



OPEN Monkeys increase scratching when encountering unexpected good fortune

Sakumi Iki[✉] & Ikuma Adachi

Elucidating how ancestral behavioural traits have been repurposed for psychological and social functions is critical to advancing our understanding of human behavioural evolution. Self-scratching, originally a hygienic response and known to exhibit social contagion, serves as a model for this process. Although human scratching behaviour is traditionally linked to negative emotions, evidence from non-human animals has produced inconsistent results, casting doubt on its association with negative emotions. Here, we examined scratching in Japanese macaques (*Macaca fuscata*) during cognitive tasks. In Experiment 1, we manipulated reward outcomes by introducing rare, unexpected increases (“fortunate” condition) or omissions (“unfortunate” condition) of rewards; scratching increased significantly under the *fortunate* condition, but not the *unfortunate* one. In Experiment 2, we presented unexpected visual stimuli without altering reward outcomes and observed increased scratching. Our results challenge the traditional view that scratching is primarily linked to negative emotions. Our findings suggest that scratching, which originally evolved as a response to unexpected skin stimulation, may later have been repurposed as a coping mechanism to manage heightened uncertainty.

Keywords Self-directed behaviour, Japanese macaques, Evolution, Surprisal, Coping strategy, Exaptation

To understand the evolution of human behaviour, it is necessary to consider how ancestral traits that originally evolved for specific adaptive functions can, over time, become linked to and reshaped by incidental psychological, social, and ecological factors^{1–3}. Self-scratching (hereafter scratching) may serve as an excellent model for examining such processes. This fixed action pattern, which is thought to have originally evolved as a hygienic and defensive behaviour against skin irritants and ectoparasites^{4,5}, is also hypothesised to be associated, in modern humans, with specific negative emotional responses and social signalling. For example, itching and scratching behaviours often increase during periods of stress, anxiety, or fear^{6,7}. Moreover, it has been suggested that observing others scratch can trigger scratching behaviour in observers^{8,9}, indicating a possible link to the social transmission of negative emotions¹⁰. How did this behaviour, which originally evolved as a simple hygienic and defensive mechanism, come to be associated with and shaped by such psychological factors and social functions?

Studies on non-human animals suggest that scratching is not necessarily associated with negative valence. On the one hand, consistent with studies on humans mentioned earlier, scratching increases in situations that evoke anxiety or fear, such as aggression (olive baboons, *Papio anubis*¹¹; tufted capuchin monkeys, *Cebus apella nigritus*¹²; Japanese macaques, *Macaca fuscata*¹³), social isolation (olive baboons¹⁴; tufted capuchin monkeys¹²), maternal separation from infants (rhesus macaques, *Macaca mulatta*¹⁵), or frustrating conditions, such as uncertain tasks or task failures (chimpanzees, *Pan troglodytes*^{16,17}; mandrills, *Mandrillus sphinx*¹⁸). Scratching also decreases in situations that alleviate anxiety, for instance, reconciliation after conflict (long-tailed macaques, *Macaca fascicularis*¹⁹; brown lemur, *Eulemur fulvus*²⁰) or the administration of anxiolytics (black-tufted marmoset, *Callithrix penicillata*²¹). On the other hand, several studies indicate that scratching does not always increase in conditions expected to elicit negative emotions, such as social isolation or predatory threat in common marmosets (*Callithrix jacchus*)²², and exposure to crowding in hamadryas baboons (*Papio hamadryas*)²³. Moreover, scratching even increases during activities such as play (common marmosets²⁴). Play is generally regarded as an autotelic, intrinsically rewarding activity for animals²⁵, and is often used as an indicator of good welfare²⁶. Among primates, play is accompanied by facial expressions thought to be homologous to human laughter²⁷. Consequently, play is typically viewed as an activity associated with positive, joyful emotions²⁸. Overall, these inconsistencies in previous studies suggest that a simple dichotomy between

Center for the Evolutionary Origins of Human Behavior, Kyoto University, Inuyama, Aichi, Japan. ✉email: sakumi.iki@gmail.com

positive and negative valence may not be the decisive factor for scratching. Instead, other psychological aspects may play a key role in the occurrence of scratching. Understanding such aspects may help explain how behaviour that originally evolved as a straightforward defensive and maintenance activity came to be associated with, and shaped by, psychological and social dimensions.

The present study focused on the fact that situations previously described as inducing scratching—whether negative (e.g., social disruption following aggression or challenging cognitive tasks) or positive (e.g., play involving flexible recombination of existing behavioural repertoires^{29,30})—can both be characterised by unexpectedness. Building on this, we proposed and tested the hypothesis that an event's unexpectedness—and the resultant surprise and arousal—rather than the valence of a situation (i.e., whether it is favourable or unfavourable), are the key factors triggering scratching behaviour.

This study investigated scratching behaviour in Japanese macaques during touchscreen-based cognitive tasks. We employed a go/no-go task where subjects distinguished between a black or white S+ (a stimulus yielding a reward pellet when touched) and S− (a stimulus resulting in a mild punishment, i.e., an increased waiting time, when touched). In Experiment 1, we compared scratching frequency across three conditions (Fig. 1): (i) the “fortunate” condition, where the reward outcome for correct responses was increased eightfold on rare occasions (6 out of 326 trials per session, corresponding to approximately 1.8% of trials; this proportion was consistent across all experimental conditions); (ii) the “unfortunate” condition, where no reward outcome was dispensed on rare occasions; and (iii) the *control* condition, where subjects consistently received the standard reward outcome. If unexpectedness and the resultant surprise and arousal—rather than valence (positive or negative)—are the key factors, scratching should increase in both the *fortunate* and *unfortunate* conditions compared to the *control* condition.

However, even if the results of Experiment 1 align with this prediction, an alternative explanation remains: changes in reward outcome, rather than unexpectedness itself, may be responsible for triggering scratching behaviour. To test this alternative explanation, we conducted Experiment 2, comparing scratching frequency

