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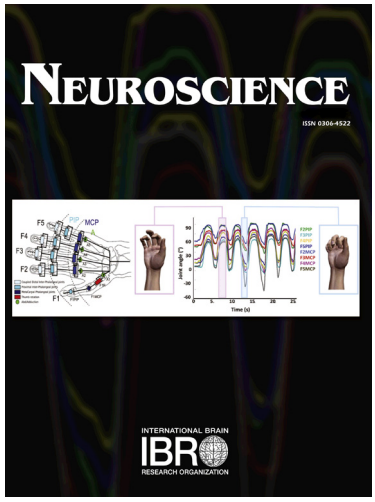

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Naoki Miura, Hiroki C. Tanabe, Akihiro Sasaki, Tokiko Harada, Norihiro Sadato

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Title: **Neural evidence for the intrinsic value of action as motivation for behavior**

Naoki Miura [(1)], Hiroki C. Tanabe [(2)], Akihiro Sasaki [(3)], Tokiko Harada [(4)], Norihiro Sadato [(4)]

(1) Department of Information and Communication Engineering, Faculty of Engineering, Tohoku Institute of Technology, 35-1 Yagiyama Kasumicho, Taihaku-ku, Sendai, Miyagi, 982-8577 Japan.

(2) Division of Psychology, Department of Social and Human Environment, Graduate School of Environmental Studies, Nagoya University, D2-1(510), Furo-cho, Chikusa-ku, Nagoya, 464-8601 Japan

(3) Pathophysiological and Health Science Team, RIKEN Center for Life Science Technologies, 6-7-3 Minatojima-minamimachi, Chuo-ku, Kobe, Hyogo, 650-0047 Japan

(4) Division of Cerebral Integration, Department of System Neuroscience, National Institute for Physiological Sciences, 38 Nishigonaka Myodaiji, Okazaki, Aichi,, 444-8585 Japan

Corresponding Author: Dr. Naoki Miura

35-1 Yagiyama Kasumicho, Taihaku-ku, Sendai, Miyagi, 982-8577 Japan.

Tel / Fax number: +81-22-305-3465 / +81-22-305-3402

E-mail address: miura.naoki@tohtech.ac.jp

Abstract

The intrinsic value of an action refers to the inherent sense that experiencing a behavior is enjoyable even if it has no explicit outcome. Previous research has suggested that a common valuation mechanism within the reward network may be responsible for processing the intrinsic value of achieving both the outcome and external reward. However, how the intrinsic value of action is neurally represented remains unknown. We hypothesized that the intrinsic value of action is determined by an action-outcome contingency indicating the behavior is controllable and that the outcome of the action can be evaluated by this feedback. Consequently, the reward network should be activated, reflecting the generation of the intrinsic value of action. To test this hypothesis, we conducted a functional magnetic resonance imaging (fMRI) investigation of a stopwatch game in which the action-outcome contingency was manipulated. This experiment involved 36 healthy volunteers and four versions of a stopwatch game that manipulated controllability (the feeling that participants were controlling the stopwatch themselves) and outcome (a signal allowing participants to see the result of their action). A free-choice experiment was administered after the fMRI to explore preference levels for each game. The results showed that the stopwatch game with the action-outcome contingency evoked a greater degree of enjoyment because the participants chose this condition over those that lacked such a contingency. The ventral striatum and midbrain were activated only when action-outcome contingency was present. Thus, the intrinsic value of action was represented by an increase in ventral striatal and midbrain activation.

Keywords

Intrinsic motivation; fMRI; ventral striatum; midbrain; action-outcome contingency.

Introduction

Humans often engage in specific behaviors with great enjoyment even when there is no external reward. Enjoyment is considered to be a positive emotion that forms in conjunction with an experienced activity in and of itself when the activity is sufficiently controllable (Pekrun, 2006). For example, enjoyment contributes to intrinsic motivation by sustaining the willingness to persist in an activity (Reeve, 1989). Educational or work performance improves when one has high intrinsic motivation for performing a target behavior (Henderlong and Lepper, 2002; Kuvaas and Dysvik, 2009). With regard to the underlying mechanism, one might expect that if a positive value is internally generated for an experienced behavior, this value will be a source of intrinsic motivation to continue the behavior (Ryan et al., 1983; Deci & Ryan, 2008).

Pekrun (2006) has proposed an educational model in which the intrinsic value of an experienced behavior consists of two components: the intrinsic value of the action itself and the intrinsic value of an expected outcome. The intrinsic value of action is associated with ongoing achievement and evokes a feeling that the behavior is enjoyable and this feeling may be generated even if there is no instrumental outcome. On the other hand, the intrinsic value of an outcome pertains to the anticipatory outcome relevant to the goal of the activity, such as a hope for achieving educational success. However, previous research has suggested that psychological outcomes (e.g., achieving success) and external rewards (e.g., monetary rewards) are processed through a common valuation mechanism that involves the corticobasal ganglia network (Murayama et al., 2010). Additionally, the relationship between intrinsic motivation and external incentives is neurally represented as the tonic and phasic modulation of activation, respectively, in common cortical regions (Marsden et al., 2015). Murayama et al. (2010) reported an undermining effect in which the existence of an external reward diminished intrinsic motivation (Deci et al., 1999; Promberger & Marteau, 2013); this was represented by decreases in activity in the ventral striatal and midbrain regions and reflected the integrated valuation process between the extrinsic reward and the intrinsic value of achieving success. However, how the intrinsic value of action itself is neurally represented in the human brain remains unknown. Hence, elucidating the neural mechanism that generates the intrinsic value of action will contribute to our understanding of human enjoyment for behavior that occurs in the absence of external

reward and may improve educational performance.

One might expect the intrinsic value of action to be determined by an action-outcome contingency, the coexistence of controllability (i.e., the feeling that one is controlling the situation) and outcome (i.e., a meaningful signal allowing one to see the result of one's action). It has been argued that intrinsic motivation is enhanced when people experience both a sense of autonomy and a feeling of competence (Deci & Ryan, 2008). One feels that a behavior is enjoyable if the behavior is perceived as sufficiently controllable (Pekrun, 2006). Furthermore, it has been reported that enjoyment may also be facilitated by a sense of mastery over the behavior via feedback (Pekrun, 2006; Hattie and Timperley, 2007; Deci and Ryan, 2008). A neuroimaging study by Tricomi et al. (2004) reported that the striatum became activated when an action-contingent reward or punishment was perceived, a result that is usually observed upon receipt of an external reward. Fitzgerald et al. (2014) suggested that reward-related activity in the ventral striatal region is modulated by action-contingency with the behavioral context. Although these studies used monetary rewards as action-contingent consequences, it is expected that the generation of intrinsic value for an action would be achieved in the same manner; that is, an action-contingent outcome would create intrinsic value for the experienced behavior. We hypothesized that the intrinsic value of an action would be highest for behavior that involves both sufficient controllability and action-contingent outcome and that it would activate the same reward network as an extrinsic reward.

