the mean z scores.

Fig. 5. Surprise neurons. A: example of error-surprise neurons in the SEF. This neuron showed elevated activity when an unpredicted error was fed back (correct→error). This postfeedback response decreased when the error was repeated in successive trials (error→error). B: population-level activity of the error-surprise neurons. C: example of a correct-surprise neuron. This neuron showed the highest activity when unpredicted correct feedback was fed back (error→correct). This activity decreased when correct feedback was repeated (correct→correct). D: population-level activity of the correct-surprise neurons. Conventions are the same as in Fig. 4.
neurons differed from neurons reflecting conventional prediction errors (signed $PE_c$ and signed $PE_e$), because the surprise neurons encoded “rectified” positive parts of the prediction errors.

To confirm the validity of the categorization of the surprise neurons, we compared the $R^2$ values of the surprise neurons in terms of the different values in the model. Of the 15 error-surprise neurons, 11 had $R^2$ values $> 0.1$ for signed prediction errors (signed $PE_e$) and 10 had $R^2$ values $> 0.1$ for error outcomes ($OV_e$) (Table 2). However, the $R^2$ values for error-surprise signals were significantly higher than those of the other two groups (paired t-test, $S_{se}$ vs. signed $PE_e$, $P = 0.009$; $S_{se}$ vs. $OV_e$, $P = 0.002$). On the other hand, among the 14 correct-surprise neurons, 9 had $R^2$ values $> 0.1$ for signed prediction errors (signed $PE_e$) and 7 had $R^2$ values $> 0.1$ for correct outcomes ($OV_c$) (Table 2). However, the $R^2$ values for correct-surprise signals were significantly higher than those in other groups (paired t-test, $S_{sc}$ vs. signed $PE_e$, $P = 0.001$; $S_{sc}$ vs. $OV_e$, $P = 0.0007$).

Finally, to investigate whether the surprise neurons were related to specific target directions, we used regression analyses to examine the directional selectivity of the neurons during saccade periods. We found that 10 error-surprise neurons (10/15) and 7 correct-surprise neurons (7/14) showed directional selectivity during the 0–300 ms period after the feedback signals (ANOVA; factor: directions of stimuli; $P < 0.01$). On the other hand, 38 error-outcome neurons (38/47) and 15 correct-outcome neurons (15/29) showed directional selectivity. This result is consistent with a previous finding that half of SEF neurons showed directional selectivity (Roesch and Olson 2003).

**Surprise Neurons and History of Behavioral Outcomes**

We investigated the relationship between the neuronal activity of surprise neurons and the outcome history. We identified two types of surprise neurons in the SEF that exhibited enhanced activity when an unexpected outcome occurred.

First, we investigated how the surprise neurons reflected changes in outcomes after pair shifts. Specifically, we analyzed the averaged firing rates of the surprise neurons in the following trials: the first error trial after a pair change (1st E), the first correct trial after a pair change (1st C), the second correct trial after a pair change (2nd C), and consecutive correct trials (CC). These trials were crucial because they provided clues about the valid targets by tracking the history of behavioral outcomes. As a result, the error-surprise neurons showed significantly enhanced responses in the first error trial after the pair shifts compared with those in the consecutive correct trials (Fig. 6A: 1st E vs. CC, $P = 0.012$). The activity in the first error trial was significantly higher compared with those in the first and second correct trials (Fig. 6A: 1st E vs. 1st C, $P = 0.029$; 1st E vs. 2nd C, $P = 0.025$). We also found that the neuronal activity level of the error-surprise neurons was higher in the first error trial than in the second error trial (1st vs. 2nd, $7.0 \pm 1.2$ vs. $4.8 \pm 0.90$, $P = 0.013$). We did not find a significant change after the third try because of the low number of trials under this condition (<3 trials per neuron). The correct-surprise neurons showed significantly higher activity in the first correct trials compared with the preceding first error trial (Fig. 6B, 1st E vs. 1st C, $P = 0.040$). Furthermore, the activity in the first correct trial of correct-surprise neurons was larger in the first try than in the second try after a pair change, but this difference was not statistically significant (1st vs. 2nd try, $6.0 \pm 0.8$ vs. $4.4 \pm 0.5$, $P = 0.16$). We did not find a significant change in the third try because of the scarcity of trials performed under this condition (<3 trials per neuron). These findings suggest that surprise neurons play a role in detecting the unexpected trials after the valid-pair changes. This result is consistent with a previous study that found that neurons in the frontomedial region showed enhanced activity during the first correct trials after a change in the task condition (Quilodran et al. 2008).  