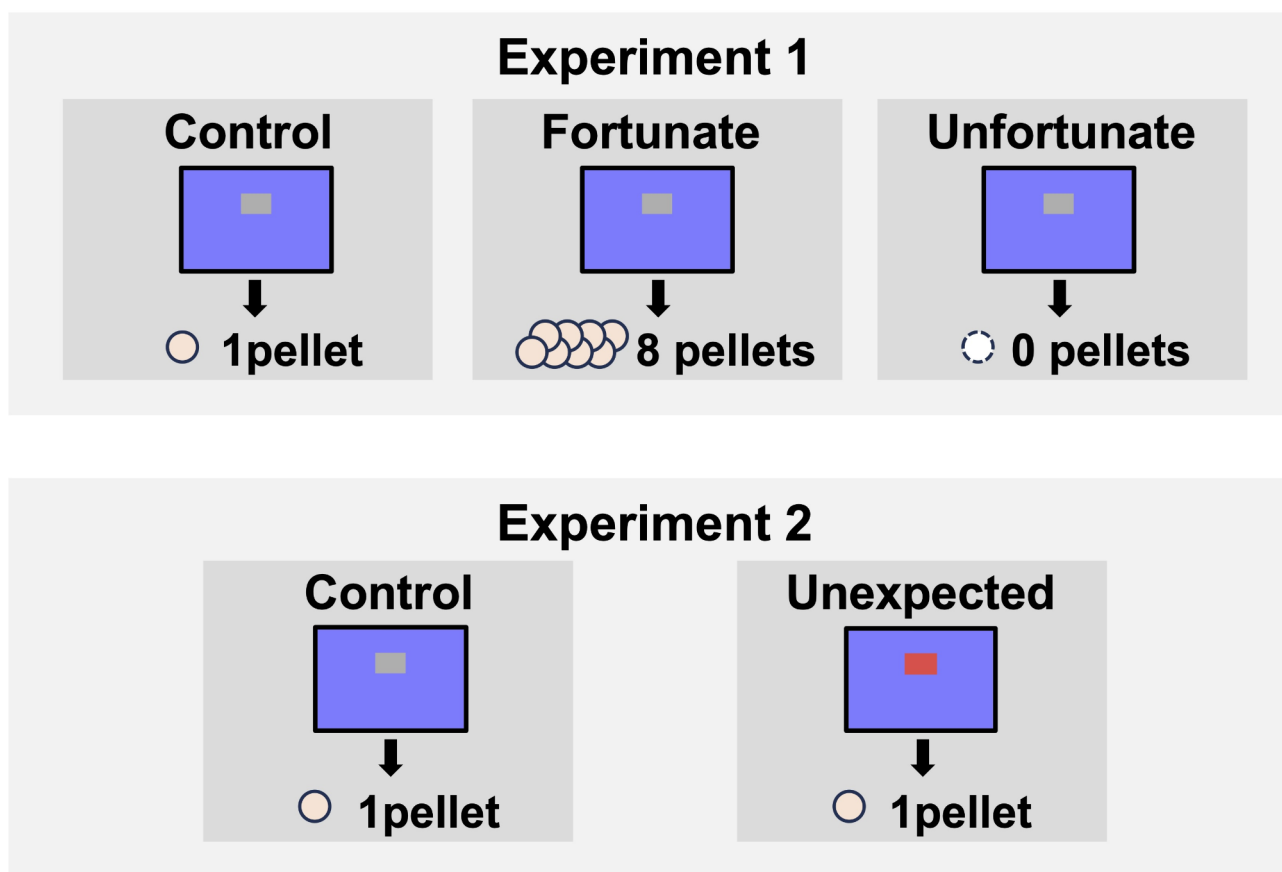


Fig. 1. Overview of Experiments 1 and 2. In both experiments, six trials, corresponding to approximately 1.8% of all trials in each session, were designated as test trials. During each trial, a button (S+) that dispensed a reward upon being touched was displayed on the screen. In Experiment 1, a pre-learned S+ (depicted here as a white button, although the allocation of black and white colours to S+ and S− was actually counterbalanced across subjects) was displayed in all conditions; however, the reward outcome associated with touching the button varied depending on the condition. In Experiment 2, the reward amount remained consistent across conditions; however, in the *unexpected* condition, novel S+ stimuli, which the subjects had never encountered before, were displayed. A total of 24 novel stimuli were used, each presented only once to each subject.

between the “unexpected” condition—in which a novel S+ button, differing from the usual white or black buttons in colour, shape, or location, was presented on rare occasions—and the *control* condition (Figs. 1 and 2). Importantly, subjects always received the standard reward amount for responding to the S+ button in both the *unexpected* and *control* conditions. Thus, unlike in Experiment 1, where changing the reward amount in response to touching a familiar S+ button served as an unexpected event, in Experiment 2, the presentation of an unfamiliar button violated the subjects’ expectations. If unexpectedness and the resultant surprise, rather than changes in reward outcomes, were the key factors, scratching would be expected to increase under the *unexpected* condition.

Results

Experiment 1

We analysed the scratching frequency using a Generalised Linear Mixed Model (GLMM; see Methods). The full model, which included condition (*fortunate*, *unfortunate*, *control*) as the key predictor along with control variables, explained significantly more variance than the null model containing only control variables (likelihood ratio test: $\chi^2 = 6.48$, $df = 2$, $p = 0.039$; Table S1). Furthermore, if subjects had developed anticipations about forthcoming novel events during the experimental conditions as trials progressed—and if their scratching was influenced by these anticipations rather than by unexpected changes in reward outcomes—an interaction effect between condition and trial number would be expected. However, including the interaction term did not significantly improve the model fit (likelihood ratio test: $\chi^2 = 1.23$, $df = 2$, $p = 0.540$; Table S1). Thus, the alternative explanation—that expectations formed over the course of the trials about changes in reward outcomes influenced scratching frequency—is not supported.

The results indicated that the unexpected increase in a reward in the *fortunate* condition significantly increased subsequent scratching frequency compared to the *control* condition (GLMM: Condition [*fortunate*], $\beta = 0.354 \pm 0.137$, $p = 0.0098$; Fig. 3; Table S2). However, there was no significant difference between the *unfortunate* and *control* conditions (GLMM: Condition [*unfortunate*], $\beta = 0.150 \pm 0.145$, $p = 0.304$; Fig. 3; Table S2). Moreover, our results showed that higher baseline scratching frequency was associated with lower scratching frequency during the experiment (GLMM: Baseline frequency, $\beta = -0.651 \pm 0.307$, $p = 0.034$; Table S2), which