To examine this hypothesis, we administered a stopwatch (SW) game as part of a functional magnetic resonance imaging (fMRI) experiment. We chose controllability and feedback as factors for manipulating the action-outcome contingency. Murayama et al. (2010) previously designed a simple SW game that was inherently pleasing; the degree of interest in this SW game was experimentally confirmed. Using this game, they found a relationship between activity in the corticobasal ganglia network and the undermining effect (Murayama et al., 2010) and argued for the importance of the ventromedial prefrontal cortex in facilitating task performance through self-determined choice (Murayama et al., 2015). However, they did not manipulate the components of the SW game itself. Here, we focused on the intrinsic value of game-related action and its relationship to the manipulation of the game's components as determined by action-outcome contingency. An fMRI experiment was conducted to (1) confirm that

participants preferred the SW game with an action-outcome contingency based on this generated value, and (2) determine whether the SW game with the action-outcome contingency would drive the reward system, thereby reflecting estimates of the intrinsic value of action.

Experimental procedures

Participants

Thirty-six healthy Japanese volunteers (18 males and 18 females, mean age: 22 ± 3, range: 18–36 years) participated in this study. None of the participants had a history of neurological or psychiatric disorders. All participants provided written informed consent in response to an experimental protocol approved by the Ethical Committee of the National Institute for Physiological Sciences and the Research Ethics Committee of Tohoku Institute of Technology. The experimental data from seven participants were excluded due to excessive head movement (head movement exceeding 2 cm on any of the actual runs or intermittent spike-like movements caused by a cough). Because the experiment targeted right-handed individuals, data from one participant were also excluded because of his handedness (laterality quotient (LQ) = 0) based on the Edinburgh handedness inventory (Oldfield 1971). Finally, the data from one additional participant were excluded because a partial low-signal-intensity region was detected in this participant's MRI data and was judged to be unsuitable for data analysis. Thus, we analyzed data from 27 participants (12 males and 15 females; 21 ± 2 years; LQ = 0.98 ± 0.04).

Experimental task

Figure 1 shows the design of the experimental task. The fMRI experiment consisted of one practice run and three runs involving actual measurement. Each run consisted of four different SW tasks and two different control tasks based on Murayama et al. (2010). That study also confirmed that the original SW game was sufficiently interesting even though there was no external reward. A block design was used for the fMRI experiment; that is, four iterations of the same trial type comprised one task block, and a task cue was presented before the first trial in each task block (Figure 1A). The duration of each task block was 32.5 seconds. In total, 18 task blocks were included in

each run, and the order of task blocks was shuffled. The SW task presented a SW that started automatically; the participant could see the timer advancing throughout each trial. The goal of each trial was to press a button with the right index finger such that the button press fell within a specified range of the 3-s mark. Participants were instructed to stop the timer as close as possible to the 3-s time mark by pressing a button during each SW task. In order to manipulate the existence of an action-outcome contingency in the SW game, four kinds of SW tasks were devised: a condition incorporating both controllability and outcome (C+O+), which represented the presence of the action-outcome contingency; a condition including only controllability (C+O-); a condition including only outcome (C-O+); and a condition including neither controllability nor outcome (C-O-; Figure 1B). In other words, these conditions were prepared so that the action-outcome contingency was included only in the C+O+ condition and not in the other three conditions. The participant recognized each type of task based on the font color of the task cue and timer; the relationship between font color and task condition was explained in advance. Controllability was manipulated by varying whether the progress of the timer actually stopped when the participant pressed the button; that is, a fixed set of blinking numbers (88:88) that corresponded to the button press under the C+O+ and C+O- conditions was displayed. Hence, participants could verify controllability in the SW game based on the displayed information. The outcome was manipulated by varying the availability of interpretable feedback. Because the task goal was to stop the timer as close as possible to the 3-s time mark, the degree of task achievement was represented by the punctuality of the button press. Under the C+O+ condition, actual feedback was presented showing the difference between the time at which the participant stopped the clock and the target time (i.e., the participant could interpret the degree of achievement based on this feedback). In contrast, pseudo-feedback that was unrelated to the participant response was presented under the C-O+ condition. When a participant received an action-contingent feedback, he/she was aware of the result of his/her own action even though controllability had been eliminated. In this manner, the pseudo-feedback was used to diminish the action-outcome contingency from the C-O+ condition. The pseudo-feedback was pseudo-randomly generated by calculating a value representing {success range × (−1.6~1.8)} for each participant. To avoid misunderstanding the pseudo-feedback, each

participant was advised prior to the fMRI experiment that the feedback information in the C-O+ condition was unrelated to the button-press response. Additionally, fixed meaningless numbers (88:88) were presented as meaningless feedback under the C+O- and C-O- conditions. The duration between the button press and feedback for all conditions was pseudo-randomly set at 1.0–1.9 s.

We also prepared two control tasks, a watch-stop task (WS) and a control-color task (color) (Figure 1C). The WS task was intended to be less enjoyable than any of the SW tasks; participants were instructed to passively view the displayed timer and press a button when the timer automatically stopped at the 3-s mark. Additionally, the color task was included as a baseline control task so that we could subtract the effects of processing visual stimuli and executing a button-press response from the fMRI data; participants were instructed to press the button when the color of the displayed numbers changed from white to yellow.

The task difficulty of the SW game was set based on each participant's success rate for initiating the button press within the target time of 3 s plus or minus 0.01 s, 0.03 s, 0.05 s, 0.07 s, 0.10 s, 0.15 s, or 0.20 s. The appropriate time range was adjusted for each participant based on the practice session. In the practice session, participants repeatedly played the C+O+ version of the SW task outside of the MRI scanner until they reached the end of a pre-programmed computer-presented practice session. The time range for each SW trial was determined based on the results of the previous eight trials, with the targeted range adapted individually for each participant based on these eight trials. Participants were instructed to stop the SW as close to the 3-second mark as possible within the limits of a visually presented range. Based on the results of the prior practice session, the appropriate time range for the actual fMRI experiment was calculated as one in which each participant was able to succeed on approximately 50% of the trials in the C+O+ version of the SW task; this information was provided to each participant before the fMRI experiment. Participants were instructed that the trial was a success if the button press occurred within the determined target interval. Additionally, participants were also informed that no external incentive was associated with their performance.