**Surprise Neurons and Exploration-Exploitation Transitions**

To investigate whether the surprise neurons in the SEF were related to the exploitative or exploratory oculomotor search pattern, we analyzed the relationship between the postfeedback activities and search patterns in the subsequent trials. According to our behavioral analysis, there were two main oculomotor search patterns: diagonal and adjacent. The use of the diagonal pattern increased in the exploration phase, but the adjacent pattern was dominant in the exploitation phase (Fig. 3A). Thus we investigated the relationship between the postfeedback activities and the oculomotor search patterns in the following trials. Specifically, we compared the neuronal activities in the trial followed by a diagonal search with those in the trials followed by an adjacent search. The results showed that error-surprise neurons had significantly higher activity levels in trials followed by a diagonal search than in those followed by an adjacent search (Fig. 6C; $P = 0.040$). Furthermore, correct-surprise neurons showed significantly higher activity levels in trials followed by an adjacent search than in those followed by a diagonal search (Fig. 6D; $P = 0.010$). In contrast, the activity levels of error- and correct-outcome neurons were not significantly correlated with their activities or search patterns in subsequent trials (Fig. 6, E and F; error-outcome neuron: $P > 0.05$, correct-outcome neuron: $P > 0.05$). These results suggest that the increased activity of the surprise neurons is related to the shifts between the oculomotor search patterns but that the activity of the simple outcome neurons is not.

To investigate the influence of postfeedback activity on subsequent behavioral adjustments further, we calculated the choice probability for surprise and outcome neurons (Fig. 6G). In this analysis, we computed the extent to which we could predict whether the subsequent search pattern was diagonal or adjacent. According to the results, the choice probability of the error-surprise neurons was higher than that of the error-outcome neurons ($P = 0.0028$). The choice probability of the correct-surprise neurons was slightly higher than that of the correct-outcome neurons, but this difference was not significant ($P = 0.33$).
In summary, the error-surprise neurons exhibited increased responses in the first error trials, and this activity was related to the behavioral shift from exploitation to exploration in the following trials. The correct-surprise neurons showed significant responses in the first correct trials, and this activity was related to the shift from exploration to exploitation in the following trials. We plotted the distribution of these SEF neurons and found no clear segregation (Fig. 7, B and C).

Fig. 7. Distribution of task-related neurons in the SEF. Data are shown in the dorsal view of the frontal lobe. A: task-related neurons. The positions of the gray dots indicate the locations of the task-related neurons of 2 monkeys relative to the gross morphological landmarks of the midline and the genu of the arcuate sulcus (AS Genu). The sizes of the dots reflect the number of neurons recorded at each location. The horizontal line indicates the frontal level of the AS genu. B: error-surprise neurons. Dots indicate the location of error-surprise neurons (light gray) and error-outcome neurons (gray). C: correct-surprise neurons. Dots indicate correct-surprise neurons (light gray) and correct-outcome neurons (gray). The relationship between the size of dots and the number of neurons is the same as in B.

DISCUSSION

We introduced a two-target search task in which monkeys had to find two adjacent targets by trial and error. Behavioral analysis revealed two distinct oculomotor search patterns during the exploration and exploitation phases and revealed that the monkeys used their memory from only the two preceding trials. We found two types of surprise neurons: error-correct surprise neurons and correct-surprise neurons. These neurons showed elevated responses to unexpected error and correct feedback, respectively. Specifically, the error-surprise neurons selectively showed increasing activity when the monkeys made the first error after a pair change. The correct-surprise neurons