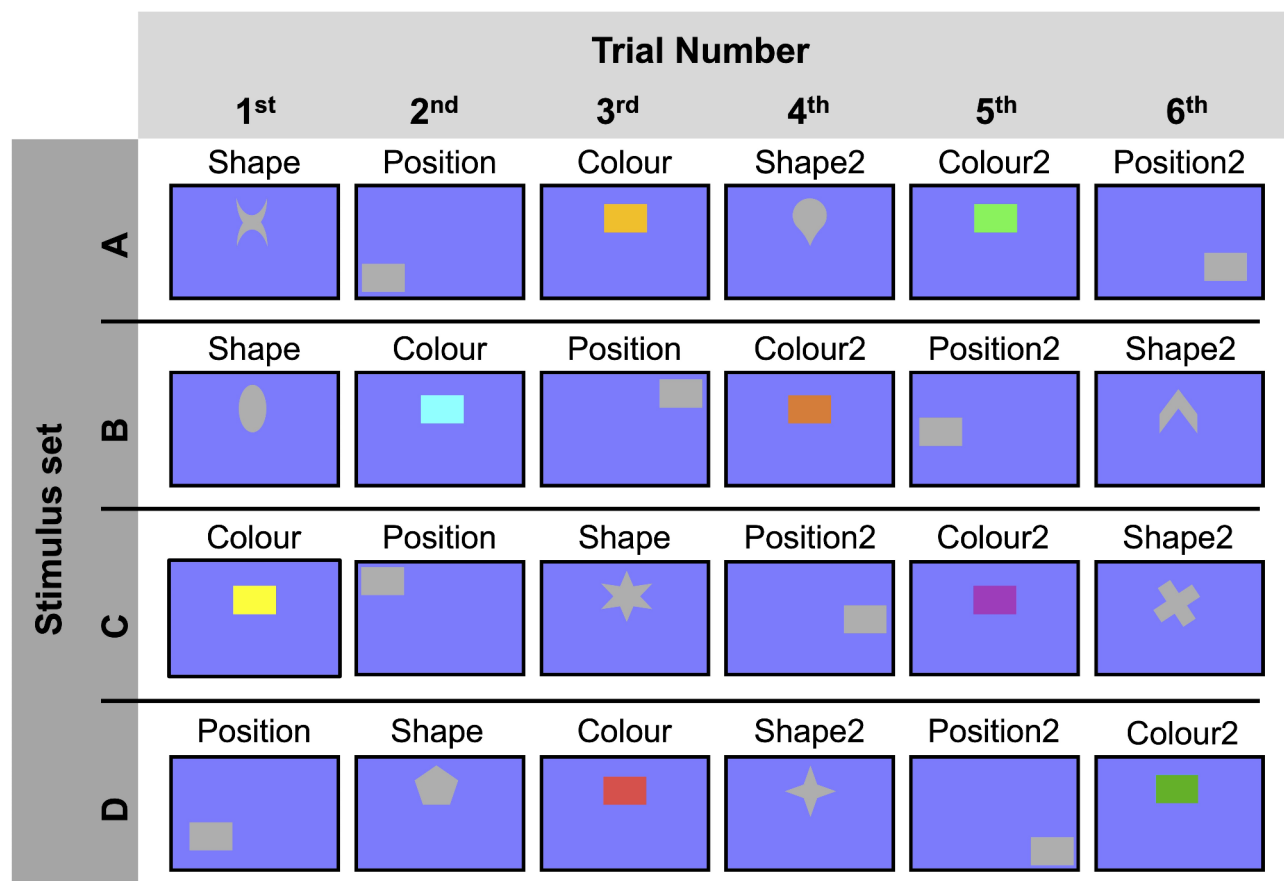


Fig. 2. Stimuli used in the unexpected condition of experiment 2. Four stimulus sets (A–D) were used, with each set presented to each subject once. The order in which the stimulus sets were assigned was pseudorandomised across subjects. Each stimulus set contained six novel stimuli: two stimuli differing from the standard S+ in shape, two differing in position, and two differing in colour. Each novel stimulus was presented once during the six test trials of a session, in the order illustrated in the figure.

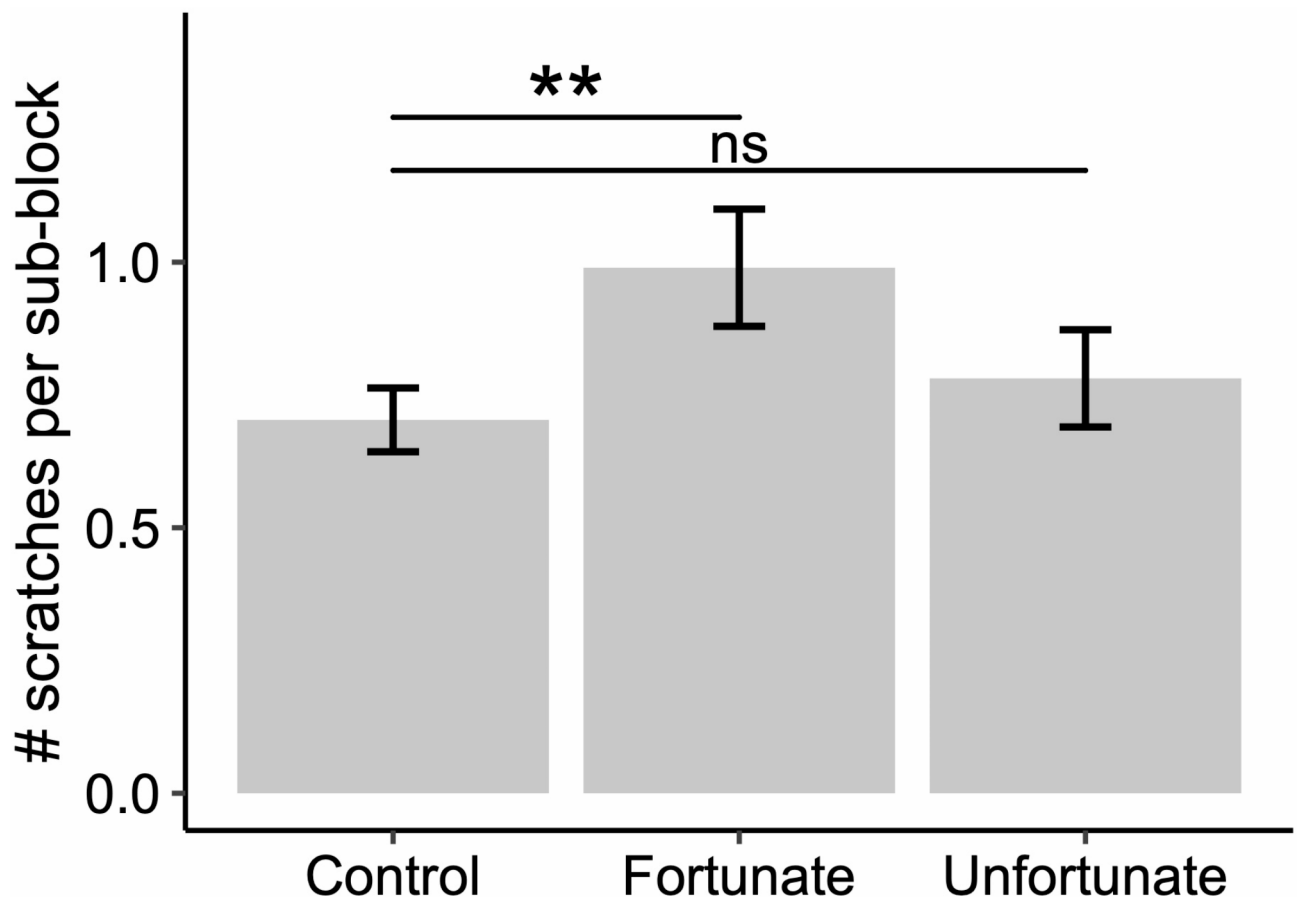


Fig. 3. Number of scratching bouts occurring in the interval between the subject's response to the S+ in one test trial and their response to the S+ in the next test trial. Error bars represent standard errors. Sample size: $N = 384$. ** $p < 0.01$; ns: non-significant (Poisson GLMM).

may suggest that frequent scratching prior to the experiment reduced the subjects' subsequent motivation to scratch during the experiment. Furthermore, the results indicated that scratching was more likely to occur in later trials (GLMM: Trial number, $\beta = 0.082 \pm 0.034$, $p = 0.015$; Table S2).