Immediately after the fMRI scan, participants engaged in a free-choice experiment outside the MRI scanner. In this free-choice experiment, each participant

was asked to stay in the examination room and to repeatedly choose and play his or her favorite task from among the four different SW tasks and the WS for 10 minutes. A task block for each condition consisted of five trials, and the duration of each task trial was approximately 5 s with an inter-trial interval of 0 s. Thus, each task block spanned approximately 25 seconds. Given that participants were also permitted to take a short break during this free-choice experiment, there were approximately 20 opportunities to choose a specific task. After 10 minutes, the experimenter concluded the free-choice experiment. The experimental setup was identical to that used in the prior practice session.

Experimental setup

During the fMRI experiment, stimulus presentation and response collection were administered using Presentation 1.21 software installed on a personal computer (Dimension 8200; Dell Computer Co., Round Rock, TX, USA). A liquid crystal display (LCD) projector (DLA-M200L; Victor, Yokohama, Japan) located outside and behind the scanner projected the stimuli via waveguide onto a translucent screen, which the participants viewed using a mirror attached to the head coil of the MRI scanner. The auditory stimuli were presented through MRI-compatible headphones (Hitachi Advanced Systems, Yokohama, Japan). Behavioral responses were recorded using a fiber-optic response box (Current Designs Inc., Philadelphia, PA, USA). The practice session was administered using Presentation software 16.1 (Neurobehavioral Systems, Albany, CA, USA) on a laptop computer (Dynabook R730; Toshiba Corporation, Tokyo, Japan).

fMRI data acquisition

All images were acquired using a 3-T Siemens Allegra scanner with a birdcage head coil (Siemens, Erlangen, Germany). To acquire a structural whole-brain image at a fine grain, magnetization-prepared rapid-acquisition gradient-echo (MP-RAGE) images were obtained (repetition time [TR], 2500 ms; echo time [TE], 4.38 ms; flip angle = 8^{o}; field of view [FoV], 230 mm; one slab; number of slices per slab = 192; voxel dimensions = 0.9 × 0.9 × 1.0 mm). The fMRI time-series data covering the entire brain were acquired using T2*-weighted gradient echo-echo planar

imaging (GE-EPI). Oblique scanning was used to cover the entire cerebrum and to exclude artifacts resulting from eye movements. The parameters of the experiment were as follows: TR, 2500 ms; acquisition time [TA], 2500 ms; TE, 30 ms; flip angle, 80°; 39 slices; FoV, 192 x 192 mm; 64 x 64 matrix; slice thickness, 3 mm; slice gap, 0.5 mm. The first two scans of each run were dummy scans for the purpose of equilibrating the state of magnetization and were discarded from the time-series data; hence, we collected 251 scans for each run. In total, 753 scans per participant were included in the analysis.

Data analysis

Data preprocessing and statistical analyses of the fMRI data were performed using Statistical Parametric Mapping (SPM) 8 (Wellcome Trust Center for Neuroimaging, London, UK) running on Matlab R2013b (Mathworks, Natick, MA, USA). The effects of head motion across scans were corrected for by realigning all scans to the mean image. The scanning time lag for each slice was adjusted to the timing of the 20th slice, which was obtained at half of the TR. The whole-head MP-RAGE image volume was then co-registered with the first EPI image. This whole-head MP-RAGE was spatially normalized to the Montréal Neurological Institute (MNI) T1 image template using a non-linear basis function. Subsequently, normalization parameters were applied to all EPI images. Finally, all normalized EPI images were smoothed with a Gaussian filter in a spatial domain (8-mm full-width at half-maximum).

The fMRI data were analyzed using a two-level approach in SPM8 (Friston et al., 1994a). At the first level, the hemodynamic responses produced under the different experimental conditions were assessed at each voxel on a subject-by-subject basis using a general linear model. Because the intrinsic value of the action would be generated to the enjoyable behavior itself, it was expected that the cortical activity reflecting the valuation process of the intrinsic value of the action would occur with the participant's voluntary action performing the SW game. Therefore, it was hypothesized that the hemodynamic responses occurring through each button press under the C+O+, C+O-, C-O+, C-O-, WS, and color conditions would be canonical hemodynamic response functions with a 0-sec duration. Hemodynamic changes in response to the observation of each visual stimulus, such as task cue, indication of SW, and feedback, were also

modeled as conditions of no interest. Under all conditions, the SW indications and feedback were each put in a summative condition. Global changes were adjusted using proportional scaling, and low-frequency confounding effects were removed using a high-pass filter with a 128-sec cutoff. Multiple regression analyses were performed on each voxel to detect the regions in which MR signal changes were correlated with the hypothesized model to obtain the partial regression coefficient for each voxel.

The second level of analysis was performed on an inter-subject basis using a two-way repeated-measures factorial analysis of variance (ANOVA) design. Factors were controllability and outcome. Contrast images obtained by subtraction (i.e., each task condition minus the lowest control (color) condition (C+O+ - color; C+O+ - color; C-O+ - color; and C-O- - color)) were used for this analysis. To identify activation specific to the action-outcome contingency occurring during the SW task, a conjunction analysis between the subtraction of {(C+O+ – color) - (C+O- – color)}, {(C+O+ – color) – (C-O+ – color)}, and {(C+O+ – color) – (C-O- – color)} was performed. Additionally, a formal analysis was performed to identify the cortical regions that showed significant main effects of controllability [{(C+O+ – color) + (C+O- – color)} - {(C-O+ – color) + (C-O- – color)}], outcome [{(C+O+ – color) + (C-O+ – color)} – {(C+O- – color) + (C-O- – color)}], and the interaction of these factors [{(C+O+ – color) + (C-O- – color)} – {(C+O- – color) + (C-O+ – color)}]. For these analyses, the statistical threshold was set at $p < 0.05$, corrected for family-wise error (FWE) by voxel-level inference (Friston et al., 1994b, 1996). The obtained activation peaks were anatomically labeled by Talairach Atlas (Talairach and Tournoux, 1988) using Talairach Client 2.4.3 (Lancaster et al., 1997, 2000), and coordinate transformations from MNI to Talairach spaces were performed using the icbm2tal procedure (Lancaster et al., 2007).

Additionally, to plot the task-specific activation for each condition (C+O+, C+O-, C-O+, C-O-, WS, and the color condition), we extracted the percent signal change relative to the button press for each activation focus with sphere radii of 4 mm, using the MarsBaR 0.43 toolbox (Brett et al., 2002). Furthermore, correlation analyses of the activation profiles of the four experimental and WS conditions and the number of times that a participant chose each task in the free-choice experiment were performed for each participant.