Fig. 6. Relationship between neuronal activity and search patterns. A: averaged activity of the error-surprise neurons. The averaged firing rates in the following trials were plotted as follows: 1st error trial after a valid-target change (1st E), 1st correct trial after a pair change (1st C), 2nd correct trial after a pair change (2nd C), and the correct trial after consecutive correct trials (CC). Dashed line shows the timing of valid-pair changes. The activity was high at the start of exploration after the valid-pair changes (1st E vs. CC, *P = 0.012). The activity in the 1st error trial was higher than that in the 1st correct and 2nd correct trials (1st E vs. 1st C, *P = 0.029; 1st E vs. 2nd C, *P = 0.0025). B: averaged activity of the correct-surprise neurons. The activity level of correct-surprise neurons was high in the 1st correct trial after the valid-pair changes (*P = 0.404). C-G: postfeedback neuronal activities and the subsequent search patterns. C: enhanced activity of the error-surprise neurons was related to the diagonal search pattern in the next trials (paired t-test; *P = 0.040). D: a higher level of activity of the correct-surprise neurons was related to the adjacent search pattern in the subsequent trials (paired t-test; *P = 0.010). E and F: the activities of the error-outcome (E) and correct-outcome (F) neurons were not related to the search patterns in the next trials (paired t-test; P → 0.05). All error bars indicate SE. ns, not significant. G: choice probabilities for error-surprise and error-outcome neurons (left) and for correct-surprise and correct-outcome neurons (right). Bar graphs show the mean choice probability value of each group. The choice probability of the error-surprise neurons was significantly higher than that of the error-outcome neurons (**P = 0.0028).
showed enhanced activity when the monkeys found the first correct target after a pair change. Furthermore, the surprise neurons were related to the exploration-exploitation transitions. Specifically, the error-surprise neurons showed enhanced activity preceding the transition from exploitative to explorative search pattern. In contrast, the correct-surprise neurons showed enhanced activity preceding the transition from explorative to exploitative search pattern. Our results suggest that the SEF is involved in behavioral transitions between exploration and exploitation by encoding the surprise signals (Fig. 1).

Behavioral Shifts During Two-Target Search Task

The unique feature of our search task was the absence of an external cue for valid targets and the attendant requirement that monkeys search for the targets by trial and error. Previous studies used visual search tasks in which monkeys had to find a target among multiple identical stimuli (Amiez et al. 2012; Mirpour and Bisley 2012; Procyk et al. 2000; Quilodran et al. 2008). In contrast, our oculomotor search task required monkeys to make alternate saccades to two valid targets during the exploration phase to motivate them to change the search pattern after a pair change. Thus the subjects had to maintain their memory of previous choices and feedback to choose subsequent behavioral patterns.

Interestingly, the behavioral analyses revealed that the monkeys remembered the outcomes of only the two preceding trials: the current \( (n) \) and the previous trial \( (n - 1) \). In a previous study, Quilodran et al. (2008) demonstrated that monkeys could remember the outcomes of three preceding trials according to their ability to choose the correct target among four possibilities after three consecutive error trials. This discrepancy between the findings of Quilodran et al. and our findings may be explained not by a limit in the monkeys’ working memory but rather by their search strategy. In the study by Quilodran et al. the monkeys had to find one correct target among four targets, but our study required the monkeys to select two valid targets alternately. Our task was more demanding, and the monkeys used the two preceding outcomes to choose the subsequent search patterns.

Surprise Signals in SEF

Our results revealed surprise neurons in the SEF. These were defined as neurons that encoded the unsigned, rectified values of the prediction error, the difference between the prediction and the outcome. These surprise neurons engaged in activity that was distinct from that displayed by outcome neurons and reward-prediction-error neurons. Their pattern of activity was similar to that of surprise neurons in the anterior cingulate cortex (ACC) and prefrontal cortex (PFC) in that they responded to unpredicted outcomes (Asaad and Eskandar 2011; Shidara and Richmond 2002). Learning-selective activity has been observed in the SEF during an associative learning task, and this type of activity appeared preferentially when a novel stimulus was introduced (Chen and Wise 1995). One recent study revealed a group of neurons that encoded valence-related reward-prediction errors (So and Stuphorn 2012). In this context, we possibly demonstrated that SEF neurons encode a different aspect of the prediction error and that distinct types of surprise neurons represent the rectified prediction errors for correct and error feedback, respectively. Our finding supports the notion that the surprise signal promotes adaptive learning in a changing world (Courville et al. 2006; Pearce and Hall 1980).