Experiment 2

To confirm that the three types of novel, unexpected S+ in Experiment 2, which differed from the usual S+ either in colour, shape, or position, elicited surprise or confusion in the subjects, we analysed response times to S+ using a GLMM. The full model, which included the type of S+ as the key predictor alongside control variables, explained significantly more variance than the null model containing only control variables (likelihood ratio test: $\chi^2 = 390.61$, $df = 3$, $p < 0.0001$; Table S1). The results showed that reaction times to all three types of novel, unexpected S+ were significantly longer than those to the usual S+ (Tukey's post-hoc test: Control vs. Colour, $\beta = -2.065 \pm 0.120$, $p < 0.0001$; Control vs. Position, $\beta = -1.921 \pm 0.119$, $p < 0.0001$; Control vs. Shape, $\beta = -2.085 \pm 0.118$, $p < 0.0001$; Fig. 4; Tables S3 and S4). This finding suggests that these novel stimuli induced confusion or surprise, leaving the subjects uncertain about how to respond. No significant differences in reaction times were observed among the three types of unexpected stimuli (Tukey's post-hoc test: Colour vs. Position, $\beta = 0.143 \pm 0.155$, $p = 0.793$; Colour vs. Shape, $\beta = -0.020 \pm 0.155$, $p = 0.999$; Position vs. Shape, $\beta = -0.163 \pm 0.153$, $p = 0.709$; Fig. 4; Tables S3 and S4). Consequently, subsequent analyses treated the three types of unexpected stimuli as a single category.

For scratching frequency, the full model, which included condition as the key predictor alongside control variables, explained significantly more variance than the null model containing only control variables (likelihood ratio test: $\chi^2 = 9.23$, $df = 1$, $p = 0.002$; Table S1). Additionally, the model containing the interaction term between trial number and condition did not improve the model fit ($\chi^2 = 1.22$, $df = 1$, $p = 0.27$). The results indicated that exposure to unexpected stimuli significantly increased subsequent scratching frequency compared to the control condition (GLMM: Condition [unexpected], $\beta = 0.486 \pm 0.157$, $p = 0.002$; Fig. 5; Table S5). No other effects were statistically significant.

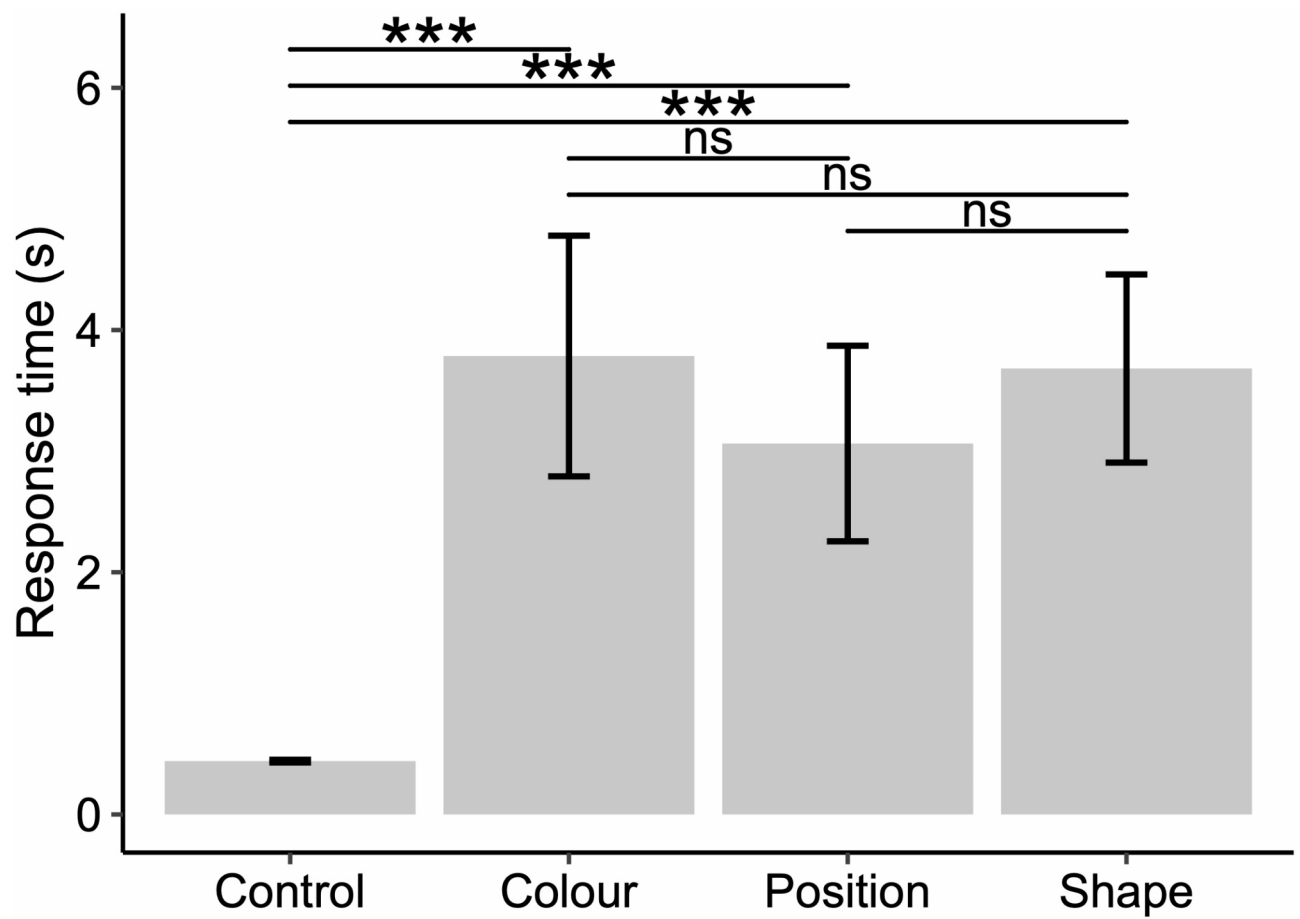


Fig. 4. Response time to different types of S+. Pre-learned, standard S+ (*control*), as well as novel stimuli differing in colour, position, or shape, were used. Sample size: $N=288$. *** $p < 0.001$; ns: non-significant (Tukey's post hoc test).

Discussion

Overall, our findings support the hypothesis that surprise—arising when animals encounter unexpected events—is a significant trigger for scratching. The results of Experiment 1 indicate that scratching increases in response to unexpected reward enhancements. The lack of improvement in model fit when incorporating the interaction between condition and trial number suggests that the alternative explanation—that scratching was induced by the subjects' prospects of forthcoming increased rewards—cannot be supported. Additionally, we did not observe an increase in scratching in the *unfortunate* condition, where subjects unexpectedly failed to receive rewards, compared to the control condition. The subjects' training history may explain this unanticipated result. In prior studies conducted more than four months before the training period of this study^{31,32}, our subjects were trained under a variable ratio reinforcement schedule and had previously experienced situations in which correct responses were sometimes not rewarded. Therefore, the *unfortunate* condition may not have been so surprising to the subjects. These findings align with our assumption that a situation's valence (i.e., favourable or unfavourable) does not play a decisive role in determining changes in scratching.