Results

Behavioral results

Figure 2 shows the average number of times that the participant chose each task in the free-choice experiment. The average number of total choices made by participants was 20.3 ± 1.0. Participants chose the C+O+ condition more frequently than they chose any other condition. A one-way repeated measures ANOVA revealed a significant difference ($F_{(2.01, 52.31)} = 29.17$, $p < 0.001$; degrees of freedom were adjusted using Greenhouse–Geisser's Epsilon) and post-hoc comparisons were performed using the modified sequentially rejective Bonferroni procedure (Shaffer, 1986) indicated that the total number of choices for the C+O+ condition was significantly greater than that for the other conditions ($p < 0.05$; the statistical value was corrected for multiple comparisons).

In the actual fMRI experiment, the success rates averaged across all participants for the C+O+, C+O-, C-O+, and C-O- conditions were 58.6 ± 16.6%, 23.1 ± 16.1%, 51.2 ± 16.8%, and 22.5 ± 17.6%, respectively. A two-way repeated-measures ANOVA for the success rates of the C+O+, C+O-, C-O+, and C-O- conditions with controllability and feedback as factors revealed significant differences for the main effects of controllability ($F_{(1, 26)} = 7.35$, $p = 0.011$) and feedback ($F_{(1, 26)} = 71.49$, $p < 0.000$) as well as their interaction ($F_{(1, 26)} = 5.24$, $p = 0.031$). Post-hoc analyses revealed that there were significant differences in success rate between the C+O+ and C-O+ ($F_{(1, 26)} = 10.44$, $p = 0.003$), C+O+ and C+O- ($F_{(1, 26)} = 71.25$, $p < 0.000$), and C-O+ and C-O- ($F_{(1, 26)} = 53.01$, $p < 0.000$) conditions. The success rates averaged across all participants for the WS and color conditions were 93.0 ± 16.2% and 98.2 ± 3.0%, respectively. The adjusted target time range based on success rates for the actual fMRI experiment was set at 0.03-s for three participants, 0.05-s for eight participants, 0.07-s for nine participants, and 0.1-s for seven participants; the average success rate for the practice session performed under the C+O+ condition was 66.7 ± 0.5%.

fMRI results

Figure 3 illustrates the peak locations of significant activation specific to the C+O+ condition; these, which were identified using a conjunction analysis of three subtraction contrasts between C+O+ and the other experimental conditions, reflect the

profiles of local signal changes for each activation peak. Significant activation was observed in regions extending over the bilateral striatal regions, the medial portion of the bilateral thalamus, and the midbrain including the ventral tegmental area. Activation peaks for the ventral striatum were located in the globus pallidus, while those in the dorsal striatum were located in the bilateral caudate nucleus. Furthermore, significant activation was also observed in the rostral portion of the anterior cingulate cortex and in the cerebellar vermis (Table 1). The bar charts representing the percent signal change associated with each task condition (shown in Figure 3) also indicate a specific increase in the BOLD signal for the C+O+ condition compared with the other task and control conditions for all activation peaks. The results of the correlation analyses for each ROI revealed a positive correlation between the degree of activation and the number of times that the participant chose each task. The average correlation coefficients obtained for each ROI were as follows: 0.48 ± 0.34 for the left caudate nucleus (Figure 3A), 0.65 ± 0.37 for the left globus pallidus (Figure 3B), 0.58 ± 0.34 for the midbrain (Figure 3C), 0.55 ± 0.45 for the anterior cingulate cortex (Figure 3D), 0.60 ± 0.38 for the left thalamus (Figure 3E), and 0.42 ± 0.51 for the cerebellar vermis (Figure 3F).

Figure 4 depicts the cortical regions showing significant main effects and an interaction as well as the comparison between each activation map and significant activation specific to the C+O+ condition. Tables A.1 and A.2 summarize the cortical areas that exhibited significant main effects of controllability and outcome, respectively. Table A.3 summarizes the cortical areas that showed significant interaction effects between controllability and outcome. Although the results of the subtraction analysis showed significant main effects of controllability in medial regions of the brain, such as the medial prefrontal cortex, the anterior cingulate gyrus, the ventral striatum extending to the medial portion of the thalamus and midbrain regions, and the cerebellar vermis (Figure 4A), these regions spatially overlapped with those for which activation specific to the C+O+ condition was observed (Figure 4B). In contrast, the results of the subtraction analysis representing the main effect of outcome showed significant differences in broad regions, including not only the medial region but also the lateral regions of the brain (Figure 4C). Among the lateral regions, the ventrolateral prefrontal regions, posterior parietal regions, and fusiform gyrus showed significant differences in both hemispheres. Among the medial regions, activation similar to that associated

specifically with the C+O+ condition was observed in the medial frontal gyrus extending over the anterior cingulate gyrus, the bilateral ventral striatum extending over the thalamus and midbrain, and the cerebellar vermis (Figure 4D). Additionally, the posterior cingulate cortex extending to the corpus callosum also showed a significant effect of outcome. The interaction effects between the factors were significantly different in the postcentral gyrus, thalamus, midbrain, and cerebellum (Figure 4E). The midbrain and part of the cerebellar region overlapped with activation associated specifically with the C+O+ condition (Figure 4F).

Discussion

Behavioral findings

The results of the free-choice experiment showed that participants exhibited greater degrees of enjoyment in the C+O+ condition than in the other conditions, with the C+O+ condition being chosen more frequently than the others. As no extrinsic reward was offered, participants' choices in this experiment reflected their degree of enjoyment in each version of the stopwatch (SW) game. We interpreted the results as indicating that the intrinsic value of the action generated by participants was greatest when both controllability and outcome were included in the task. This result supports previous psychological theories (Pekrun, 2006; Deci and Ryan, 2008). It is probable that the specific preference for the C+O+ condition was established during the fMRI experiment, given that the free-choice experiment was administered immediately after the fMRI experiment and participants chose their preferred game based on their experience of playing the various versions of the SW task in that experimental setting.

Effects of action-outcome contingency on ventral striatal and midbrain activations

Specific increases in neural activity were observed for the C+O+ condition in the bilateral striatal regions, including the globus pallidus and caudate nucleus, and the midbrain, including the ventral tegmental area. It has been suggested that the globus pallidus (Elliot et al., 2000; Pessiglione et al., 2007) and ventral tegmental area (Elliott et al., 2000; D'Ardenne et al., 2008) constitute part of the reward network. In a previous study using the SW game, the ventral striatal and midbrain regions functioned as a common valuation system for both internal and external rewards (Murayama et al.,

2010). Activity in the ventral pallidum was also observed when a task cue for self-determination was presented in the SW game, although this effect did not reach statistical significance (Murayama et al., 2015). Additionally, ventral striatal activation during an experimental task without an extrinsic reward was found to be augmented by the presence of feedback (Tricomi et al., 2006), and striatal activation was found to be selectively sensitive to self-acquired rewards during video game play (Kätsyri1 et al., 2013). Given the results of our free-choice experiment, we interpreted the specific activation in these reward-related regions as reflecting the processing of the intrinsic value of an action generated by participants. Furthermore, the intrinsic value of an action may be assessed by a valuation mechanism in the reward network that is similar to that found for other types of reward, such as the intrinsic value of achieving success. Fitzgerald et al. (2014) reported that ventral striatal activity was dynamically modulated by action selection. Similarly, increases in tonic dopamine release in the ventral striatum promoted the selection of an extended sequence of goal-directed behavior (Westbrook and Braver, 2016). In contrast, O'Doherty et al. (2004) showed that ventral striatal activation could be induced by Pavlovian rewards that did not depend on action. The present findings support the former study and expand its implications regarding situations where no external reward is present (i.e., ventral striatal and midbrain activation are associated with the internal valuation of the experienced behavior itself).