The SEF encodes two types of prediction errors: one is based on the amount of reward and the other on the subjective probabilities of feedback. The former type of prediction error was identified with a behavioral task that involved changing the amount of the reward systematically (So and Stuphorn 2012). On the other hand, we investigated the latter type of prediction error as a surprise signal. We computed surprise signals based on the subjective probability of feedback, because we assumed that the SEF was able to evaluate outcomes based on the subjects’ behavioral history. This is consistent with a recent study in which SEF neurons showed metacognition-related activity that reflected the subjective probability of correct choices (Middlebrooks and Sommer 2012).

We found that a portion of the surprise neurons showed directional selectivity during saccade periods, implying that they integrated directional information and outcome signals. We assumed that the directional information in the saccade period and the outcome information during the postfeedback period would be combined to adjust subsequent behavior. On the other hand, a previous report showed that reward value and directional information were represented separately in the SEF, but these signals were expected to be used in concert to adjust behavior (So and Stuphorn 2012). Future studies should address how information regarding action and outcome is integrated to adjust subsequent behavior.

Surprise Signals in Frontal Areas

Surprise signals, responses to unpredicted outcomes, were also observed in other frontal areas, such as the ACC, in single-cell recording studies (Amiez et al. 2005; Hayden et al. 2011; Shidara and Richmond 2002). Correct/error-related activity was reported in single-cell recording studies (Ito et al. 2003; Matsumoto et al. 2007) as well as in event-related potential studies (Emeric et al. 2008; Gembä et al. 1986). Neurons in the lateral prefrontal cortex (LPFC) were also reported to reflect positive or negative prediction errors (Asaad and Eskandar 2011; Seo and Lee 2007). The SEF is connected anatomically to the ACC and LPFC (Huerta and Kaas 1990; Wang et al. 2005). These functional and anatomical studies suggest that surprise signals are encoded in the frontal network in the SEF, ACC, and LPFC.

Furthermore, human electroencephalogram studies have reported event-related potentials in the medial frontal region in response to unexpected negative, unexpected positive, or novel stimuli (Falkenstein et al. 1991; Gehring et al. 1993; Holroyd et al. 2008; Ridderinkhof et al. 2004; Wessel et al. 2012). Indeed, the relationship between error-related responses and neuronal activity should be investigated in future research.

Surprise Signals and Exploration-Exploitation Transitions

We found that the elevated activities of the surprise neurons in the SEF were followed by specific search patterns. Combined with behavioral analysis that showed distinctive explorative and exploitative search patterns, our results suggest that the SEF neurons are related to the transitions between exploration and exploitation in visual searches (Fig. 1). As a frontomedial region, the ACC is functionally significant in adaptive, exploratory behavior (Daw et al. 2006; Procyk et al. 2000;
cause of sensory inputs based on a generative model and that predictive coding theory, which holds that the brain infers the outcome was repeated. This pattern of responses fits well with outcome was unexpected and decreased activity when the same and Timing

Surprise Signals from the Perspective Of Predictive Coding

between exploration and exploitation strategies appropriately. According to our findings, study of a patient with a focal SEF lesion (Husain et al. 2003). Investigates how the oculomotor system is involved in the task. Understood to the subcortical systems, such as the locus coeruleus (LC) or dopaminergic network. The subcortical systems regulate decision-making processes (Doya 2002; Yu and Dayan 2005), and this activity has been related to behavioral transitions (Barnes et al. 2005; Graybiel 2008). Cortical and subcortical contributions to exploration and exploitation have also been supported by studies evaluating genetic factors in humans (Frank et al. 2009). In light of these findings, our data suggest that, along with the ACC and OFC, the SEF plays an evaluative role. Indeed, anatomical studies have shown that the SEF is connected to the LC (Arnsten and Goldman-Rakic 1984; Shook et al. 1990) and the ACC (Huerta and Kaas 1990; Wang et al. 2005). Thus the SEF is expected to manage the balance between exploration and exploitation by sending surprise signals to the subcortical systems, such as the LC.