The results of Experiment 1 were inconclusive in determining whether changes in reward outcomes themselves or the unexpectedness of those changes were the key factors driving the occurrence of scratching. Experiment 2 aimed to clarify this point further. Our findings demonstrated that subjects exhibited confusion when exposed to unexpected stimuli and were subsequently more likely to engage in scratching. Importantly, since there was no difference in the reward amount between the *control* and *unexpected* conditions, the alternative explanation—that scratching occurred solely due to changes in reward outcomes—can be ruled out. These results further strengthen the hypothesis that unexpectedness and resultant surprise are the critical factors.

Taken together, our results support the hypothesis that scratching behaviour is driven not by a situation's negative or positive valence, but by surprise and arousal triggered when facing unexpected circumstances. This interpretation may help reconcile previously inconsistent findings, as earlier research has shown that scratching increases in both positively valenced contexts, such as play²⁴, and negatively valenced ones, including aggression^{11–13} or challenging tasks^{16–18}. These contexts share a critical underlying feature—unpredictability: play involves the flexible combination of diverse motor patterns borrowed from other contexts^{29,30}, social disruption emerges following aggressive interactions, and difficult tasks often yield unpredictable outcomes. In all such cases, this shared element of unexpectedness may be the key factor underlying the observed increase

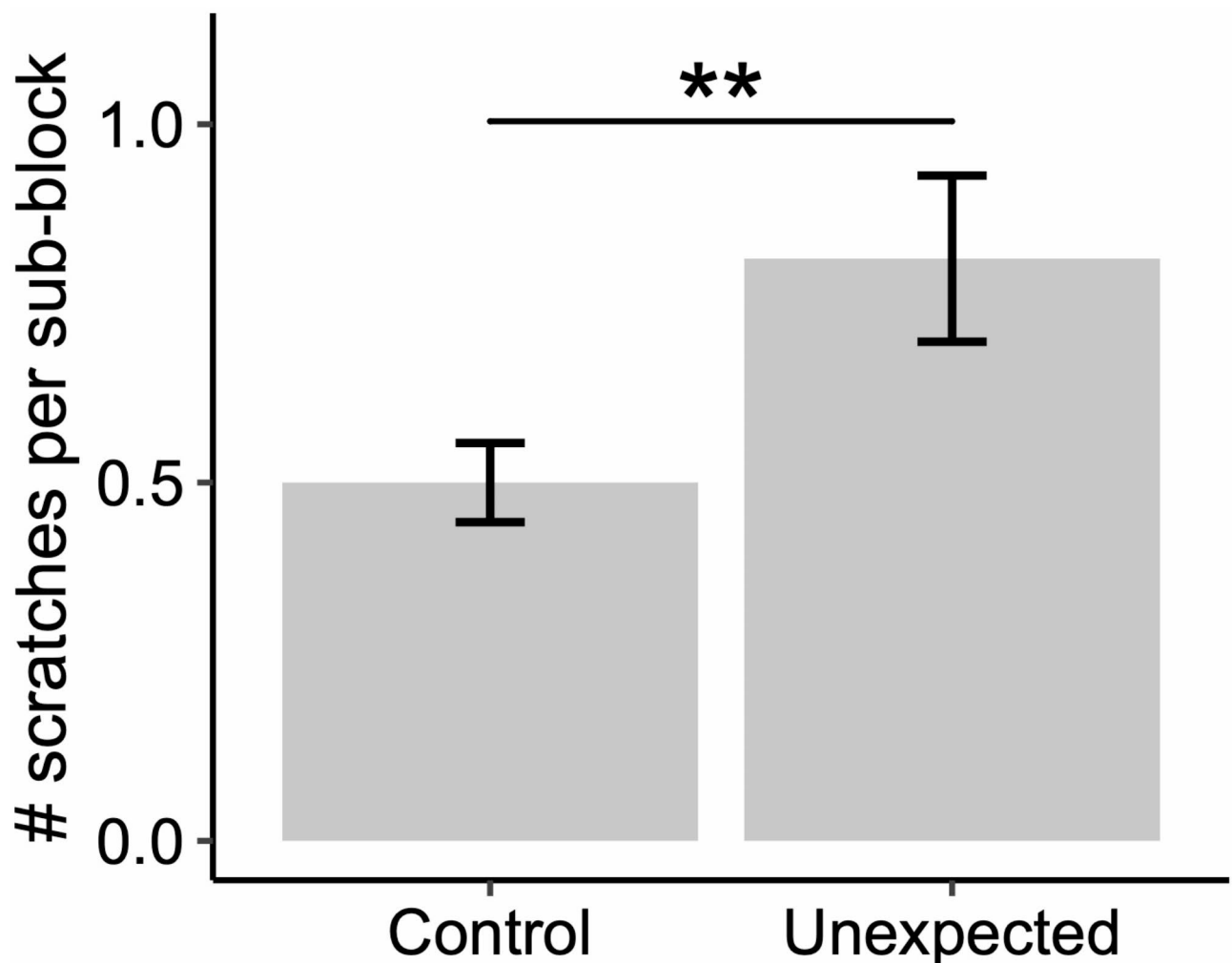


Fig. 5. Number of scratching bouts occurring in the interval between the display of the S+ in one test trial and the display of the S+ in the next test trial. Error bars represent standard errors. Sample size: $N = 288$. $**p < 0.01$ (Poisson GLMM).

in scratching. Furthermore, the reported reduction in scratching following anxiolytic administration²¹ may not stem from the alleviation of negative valence itself, but rather from changes in arousal triggered by environmental events³³.

By extrapolating from the findings of this study, we can propose a hypothesis regarding the potential function of scratching: scratching may serve as a coping strategy for animals to alleviate internal conflict when facing heightened uncertainty (cf.^{34,35}). This proposal aligns with neurobehavioural theories suggesting that organisms act to minimise prediction errors by updating internal models^{36,37}. Specifically, scratching may allow animals to produce highly predictable sensations as their brains, utilizing a copy of their motor command (i.e., an efference copy:^{38,39}), can predict the sensory input caused by scratching, thereby minimizing the mismatch between the predicted and actual sensations. This putative function may have been acquired through the process of ‘co-opting’ (*sensu*^{1,40}) what was originally a simple hygienic and defensive behaviour against unexpected sensations on the skin caused by ectoparasites or irritants. Moreover, contagious scratching (Japanese macaques:⁴¹; mice:⁴²; orangutans, *Pongo pygmaeus*:⁴³; spider monkeys, *Ateles geoffroyi*:⁴⁴; black-and-white ruffed lemurs, *Varecia variegata*, and red ruffed lemurs, *Varecia rubra*:⁴⁵; but see^{32,46}) may arise because an individual scratching in reaction to heightened uncertainty introduces additional unpredictability to surrounding conspecific observers. To confirm these hypotheses, future research is needed to determine, from physiological, psychological, and behavioural perspectives, whether scratching indeed helps alleviate the animal’s internal conflict and minimise prediction error.