A specific feature of the C+O+ condition was that participants received quantitative results regarding their performance based on action-contingent feedback; the other conditions did not provide this feature. Thus, the activation of the ventral striatal and midbrain regions would have been induced by the action-outcome contingency of the SW game. Several studies have reported that activation in typical reward-related regions is associated with an action contingent to external incentives (Tricomi et al., 2004; O'Doherty et al., 2004; Bhanji and Delgado, 2014). Additionally, a voluntary choice of options modulates the activation of corticostriatal regions (Cockburn et al., 2009; Leotti and Delgado, 2011; Sharot et al., 2014). Taken together, these studies suggest that reward-related activations formed by an external incentive are reinforced when the controllability of behavior exists. In contrast, the present study manipulated the existence of both controllability and feedback and did not prepare any external incentives for the SW game; therefore, those points would be unique

characteristics of the experimental design. Because the participants were aware of the degree of error for each trial via feedback, they might have achieved a feeling of competence when the degree of error was sufficiently small. Clark et al. (2009) suggested that near-miss outcomes are also processed as a reward by the human reward system. Thus, the feedback of the C+O+ condition might be processed as a positive outcome and result in valuing the gameplay itself. In sum, the present findings suggest that the SW game with an action-outcome contingency would drive the reward system and reflect estimates of the intrinsic value of action for playing the SW game.

The present results also contribute to the understanding of how a teacher or manager prepares a target behavior and the manner in which students or workers translate reward processing in the brain into behavior. Previous studies have indicated that the feeling of enjoyment is an important factor involved in the generation of intrinsic motivation for a target behavior in educational and work places (Henderlong and Lepper, 2002; Isen and Reeve, 2006; Pekrun, 2006; Kuvaas et al., 2009). For example, gamification, which utilizes game elements in a non-game context, was recently employed to foster motivation in various fields (Sailer et al., 2013; Dale, 2014; Oprescu et al., 2014; Dicheva et al., 2015). Because games are a type of play (Elis, 1978) in which a player voluntarily enjoys the activity itself without external reward, the intrinsic value of action would act as an essential reward while playing the game. The present findings showed that the existence of an action-outcome contingency on experienced behavior induced activation of the ventral striatal and midbrain regions. If a target behavior does not provide a sufficient action-outcome contingency, even if some game elements are embedded in the behavior, the reward network would not become active and the player might not be intrinsically motivated to perform that behavior. Thus, the present findings may provide information regarding how to make a student or worker experience intrinsic reward while performing a behavior in and of itself. In particular, the combination of controllability and an action-contingent outcome as essential components of a behavior will be important when applying various procedures, such as gamification.

Specific activations associated with the action-outcome contingency in other regions

Significant activation specific to the C+O+ condition was observed in the

anterior cingulate cortex, thalamus, and cerebellar vermis regions, as well as in the ventral striatal and midbrain regions. Participants who diligently played the SW game would attempt to stop the timer as close as possible to the 3-second mark by using feedback to accomplish this task. Consequently, participants tried to adjust the timing of their button presses based on the results of preceding trials if action-contingent feedback was available for use. The success rates significantly differed such that the success rate in the C+O+ condition was higher than that in the other conditions. This result supports the study expectations in that the participants successfully adjusted their button response in the C+O+ condition and, thus, cognitive processing was specifically enhanced in this condition. Several areas of the basal ganglia are involved in reward-based learning of motor control (Doya, 2000; Haruno and Kawato, 2006). The caudate nucleus is involved in motor control involving feedback related to goal-directed action (Packard and Knowlton, 2002), the perception of a contingency between button-press responses and outcomes (Tricomi et al., 2004), and feedback processing in the presence of intrinsic or extrinsic rewards (Tricomi et al., 2006; Murayama et al., 2010). The anterior cingulate cortex is also associated with the processing of positive feedback related to associative learning (Marco-Pallarés et al., 2007) and to performance adjustment (Ridderinkhof et al., 2004). It has been argued that the ventral thalamic region, in tandem with the striatum, plays an important role in reinforcement learning and action selection (see Smith et al., 2011 for a review). Similarly, the cerebellar vermis is associated with motor learning accompanied by feedback (Jueptner and Weiller, 1998; Doya, 2000). Thus, increased activation in these regions has been associated with the adjustment of motor control based on action-contingent outcome. This adjustment process is linked to the generation of an intrinsic value of an action, which allows participants to derive value from their own actions in the SW game.

Effects of controllability and outcome on cortical activation

The subtraction analyses for the two main effects indicated overlap between the two factors with respect to almost all activated regions in the medial region of the brain; these regions also overlapped with regions showing activation specific to the C+O+ condition. This suggests that the magnitude of activation under the C+O+ condition strongly influenced the computation of contrast images for those subtraction

analyses. Thus, the presence of either factor alone in the SW game could not fully explain the activation in these medial regions. Under the conditions that included controllability, the information that was displayed depended on participants' button-press responses. Consequently, participants had a sense of autonomy due to action-contingent changes in the visual stimulus. However, participants were unable to precisely evaluate their actions under the C+O- condition due to lack of feedback. Hence, they were unable to fully achieve a sense of competence under this condition—that is, an intrinsic value for the action was not generated under this condition. In contrast, the SW tasks with outcome included quantitative information about performance. However, the C-O+ condition did not include controllability; hence, the information displayed did not change when the participant pressed the button. Additionally, the pseudo-feedback was not contingent on the button-press response, which was explained prior to the fMRI measurement. Therefore, the participants did not receive a sufficient sense of autonomy from the changes in visual stimuli in the C-O+ condition. On the other hand, the participants could see the elapsed time on the screen until the pseudo-feedback was presented and, thus, could estimate an anticipated outcome from the elapsed time. The anticipated outcome was uncertain and might have been influenced by the pseudo-feedback because incongruity between the estimated result and pseudo-feedback could diminish one's sense of competence. This prevented participants from achieving a sufficient experience of autonomy and competence and, as a result, high levels of intrinsic value of action were not generated under the C-O+ condition. Furthermore, the local signal change of the ROI in the ventral striatum in the C-O+ condition was greater than that in the C-O- condition (Figure 3); a similar tendency was observed in the ROI of the midbrain. If the absence of an action-contingent outcome solely determines the intrinsic value of action, then the activation patterns of C-O+ and C-O- conditions should become equivalent. However, the present results showed contradictory patterns. Taken together, these findings indicate that both controllability and outcome proved essential for generating an intrinsic valuation of action; the reward system was not activated when either factor was excluded.