Exploration-Exploitation Transition as Set Shifting

Our task resembles the Wisconsin Card Sorting Test (WCST) in that it requires cognitive flexibility in switching mental “sets” (Milner 1963; Stuss et al. 2000). Functional MRI and single-cell recordings from monkeys performing an analog of the WCST have shown that the medial and lateral PPCs are involved in set shifting (Kamigaki et al. 2012; Konishi et al. 2010; Nakahara et al. 2002). Another study showed that ACC neurons responded to correct or error feedback and changed activity depending on the outcome of the previous trial (Mansouri et al. 2006). Compared with the WCST, our task requires understanding of the spatial combinations of the targets, but it investigates how the oculomotor system is involved in the task.

From a clinical perspective, our finding is consistent with a study of a patient with a focal SEF lesion (Husain et al. 2003). This patient demonstrated difficulty in adapting to unexpected rule changes in a rule-reversal task. According to our findings, the patient may have been impaired in the ability to switch between exploration and exploitation strategies appropriately.

Surprise Signals from the Perspective Of Predictive Coding and Timing

The surprise neurons showed increased activity when the outcome was unexpected and decreased activity when the same outcome was repeated. This pattern of responses fits well with predictive coding theory, which holds that the brain infers the cause of sensory inputs based on a generative model and that prediction errors are used to adjust the model until the error is minimized (Friston 2005). The framework of the predictive coding explains the neuronal mechanism for repetition suppression, in which stimulus-evoked neural activity is attenuated when the same stimulus is presented repeatedly and activity is enhanced when the stimulus is unpredictable (Summerfield et al. 2008; Todorovic and de Lange 2012). Thus the surprise signal in our task corresponds to the prediction error in predictive coding theory (Friston 2005).

We also found that a group of SEF neurons showed increased activity until the predicted event occurred. This type of activity is consistent with predictive timing theory, which posits that the brain estimates the timing of events and holds that prediction errors are generated when expected events do not occur (Arnal and Giraud 2012; Nobre et al. 2007). The predictive timing theory may explain various types of activity in SEF neurons, such as those that responded to predictable target motion (Heinen and Liu 1997) and error feedback (Stuphorn et al. 2000), reward-predicting (Amador et al. 2000), event-predicting, and event-detecting neurons (Campos et al. 2010). Additionally, the presupplementary motor area has been reported to encode elapsed time (Mita et al. 2009). Combined with these data, our results provide evidence that the SEF is involved in both predictive coding and predictive timing. Furthermore, our study also suggests that the signals generated according to these theories are important for making subsequent behavioral adjustments.

Effects of Feedback Signals on Outcomes and Surprise Neurons

We found a substantial difference in the number of neurons and the activity patterns of the error- and correct-outcome neurons. Two possibilities for this difference are discussed below. The first possibility is that these differences were due to variations in the visual stimuli that signal error and correct feedback. Error feedback was signaled by the disappearance of visual stimuli, whereas correct feedback was signaled by a change in the color of a fixation target. The second possibility involves the difference in behavioral context. In our task, error feedback was critical when exploitation was switched to exploration; in contrast, correct feedback was related to the maintenance of current exploitation and the switch from exploitation to exploitation. The context-dependent difference in response to error or correct feedback is consistent with the previous finding that error/correct-related activities were influenced by the likelihood of error in the behavioral task (Jessup et al. 2010; Wessel et al. 2012).

We found 15 error-surprise neurons (10% of all feedback-related neurons) and 14 correct-surprise neurons (10%). These numbers seem small compared with the numbers reported in previous studies showing reward-prediction errors in the ACC (Hayden et al. 2011) and LPFC (Asaad and Eskandar 2011; Seo and Lee 2007). However, our result is comparable with other studies evaluating the SEF (So and Stuphorn 2012) and ACC (Matsumoto et al. 2007). The differences in the numbers of neurons that encode reward-prediction errors may be explained by the type of feedback. Like the present study, the research conducted by the So and Matsumoto groups investigated neuronal activities during the postfeedback period, and feedback was provided in the form of visual signals. In con-
Contrast, the feedback in the former studies was an actual reward. Thus differences in the type of feedback may be a key contributor to the responsiveness of cortical neurons to unexpected outcomes.