When generalising the results of this study, several caveats must be considered. First, our study was based on a limited number of subjects. Future studies involving a larger sample size are required to verify the robustness of our findings. Moreover, a higher number of subjects may help identify individual attributes or personality traits that make certain individuals more susceptible to unexpected events. Second, our findings should be examined in follow-up studies that expose subjects to different types of unexpected events. One potential approach would be to create an alternative condition in which subjects unexpectedly receive a reward after touching an S– button.

Furthermore, previous studies have shown that both human infants and non-human primates display varied responses depending on the degree of stimulus novelty or unfamiliarity^{47,48}. An intriguing direction for future work would be to investigate how scratching frequency changes in response to stimuli with different levels of novelty or unfamiliarity presented to the subjects.

In conclusion, our results demonstrate that scratching—traditionally viewed as associated primarily with negative emotions—is more likely to occur in response to unexpectedly elevated reward outcomes and in situations where animals encounter unexpected stimuli without changes in reward outcomes. These findings undermine the explanation that the negative valence of an event serves as the decisive trigger for scratching. Instead, they suggest that surprise and arousal accompanying unexpected events—regardless of whether they are favourable or unfavourable—are the key factors driving scratching. However, it should be noted that this study does not entirely refute the relationship between negative emotions and scratching. This is because unexpected events in animals' natural habitats are more often potentially dangerous occurrences warranting caution, rather than purely fortuitous and positive events. Future research should build upon the insights provided by this and other studies to explore the function of scratching as a coping strategy in the face of unexpected events. Investigations in this direction could provide valuable models for understanding the evolutionary processes of human behaviour, where traits originally selected for relatively simple ancestral functions become linked with and shaped by psychological and social factors over time.

Methods

Study subjects

We conducted experiments on four adult Japanese macaques at the Center for the Evolutionary Origins of Human Behavior (EHUB), Kyoto University. The subjects were two males and two females, aged 9 to 15 years (mean \pm SD: 12.5 \pm 3.0 years). The macaques were housed either individually or in pairs. For the macaques housed in pairs, a partition was placed between them at least 20 min before the experiment to separate the individuals. No food was provided before the trials to control the subjects' motivation for rewards. After completing each day's experiment, the experimenter fed the subjects their daily rations. Water was available ad libitum throughout the study. This study was approved by the Animal Welfare and Care Committee of the EHUB, Kyoto University (#2024–039). All procedures adhered to the Japanese Act on the Welfare and Management of Animals and are reported in accordance with ARRIVE guidelines.

Apparatus

The computerised Go/No-go visual discrimination task was conducted using a touchscreen (Microsoft Surface Pro 8 EIV-00010). Upon a correct Go response, a food dispenser (Med Associates, Fairfax, Vermont, USA) automatically released a 190 mg banana-flavoured pellet (Bio-Serv DPP) into a tray beneath the screen accompanied by a one-second beep. An incorrect response triggered a buzzing sound. The experimental apparatus was controlled using Visual Basic 2010 (Microsoft Corporation, Redmond, Washington, USA). During the experiment, the subjects' scratching was recorded using GoPro Hero11 video cameras positioned above the touchscreen and the cage. A scratching event occurring more than 3 s after the previous one was classified as a new bout.

Discrimination training

The subjects underwent training in a Go/No-go visual discrimination task from June to July 2024. Black (RGB 75/75/75) and white rectangular stimuli (RGB 175/175/175) served as predictors of reward (S+) and mild, non-invasive punishment (S−). The allocation of black and white colours to S+ and S− was counterbalanced across subjects. When the subjects touched the self-start key located in the lower centre of the screen, S+ or S− was displayed in the upper centre for two seconds. The order of S+ and S− was pseudorandomised, with S+ always presented at the beginning of each training session. The inter-trial interval (ITI) was set to 2 s. The stimulus disappeared when a subject touched S+, and a reward pellet was dispensed. When a subject touched S−, the stimulus disappeared, and the subject was required to wait for an 8 s time-out in addition to the ITI before proceeding to the next trial.

Training sessions were conducted on weekdays, and subjects performed as many discrimination trials as possible within one hour. Prior to the start of each session, the touchscreen display was set to a blank screen. The experimenter pressed the start button on the keyboard and then left the experimental room. Ninety seconds later, the screen transitioned to a start screen with a green background for two minutes. After two minutes, the background changed to light blue, the self-start key appeared, and the training session began. At the end of each day's training, we calculated the proportions of correct Go and No-go responses. Subjects who completed at least 300 training trials daily and achieved a proportion of correct Go and No-go responses of 0.9 or higher for at least three consecutive days progressed to the testing phase. All four subjects met the learning criteria.

Experimental procedure

Experiment 1

Experiment 1 was conducted from July to August 2024. Black (RGB 75/75/75) and white stimuli (RGB 175/175/175) were used as S+ and S−. Testing was conducted on weekdays using a block design in which the condition alternated daily among *fortunate*, *unfortunate*, and *control* conditions. The conditions were presented in one of two fixed orders: *control* \rightarrow *fortunate* \rightarrow *control* \rightarrow *unfortunate* or *control* \rightarrow *unfortunate* \rightarrow *control* \rightarrow *fortunate*, repeated across four cycles. The orders were counterbalanced across subjects. Each test session consisted of 326 trials, with six (about 1.8%) designated as test trials. Following the same procedure as the training phase, the session began with the display of a 2-minute green start screen. After this, the background

transitioned to light blue, the self-start key appeared, and the testing session began. The detailed procedure for the testing sessions was as follows:

1. 80 filler trials (40 S+ and 40 S−) of the discrimination task were conducted in pseudorandom order.
2. A single test trial was conducted in which a normal S+ button was displayed on the screen and remained until touched by the subject. The reward for responding to S+ varied by condition (Fig. 1):
 - In the *control* condition, one pellet was dispensed, as in filler trials.
 - In the *fortunate* condition, eight pellets were dispensed consecutively at 0.5-second intervals.
 - In the *unfortunate* condition, no pellets were dispensed.
3. Forty filler trials (20 S+ and 20 S−) of the discrimination task were conducted in pseudorandom order.
4. Steps 2 and 3 were repeated six times.

Because the experiment used a block design, all trials corresponded to the same condition on any given experimental day. We used video cameras to record and calculate the number of scratching bouts occurring during each sub-block, defined as the interval between the subject's response to the S+ in one test trial and their response to the S+ in the next test trial. A total of 16 sessions were conducted per subject, comprising 8 *control* sessions, 4 *fortunate* sessions, and 4 *unfortunate* sessions. This resulted in data on the number of scratches in 384 sub-blocks (6 test trials per session × 16 sessions per subject × 4 subjects).