Significant activation reflecting the main effect of outcome was observed not only in the medial region but also in the lateral regions of the brain. Under the SW

conditions with outcome, participants could see the elapsed time on the screen until they stopped the SW. That is, they could adjust the timing of their button press by using the displayed timer. Such adjustment was difficult in SW tasks without outcome because the displayed timer was masked after 1.5 seconds. The success rates under each SW condition differed considerably depending on the presence of feedback. These results suggest that the cognitive processing of visuo–motor coordination was substantially involved in the execution of accurate motor responses via button press under conditions with the timer displayed. Previous studies have suggested that the parieto–frontal network is involved in the neural mechanism underlying visuo–motor coordination, such as in visually guided grasping (Grol et al., 2007). Visuo–motor coordination has been found to be involved not only in visuo–spatial manipulation tasks but also in temporal pattern processing (Schubotz et al., 2000). In our study, increased cortical activation within the parieto–frontal network occurred as a result of the visuo–motor coordination needed to control the button press based on timer information. Furthermore, participants could predict their degree of error for each trial because they were able to see the time at which they pressed the button under the SW conditions with outcome, resulting in enhanced anticipation of the result in the SW game with feedback. Risk anticipation and prediction of error have been reported to be among the cognitive functions of the anterior insula (Preuschoff et al., 2008). Similarly, Brown and Braver (2005) have reported that the rostral portion of the anterior cingulate cortex is involved in learning to predict error likelihood. Activation of the posterior cingulate cortex and medial prefrontal cortex is associated with subjective value estimation in a risky lottery task (Levy et al., 2010). Therefore, activation of the anterior and posterior cingulate regions and the anterior insular region reflects anticipation of behavioral error as represented by the predicted difference between target and stopped times.

The present study had several potential limitations that should be noted. First, the participants were instructed that the feedback information in the C-O+ condition was unrelated to the button response in order to ensure the effects of the pseudo-feedback. However, the participants did not confirm whether they recognized the pseudo-feedback during the fMRI measurement; therefore, it is possible that some participants misunderstood the pseudo-feedback as action-contingent information.

Additionally, the cortical activation induced by the C+O- condition might have contained a valuation of the intrinsic value of the action. However, activations of the various aspects of the reward network revealed a clear and significant difference between the C+O+ and C+O- conditions. Second, in the experimental design, the feedback in each trial was displayed 1.0–1.9 s after the button press because the immediate feedback given to the participant produced an action contingency. Accordingly, cortical activations induced by the button press and observation of feedback for each condition could not be perfectly separated in the first-level analysis. For the fMRI data analysis, it was expected and modeled that the hemodynamic responses would be associated with the valuation process of the intrinsic value of the action induced by the button press during the SW game because the valuation process might occur during the participant's voluntary action performing the game. Moreover, the feedback was a visual stimulus and was modeled as a condition of no interest. However, the present fMRI results indicate, at least in part, that this cortical activation might have been induced by the observation of the meaningful feedback due to restrictions of the task design. It has been suggested that positive feedback is processed as a reward (Tricomi et al., 2006; Marco-Pallares et al., 2007) and, although this fact may be interpreted as a limitation of the present study, the present findings suggest that there were differences in cortical activity during the performance of the SW game regarding the intrinsic value of the action, irrespective of these limitations.

Conclusion

We found that the SW game with an action-outcome contingency was chosen most frequently in the free-choice session. This indicates that the intrinsic value of action was enhanced by coexistence of controllability and outcome in the SW game. Moreover, the fMRI data showed that the ventral striatal and midbrain regions were significantly activated when both controllability and outcome were included in the SW game. These results suggest that, in a manner similar to the processing of external rewards or the intrinsic value of achieving success, the intrinsic value of an action in the SW game corresponded to incremental activation in the reward network.

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Reference

Bhanji JP, Delgado MR (2014) Perceived control influences neural responses to setbacks and promotes persistence. Neuron, 83(6):1369-1375.

Brett M, Anton J-L, Valabregue R, Poline, J-B (2002) Region of interest analysis using the MarsBar toolbox for SPM 99. Neuroimage, 16(2):S497.

Brown JW, Braver TS (2005) Learned predictions of error likelihood in the anterior cingulate cortex. Science, 307(5712):1118-1121. doi:10.1126/science.1105783

Clark L, Lawrence AJ, Astley-Jones F, Gray N (2009) Gambling near-misses enhance motivation to gamble and recruit win-related brain circuitry. Neuron, 61(3):481-490. doi:10.1016/j.neuron.2008.12.031

Cockburn J, Collins AG, Frank MJ (2014) A reinforcement learning mechanism responsible for the valuation of free choice. Neuron, 83(3):551-557. doi:10.1016/j.neuron.2014.06.035

Dale S (2014) Gamification: Making work fun, or making fun of work?. Bus Inf Rev, 31(2):82-90.

D'Ardenne K, McClure SM, Nystrom LE, Cohen JD (2008) BOLD responses reflecting dopaminergic signals in the human ventral tegmental area. Science, 319(5867):1264-1267. doi:10.1126/science.1150605

Deci EL, Koestner R, Ryan RM (1999) The undermining effect is a reality after all—Extrinsic rewards, task interest, and self-determination: Reply to Eisenberger, Pierce, and Cameron (1999) and Lepper, Henderlong, and Gingras (1999).

Deci EL, Ryan RM (2008) Facilitating Optimal Motivation and Psychological Well-Being Across Life's Domains. Canadian Psychol, 49(1):14-23.

Dicheva D, Dichev C, Agre G, Angelova G (2015) Gamification in education: A systematic mapping study. Educ Technol Soc, 18(3), 75-88.

Doya K (2000) Complementary roles of basal ganglia and cerebellum in learning and motor control. Curr Opin Neurobiol, 10(6):732-739.

Elliott R, Friston KJ, Dolan RJ (2000) Dissociable neural responses in human reward systems. J Neurosci, 20(16):6159-6165.

Ellis, M.J. (1973). Why People Play, Prentice-Hall.