Limitations in the Original Model and Alternatives to the Model

We found that the correct-surprise and correct-outcome neurons were suppressed strongly in response to error feedback. These neurons were categorized as correct-outcome or surprise neurons because we fitted each model to the postfeedback activity according to its relative firing rates in correct and error trials. This result raises the possibility that SEF neurons change their response preferentially to behavioral errors rather than to correct feedback. This preference for error responses in the SEF is consistent with findings of the dominance of error-related negativity in event-related potential studies (Falkenstein et al. 1991; Gehring et al. 1993; Holroyd and Coles 2002).

The correct-surprise neurons showed seemingly “signed” responses to the feedback (Fig. 5, C and D), because they exhibited error-related suppression. However, this activity was explained better by the model of “unsigned” surprise signals. Indeed, the difference between actual and expected outcomes was reflected only in an increase in the activity and not in a reduction in the activity of the correct-surprise neurons. To resolve this apparent discrepancy, we hypothesized an additional model of correct-surprise signals based on a combination of the two types of outcome activity (Fig. 8). In this model, the correct-outcome value was increased in response to correct feedback and the error-outcome value was reduced in response to error feedback. Previous studies have demonstrated that SEF neurons reflect both types of outcome values, as predicted by this model (Amador et al. 2000; Roesch and Olson 2003; So and Stuphorn 2012; Stuphorn et al. 2000). New types of unsigned surprise signals should be investigated in the future.

Conclusions

We found two types of surprise neurons in the SEF during the two-target oculomotor search task. Error-surprise neurons responded to unexpected error feedback and were involved in the transition from exploitation to exploration. Correct-surprise neurons responded to unexpected correct feedback and were involved in the transition from exploration to exploitation. Our results suggest that the SEF contributes to the control of exploration-exploitation transitions by detecting unexpected behavioral outcomes.

APPENDIX

In this section, we present the values used in and theoretical background of our model.

Outcome values represent whether a specific outcome was fed back. Outcome values at time $t$ were divided into two types: the outcome value of correct feedback ($OV_{c,t}$) and the outcome value of error feedback ($OV_{e,t}$). We set the $OV_{c,t}$ as 1 and the $OV_{e,t}$ as 0 for correct feedback. In contrast, we set the $OV_{c,t}$ as 0 and the $OV_{e,t}$ as 1 for error feedback.

Prediction values represent the probability that a specific outcome occurred at time $t$. Prediction values were divided into two types: the prediction value of correct feedback ($PV_{c,t}$) and the prediction value of error feedback ($PV_{e,t}$). $PV_{c,t}$ and $PV_{e,t}$ represented the subjective probability of correct and error feedback at time $t$, respectively. These values were updated at each time $t$ with a temporal difference algorithm (Alexander and Brown 2011; Sutton and Barto 1998). Each iteration (dt) represents 10 ms of real time. The prediction values at time $t$ ($PV_{c,t}$) were computed as

$$PV_{c,t} = \sum_{i} X_i \times W_t$$

where $X_i$ is a set of task-related stimuli modeled as a temporal delay chain. $W_t$ is a learned weight and constrained by $W_t \rightarrow 0$. $W_t$ was computed as follows:

$$W_{t+1} = W_t + \alpha \delta e_t$$

where $\alpha$ is the learning rate ($0.1 \leq \alpha \leq 0.3$) and $e_t$ is an eligibility trace at time $t$. $\delta e_t$ and $\delta c_t$ were the temporal difference errors in correct or error feedback, respectively, at time $t$ and were defined as follows:

$$\delta e_t = OV_{e,t+1} + \gamma PV_{e,t+1} - PV_{e,t}$$
$$\delta c_t = OV_{c,t+1} + \gamma PV_{c,t+1} - PV_{c,t}$$

where $OV_{c,t}$ and $OV_{e,t}$ represent occurrences of correct and error feedback, respectively, at time $t$. $PV_{c,t}$ and $PV_{e,t}$ are the prediction values of correct and error feedback, respectively, at time $t$. $\gamma$ is a temporal discounting factor ($0 \leq \gamma \leq 1$). $PV_{c,t}$ and $PV_{e,t}$ reflect the subjective probability of correct and error feedback based on the histories of outcomes, regardless of actions.