Experiment 2

Experiment 2 was conducted from October to November 2024. The same black and white stimuli as in Experiment 1 were used as S+ and S−. Testing was conducted on weekdays. The conditions followed the fixed order *control* → *control* → *unexpected*, repeated across four cycles. To enhance the salience of the *unexpected* condition, subjects were first exposed to two sessions of the *control* condition, where nothing unexpected occurred, before experiencing the *unexpected* condition. Thus, the order of conditions was not randomised. As in Experiment 1, each test session consisted of 326 trials, with six (about 1.8%) designated as test trials. The testing session began following the same procedure as in Experiment 1. The detailed procedure for the testing sessions was as follows:

1. 80 filler trials (40 S+ and 40 S−) of the discrimination task were conducted in pseudorandom order.
2. A single test trial was conducted, during which the S+ button differed by condition (Fig. 1):
 - In the *control* condition, the standard black or white S+ button was displayed.
 - In the *unexpected* condition, an S+ button that differed from the standard S+ in either colour, shape, or location was displayed. We employed these novel S+ buttons, which varied across three dimensions, to prevent the subjects from becoming accustomed to variation along only one specific dimension. These novel S+ buttons had never been presented to the subjects before. A different novel S+ was used for each test trial, ensuring that each subject was exposed to each novel S+ only once (Fig. 2).
 - In test trials, the S+ button remained on the screen until touched by the subject. In both conditions, responding to the S+ resulted in dispensing a single pellet.
3. 40 filler trials (20 S+ and 20 S−) of the discrimination task were conducted in pseudorandom order.
4. Steps 2 and 3 were repeated six times.

As in Experiment 1, the experiment followed a block design. We used video cameras to record and calculate the number of scratching bouts occurring during each sub-block, defined as the interval between the display of the S+ in one test trial and the display of the S+ in the next test trial. A total of 12 sessions were conducted per subject, comprising 8 *control* sessions and 4 *unexpected* sessions. This resulted in data on the number of scratches in 288 sub-blocks (6 test trials per session × 12 sessions per subject × 4 subjects).

Statistics

We analysed the data using GLMMs with the *glmer* function in the *lme4* package in R (version 4.1.2). The alpha level was set to 0.05.

For both Experiments 1 and 2, we employed a GLMM with a Poisson error structure and a log link function to analyse the scratching frequency. The response variable was the number of scratches occurring during the sub-block between the current and subsequent test trials. We used the log-transformed value of the sub-block duration (in minutes) as the offset term. The key predictor variable was the condition (Experiment 1: *control*, *fortunate*, *unfortunate*; Experiment 2: *control*, *unexpected*). To account for confounding effects, we included the following control variables: session number (continuous: Day 1–16 for Experiment 1; Day 1–12 for Experiment 2), trial number (continuous: 1–6), subject's sex (categorical), and baseline frequency of scratching (continuous). The baseline frequency was calculated by dividing the number of scratches occurring during the period from the two-minute start-screen to the first test trial by the duration (in minutes) of that period. To address potential pseudoreplication, we included subject ID as a random intercept. The significance of the full model was tested by comparing it to a null model that included only the control variables and the random intercept, using a likelihood ratio test with the *anova* function. Additionally, we compared the full model containing the interaction between the condition and trial number to a model without the interaction term, using a likelihood ratio test. If the inclusion of the interaction did not significantly improve model fit, we reported the results from the simpler model without the interaction.

To confirm that the three types of novel, unexpected S+ in Experiment 2, which differed from the usual S+ either in colour, shape, or position, elicited surprise or confusion in the subjects, we analysed response times to S+ using a GLMM with a Gamma error structure and a log link function. The key predictor was the type of S+ (normal S+ used in the *control* condition, S+ with a different colour, S+ with a different shape, or S+ with a different location). To account for confounding effects, we included the following control variables: session number (continuous: Day 1–12), trial number (continuous: 1–6), and subject's sex (categorical). Post-hoc comparisons among the four levels of S+ types were conducted using Tukey's test. The significance of the full model was assessed by comparing it to a null model containing only the control variables and a random intercept, using a likelihood ratio test with the *anova* function.

Data availability

All data and R codes have been deposited on OSF: <https://osf.io/zqhds/>.