FitzGerald TH, Schwartenbeck P, Dolan RJ (2014) Reward-related activity in ventral

striatum is action contingent and modulated by behavioral relevance. J Neurosci, 34(4):1271-1279. doi:10.1523/JNEUROSCI.4389-13.2014

Friston KJ, Holmes A, Poline J-B, Price CJ, Frith CD (1996) Detecting activations in PET and fMRI: levels of inference and power. Neuroimage, 4(3):223-235.

Friston KJ, Holmes AP, Worsley KJ, Poline J-P, Frith CD, Frackowiak RS (1994) Statistical parametric maps in functional imaging: a general linear approach. Hum Brain Mapp, 2(4):189-210.

Friston KJ, Worsley KJ, Frackowiak R, Mazziotta JC, Evans AC (1994) Assessing the significance of focal activations using their spatial extent. Hum Brain Mapp, 1(3):210-220.

Grol MJ, Majdandzic J, Stephan KE, Verhagen L, Dijkerman HC, Bekkering H, Verstraten FA, Toni I. (2007) Parieto-frontal connectivity during visually guided grasping. J Neurosci, 27(44):11877-11887. doi:10.1523/JNEUROSCI.3923-07.2007

Haruno M, Kawato M. (2006) Heterarchical reinforcement-learning model for integration of multiple cortico-striatal loops: fMRI examination in stimulus-action-reward association learning. Neural Netw, 19(8):1242-1254. doi:10.1016/j.neunet.2006.06.007

Hattie J, Timperley H (2007) The Power of Feedback. Rev Educational Res, 77(1):81-112. doi:10.3102/003465430298487

Henderlong J, Lepper MR (2002) The effects of praise on children's intrinsic motivation: A review and synthesis. Psychol Bull, 128(5):774-795. doi:10.1037//0033-2909.128.5.774.

Isen AM, Reeve J (2005) The influence of positive affect on intrinsic and extrinsic motivation: Facilitating enjoyment of play, responsible work behavior, and self-control. Motivation and emotion, 29(4):295-323.

Jueptner M, Weiller C (1998) A review of differences between basal ganglia and cerebellar control of movements as revealed by functional imaging studies. Brain, 121(8):1437-1449.

Katsyri J, Hari R, Ravaja N, Nummenmaa L (2013) Just watching the game ain't enough: striatal fMRI reward responses to successes and failures in a video game during active and vicarious playing. Front Hum Neurosci, 7:278.

doi:10.3389/fnhum.2013.00278

Kuvaas B, Dysvik A (2009) Perceived investment in employee development, intrinsic motivation and work performance. Hum Resour Manag J, 19(3):217-236.

Lancaster JL, Rainey LH, Summerlin, JL, Freitas CS, Fox PT, Evans AC, Toga AW, Mazziotta JC (1997) Automated Labeling of the Human Brain: A Preliminary Report on the Development and Evaluation of a Forward-Transform Method. Hum Brain Mapp, 5(4):238-242.

Lancaster JL, Tordesillas-Gutierrez D, Martinez M, Salinas F, Evans AC, Zilles K, Mazziotta JC, Fox PT (2007) Bias between MNI and Talairach coordinates analyzed using the ICBM-152 brain template. Hum Brain Mapp, 28(11):1194-1205. doi:10.1002/hbm.20345

Lancaster JL, Woldorff MG, Parsons LM, Liotti M, Freitas CS, Rainey LH, Kochunov PV, Nickerson D, Mikiten SA, Fox PT (2000) Automated Talairach atlas labels for functional brain mapping. Hum Brain Mapp, 10(3):20-131.

Leotti LA, Delgado MR (2011) The inherent reward of choice. Psychol Sci, 22(10):1310-1318. doi:10.1177/0956797611417005

Levy I, Snell J, Nelson AJ, Rustichini A, Glimcher PW (2010) Neural representation of subjective value under risk and ambiguity. J Neurophysiol, 103(2):1036-1047. doi:10.1152/jn.00853.2009

Marco-Pallares J, Muller SV, Munte, TF (2007) Learning by doing: an fMRI study of feedback-related brain activations. Neuroreport, 18(14):1423-1426. doi:10.1097/WNR.0b013e3282e9a58c

Marsden K.E, Ma WJ, Deci EL, Ryan RM, Chiu PH (2015) Diminished neural responses predict enhanced intrinsic motivation and sensitivity to external incentive. Cogn Affect Behav Neurosci, 15(2):276-286.

Murayama K, Matsumoto M, Izuma K, Matsumoto K (2010) Neural basis of the undermining effect of monetary reward on intrinsic motivation. Proc Natl Acad Sci, 107(49):20911-20916. doi:10.1073/pnas.1013305107

Murayama K, Matsumoto M, Izuma K, Sugiura A, Ryan RM, Deci EL, Matsumoto K (2015) How self-determined choice facilitates performance: a key role of the ventromedial prefrontal cortex. Cereb Cortex, 25(5):1241-1251. doi:10.1093/cercor/bht317

O'Doherty J, Dayan P, Schultz J, Deichmann R, Friston KJ, Dolan RJ (2004) Dissociable roles of ventral and dorsal striatum in instrumental conditioning. Science, 304(5669):452-454. doi:10.1126/science.1094285

Oldfield RC (1971) The assessment and analysis of handedness: the Edinburgh inventory. Neuropsychologia, 9(1):97-113.

Oprescu F, Jones C, Katsikitis M (2014) I PLAY AT WORK—ten principles for transforming work processes through gamification. Front in Psychol, 5:14.

Packard MG, Knowlton BJ (2002) Learning and memory functions of the Basal Ganglia. Annu Rev Neurosci, 25:563-593. doi:10.1146/annurev.neuro.25.112701.142937

Pekrun R (2006) The Control-Value Theory of Achievement Emotions: Assumptions, Corollaries, and Implications for Educational Research and Practice. Educational Psychol Rev, 18(4), 315-341:doi:10.1007/s10648-006-9029-9

Pessiglione M, Schmidt L, Draganski B, Kalisch R, Lau H, Dolan RJ, Frith CD (2007) How the brain translates money into force: a neuroimaging study of subliminal motivation. Science, 316(5826):904-906. doi:10.1126/science.1140459

Preuschoff K, Quartz SR, Bossaerts P (2008) Human insula activation reflects risk prediction errors as well as risk. J Neurosci, 28(11):2745-2752. doi:10.1523/JNEUROSCI.4286-07.2008

Promberger M, Marteau TM (2013) When do financial incentives reduce intrinsic motivation? comparing behaviors studied in psychological and economic literatures. Health Psychol, 32(9):950-957. doi:10.1037/a0032727

Reeve J (1989) The interest-enjoyment distinction in intrinsic motivation. Motivation and Emotion, 13(2), 83-103.