Multiple prediction errors.

In this model, signed and unsigned prediction errors were computed based on differences between predicted and actual outcomes. First, we defined signed prediction errors for correct and error feedback (signed $PE_{c,t}$ and signed $PE_{e,t}$) as follows:

signed $PE_{c,t} = OV_{c,t} - PV_{c,t}$
signed $PE_{e,t} = OV_{e,t} - PV_{e,t}$

where $OV_{c,t}$ and $OV_{e,t}$ represent occurrences of correct and error feedback, respectively, at time $t$. $PV_{c,t}$ and $PV_{e,t}$ are prediction values for correct and error feedback, respectively, at time $t$.

Next, we defined surprise signals ($SS_{e,t}$) as rectified unsigned prediction errors. The surprise signals were divided into correct- or error-responsive types. An error-surprise signal ($SS_{e,t}$) was generated when an unexpected error outcome was received at time $t$. A correct-surprise signal ($SS_{c,t}$) was generated when an unexpected correct outcome was received at time $t$. Thus these two values were produced.

Fig. 8. Hypothetical model of correct-surprise signals. This surprise signal may explain the correct-surprise signals observed in Fig. 5, C and D. In this model, a differential response to correct and error feedback was hypothesized, and the surprise signals were associated with increasing activity in response to correct feedback and decreasing activity in response to error feedback.
to respond to the unpredicted outcome of correct and error feedback at time $t$. The values were defined as follows:

$$SS_{c,t} = [OV_{c,t} - PV_{c,t}]$$
$$SS_{e,t} = [OV_{e,t} - PV_{e,t}]$$

where $[OV_{c,t} - PV_{c,t}]^+$ and $[OV_{e,t} - PV_{e,t}]^+$ are the rectified positive parts of the prediction errors. $OV_{c,t}$ and $OV_{e,t}$ represent occurrences of correct and error feedback, respectively, at time $t$. $PV_{c,t}$ and $PV_{e,t}$ are prediction values of correct and error feedback, respectively, at time $t$. The $SS_{c,t}$ and $SS_{e,t}$ are high when the prediction values are low and unpredicted feedback occurs. These values are shown in Fig. A1. The values are emphasized for visualization purpose.

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the author(s).

AUTHOR CONTRIBUTIONS

Author contributions: N.K., K.S., N.S., and Y.F. performed experiments; N.K. and K.S. analyzed data; N.K. prepared figures; N.K. drafted manuscript; N.K., K.S., and H.M. edited and revised manuscript; J.T. and H.M. conceived and designed research; M.A. and H.M. approved final version of manuscript.

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Fig. A1. Model of the error- and correct-surprise signals. The surprise signal (SS) was calculated by the 2 basic values, the prediction value (PV) and the outcome value (OV). The OV represents whether preferred feedback occurred (framed by gray line). The PV represents the subjective probability of the preferred feedback. We categorized the PV into 2 types: higher and lower probability. The OV shows transient increases during feedback, and the PV shows increases before feedback and decreases after feedback. Dashed lines indicate the timing of the feedback. Both outcome values and surprise signals were divided into 2 types depending on the preference for correct or error feedback. A: simulated value of the error-surprise signal (SS$_e$). The value is the rectified portion of the prediction error produced by subtracting PV$_e$ from OV$_e$. SS$_e$ is high when the error feedback was not expected but an error occurred (blue, framed by black line). The postfeedback response is lower when the error feedback occurred repeatedly (sky blue). B: correct-surprise signal (SS$_c$). The value is the rectified portion of the prediction error produced by subtracting PV$_c$ from OV$_c$. SS$_c$ is high when the correct feedback was expected but an error occurred (red, framed by black line). The response was lower when correct feedback was expected and occurred repeatedly (magenta).

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