Received: 15 January 2025; Accepted: 26 February 2025

Published online: 11 March 2025

References

- Gould, S. J. & Vrba, E. S. Exaptation—a missing term in the science of form. *Paleobiology* **8**, 4–15 (1982).
- Eastwick, P. W. Beyond the Pleistocene: using phylogeny and constraint to inform the evolutionary psychology of human mating. *Psychol. Bull.* **135**, 794–821 (2009).
- Reeve, H. K. & Sherman, P. W. Adaptation and the goals of evolutionary research. *Q. Rev. Biol.* **68**, 1–32 (1993).
- Ventura, R., Majolo, B., Schino, G. & Hardie, S. Differential effects of ambient temperature and humidity on allogrooming, self-grooming, and scratching in wild Japanese macaques. *Am. J. Phys. Anthropol.* **126**, 453–457 (2005).
- Duboscq, J., Romano, V., Sueur, C. & MacIntosh, A. J. J. Scratch that itch: revisiting links between self-directed behaviour and parasitological, social and environmental factors in a free-ranging primate. *R. Soc. Open Sci.* **3**, 160571 (2016).
- Golpanian, R. S., Kim, H. S. & Yosipovitch, G. Effects of stress on itch. *Clin. Ther.* **42**, 745–756 (2020).
- Sanders, K. M. & Akiyama, T. The vicious cycle of itch and anxiety. *Neurosci. Biobehav. Rev.* **87**, 17–26 (2018).
- Lu, J. S. et al. Contagious itch can be induced in humans but not in rodents. *Mol. Brain* **12**, 38 (2019).
- Holle, H., Warne, K., Seth, A. K., Critchley, H. D. & Ward, J. Neural basis of contagious itch and why some people are more prone to it. *Proc. Natl. Acad. Sci. U. S. A.* **109**, 19816–19821 (2012).
- Helt, M. S. et al. Contagious itching is heightened in children with autism spectrum disorders. *Dev. Sci.* **24**, e13024 (2021).
- Castles, D. L. & Whiten, A. Post-conflict behaviour of wild Olive baboons. II. Stress and self-directed behaviour. *Ethology* **104**, 148–160 (1998).
- di Polizzi, E., Schino, G., Tiddi, B. & Aureli, F. Scratching as a window into the emotional responses of wild tufted capuchin monkeys. *Ethology* **118**, 1072–1084 (2012).
- Kutsukake, N. & Castles, D. L. Reconciliation and variation in post-conflict stress in Japanese macaques (*Macaca fuscata fuscata*): testing the integrated hypothesis. *Anim. Cogn.* **4**, 259–268 (2001).
- Castles, D. L., Whiten, A. & Aureli, F. Social anxiety, relationships and self-directed behaviour among wild female Olive baboons. *Anim. Behav.* **58**, 1207–1215 (1999).
- Maestripietri, D. Maternal anxiety in rhesus macaques (*Macaca mulatta*). *Ethology* **95**, 19–31 (1993).
- Itakura, S. Emotional behavior during the learning of a contingency task in a chimpanzee. *Percept. Mot. Skills* **76**, 563–566 (1993).
- Leavens, D. A., Aureli, F., Hopkins, W. D. & Hyatt, C. W. Effects of cognitive challenge on self-directed behaviors by chimpanzees (*Pan troglodytes*). *Am. J. Primatol.* **55**, 1–14 (2001).
- Leeds, A. & Lukas, K. E. Experimentally evaluating the function of self-directed behaviour in two adult mandrills (*Mandrillus sphinx*). *Anim. Welf.* **27**, 81–86 (2018).
- Aureli, F., Van Schaik, C. P. & Van Hooff, J. A. R. A. M. Functional aspects of reconciliation among captive long-tailed macaques (*Macaca fascicularis*). *Am. J. Primatol.* **19**, 39–51 (1989).
- Palagi, E. & Norscia, I. Scratching around stress: hierarchy and reconciliation make the difference in wild brown lemurs (*Eulemur fulvus*). *Stress* **14**, 93–97 (2011).
- Barros, M., Boere, V., Huston, J. P. & Tomaz, C. Measuring fear and anxiety in the marmoset (*Callithrix penicillata*) with a novel predator confrontation model: effects of diazepam. *Behav. Brain Res.* **108**, 205–211 (2000).
- Kato, Y. et al. Vocalizations associated with anxiety and fear in the common marmoset (*Callithrix jacchus*). *Behav. Brain Res.* **275**, 43–52 (2014).
- Judge, P. G., Griffaton, N. S. & Fincke, A. M. Conflict management by hamadryas baboons (*Papio hamadryas hamadryas*) during crowding: a tension-reduction strategy. *Am. J. Primatol.* **68**, 993–1006 (2006).
- Neal, S. J. & Caine, N. G. Scratching under positive and negative arousal in common marmosets (*Callithrix jacchus*). *Am. J. Primatol.* **78**, 216–226 (2016).
- Burghardt, G. M. *The Genesis of Animal Play: Testing the Limits*. (MIT Press, 2005).
- Held, S. D. E. & Špinka, M. Animal play and animal welfare. *Anim. Behav.* **81**, 891–899 (2011).
- Iki, S. & Kutsukake, N. Play face in Japanese macaques reflects the sender's play motivation. *Anim. Cogn.* **26**, 849–859 (2023).
- Nelson, X. J. et al. Joyful by nature: approaches to investigate the evolution and function of joy in non-human animals. *Biol. Rev.* **98**, 1548–1563 (2023).
- Fagen, R. *Animal Play Behavior*. (Oxford University Press, 1981).
- Iki, S. & Kutsukake, N. Victims of play escalation rank below aggressors in Japanese macaques (*Macaca fuscata*). *Int. J. Primatol.* **43**, 365–383 (2022).
- Iki, S. & Adachi, I. Fearful snake pictures make monkeys Pessimistic. *iScience* **26**, 107622 (2023).
- Iki, S. & Adachi, I. Affective bodily responses in monkeys predict subsequent pessimism, but not vice versa. *Proc. R. Soc. B* **292**, 20242549 (2025).
- McNaughton, N. & Gray, J. A. Anxiolytic action on the behavioural Inhibition system implies multiple types of arousal contribute to anxiety. *J. Affect. Disord.* **61**, 161–176 (2000).
- Kikuchi, Y. & Noriuchi, M. Power of self-touch: its neural mechanism as a coping strategy in *Emotional Engineering*, Vol. 7: *The Age of Communication*. 33–47 (eds Fukuda, S.) (Springer, 2019).
- Boehme, R. & Olsson, H. Differentiating self-touch from social touch. *Curr. Opin. Behav. Sci.* **43**, 27–33 (2022).
- Friston, K. J., Daunizeau, J. & Kiebel, S. J. Reinforcement learning or active inference? *PLoS One* **4**, e6421 (2009).
- Clark, A. Whatever next? Predictive brains, situated agents, and the future of cognitive science. *Behav. Brain Sci.* **36**, 181–204 (2013).
- Blakemore, S. J., Wolpert, D. & Frith, C. Why can't you tickle yourself? *Neuroreport* **11**, R11–R16 (2000).

39. Kilteni, K., Engeler, P. & Ehrsson, H. H. Efferece copy is necessary for the attenuation of self-generated touch. *iScience* **23**, 100843 (2020).
40. Gould, S. J. Exaptation: a crucial tool for an evolutionary psychology. *J. Soc. Issues* **47**, 43–65 (1991).
41. Nakayama, K. Observing conspecifics scratching induces a contagion of scratching in Japanese monkeys (*Macaca fuscata*). *J. Comp. Psychol.* **118**, 20–24 (2004).
42. Yu, Y. Q., Barry, D. M., Hao, Y., Liu, X. T. & Chen, Z. F. Molecular and neural basis of contagious itch behavior in mice. *Science* **355**, 1072–1076 (2017).
43. Laméris, D. W., Berlo, E., Sterck, E. H. M., Bionda, T. & Kret, M. E. Low relationship quality predicts scratch contagion during tense situations in orangutans (*Pongo pygmaeus*). *Am. J. Primatol.* **82**, e23138 (2020).
44. Valdivieso-Cortadella, S., Bernardi-Gómez, C., Aureli, F., Llorente, M. & Amici, F. Yawning and scratching contagion in wild spider monkeys (*Ateles geoffroyi*). *Sci. Rep.* **13**, 8367 (2023).
45. Lemes, W. P. & Amici, F. Contagious yawning and scratching in captive lemurs. *Sci. Rep.* **14**, 26672 (2024).
46. Whitehouse, J., Micheletta, J., Kaminski, J. & Waller, B. M. Macaques attend to scratching in others. *Anim. Behav.* **122**, 169–175 (2016).
47. Wang, M. Z. & Hayden, B. Y. Monkeys are curious about counterfactual outcomes. *Cognition* **189**, 1–10 (2019).
48. Kidd, C., Piantadosi, S. T. & Aslin, R. N. The Goldilocks effect: human infants allocate attention to visual sequences that are neither too simple nor too complex. *PLoS One* **7**, e36399 (2012).

Acknowledgements

This study was supported by JSPS KAKENHI Grant Numbers JP19K12730, JP22KJ1783, and JP23K17642.

Author contributions

S.I. and I.A. conceived the study, acquired the funding, and finalized the manuscript. S.I. gathered the data, performed the statistical analyses, and drafted the manuscript.

Declarations

Competing interests

The authors declare no competing interests.

Additional information

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1038/s41598-025-92251-x>.

Correspondence and requests for materials should be addressed to S.I.

Reprints and permissions information is available at www.nature.com/reprints.

Publisher's note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Open Access This article is licensed under a Creative Commons Attribution-NonCommercial-NoDerivatives 4.0 International License, which permits any non-commercial use, sharing, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if you modified the licensed material. You do not have permission under this licence to share adapted material derived from this article or parts of it. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by-nc-nd/4.0/>.

© The Author(s) 2025