Ridderinkhof KR, Ullsperger M, Crone EA, Nieuwenhuis S (2004) The role of the medial frontal cortex in cognitive control. Science, 306(5695):443-447. doi:10.1126/science.1100301

Ryan RM, Mims V, Koestner R (1983) Relation of reward contingency and interpersonal context to intrinsic motivation: A review and test using cognitive evaluation theory. J Personal and soc psychol, 45(4):736.

Sailer M, Hense J, Mandl H, Klevers M (2013) Psychological Perspectives on Motivation through Gamification. IxD&A, 19, 28-37.

Schubotz RI, Friederici AD, von Cramon DY (2000) Time perception and motor timing:

a common cortical and subcortical basis revealed by fMRI. Neuroimage, 11(1):1-12. doi:10.1006/nimg.1999.0514

Sharot T, De Martino B, Dolan RJ (2009) How choice reveals and shapes expected hedonic outcome. J Neurosci, 29(12):3760-3765. doi:10.1523/JNEUROSCI.4972-08.2009

Shaffer JP (1986) Modified sequentially rejective multiple test procedures. J. of the American Stat Assoc, 81(395):826-831.

Smith Y, Surmeier DJ, Redgrave P, Kimura M (2011) Thalamic contributions to Basal Ganglia-related behavioral switching and reinforcement. J Neurosci, 31(45):16102-16106. doi:10.1523/JNEUROSCI.4634-11.2011

Talairach J, Tournoux P (1988) Co-planar stereotaxic atlas of the human brain. 3-Dimensional proportional system: an approach to cerebral imaging, New York.

Tricomi E, Delgado MR, McCandliss BD, McClelland JL, Fiez JA (2006) Performance feedback drives caudate activation in a phonological learning task. J Cogn Neurosci, 18(6):1029-1043.

Tricomi EM, Delgado MR, Fiez JA (2004) Modulation of caudate activity by action contingency. Neuron, 41(2):281-292.

Westbrook A, Braver TS (2016) Dopamine does double duty in motivating cognitive effort. Neuron, 89(4):695-710.

Legends

Figure 1.

Details of the fMRI experimental task design. (A) Timeline of the fMRI experiment. (B) The time course of a single trial in each stopwatch (SW) task. Font color indicates the task type, the relation between the font color and task type is notified in advance. Following an inter-trial interval, a SW started automatically. In the C+O- (the condition including only controllability) and C-O- (the condition including neither controllability nor outcome) conditions, the displayed time was masked by numbers that changed randomly after 1.5 seconds to prevent participants from viewing information regarding the timing of the button press in the SW tasks without feedback. After the button press, a fixed set of blinking numbers (88:88) was presented under the C+O+ (the condition incorporating both controllability and outcome) and C+O- conditions. In contrast, accurate times or random numbers were continuously presented under the C-O+ (the condition including only outcome) and C-O- conditions, respectively. At the end of the trial, actual feedback showing the result of trial was presented under the C+O+ condition, and pseudo-feedback was presented under the C-O+ condition, with the other two conditions (C+O- and C-O-) presenting fixed meaningless numbers (88:88). (C) The time course of a single trial in each control task. In the watch-stop (WS) task, the timer automatically stopped at 3 seconds, irrespective of the button-press response. And, fixed meaningless numbers (88:88) with yellow font-color was presented in the feedback period. In the color task, fixed numbers (88:88) were presented, and their font color changed at the 3-s mark. Fixed numbers representing meaningless feedback were presented at the end of the trial.

Figure 2.

Results of the free-choice experiment. Bar charts show the average number of times that participants chose each task, with error bars indicating the standard error of the mean.

Figure 3.

Regions showing activation specific to the C+O+ condition: (A) left caudate nucleus, (B) left globus pallidus, (C) midbrain, (D) anterior cingulate cortex, (E) left thalamus, and (F) cerebellar vermis ($p < 0.05$, corrected for FWE by voxel level). The crosshairs on the sectional image (left) show the location of the activation peak, and the color scale indicates T-values. Activation clusters were anatomically labeled using Talairach Software. The bar chart (right) shows the percent signal change relative to the button press for each SW task and control condition with respect to each activation peak, as calculated using the MarsBar toolbox. The error bar shows the standard error of the mean.

Figure 4.

Regions showing significant main effects and interaction: (A) regions showing significant differences due to controllability, (B) clusters showing overlap between activation specific to the C+O+ condition and activation reflecting the main effect of controllability in the ventral striatum and midbrain regions, (C) regions showing significant differences due to the availability of outcome, and (D) clusters showing overlap between activation specific to the C+O+ condition and activation reflecting the main effect of outcome, (E) regions showing significant differences due to the interaction effect between controllability and outcome, and (F) clusters showing overlap between activation specific to the C+O+ condition and activation reflecting the interaction ($p < 0.05$, corrected for FWE by voxel level). Each activation map in (A), (C) and (E) was projected onto the bilateral surface and sagittal sectional image ($x = 8$ mm) of the MNI single-subject template. The coordinate value of each sagittal slice (y-axis) in (B), (D) and (F) was determined by activation peaks in the striatal and midbrain regions showing activation specific to the C+O+ condition (as shown in Figure 3 (A), (B) and (C)). Color scales indicate T-values for activation specific to the C+O+ condition (red – white) and for the main effects of controllability (blue – green), outcome (blue – light blue) and interaction (black – light green).

Table

Table 1.

Significant activation specific to the C+O+ condition. The threshold size of activation was $p < 0.05$, corrected for FWE by voxel level. L/R indicates left (L) or right (R) hemisphere.

Cluster size (mm^3)	**MNI coordinate (mm)**			**z-value**	**Location**	
	x	y	z		L/R	Anatomical label
10944	10	10	-2	5.79	R	Caudate nucleus
	-10	10	8	5.95	L	Caudate nucleus
	12	0	-6	6.10	R	Globus pallidus
	-10	-2	-4	6.03	L	Globus pallidus
	8	-12	-2	5.94	R	Thalamus
	-6	-24	-4	6.08	L	Thalamus
	6	-26	-2	5.79	R	Thalamus
	4	-28	-18	6.34	R	Midbrain
2224	2	-50	-18	5.20	R	Cerebellar vermis
	0	-62	-26	5.38		Cerebellar vermis
	0	-70	-34	5.83		Cerebellar vermis
536	8	30	22	5.26	R	Anterior cingulate cortex
8	-16	-68	-22	4.66	L	Cerebellar posterior lobule

Appendices

Table A.1.

Regions showing a significant main effect of controllability. The threshold size of activation was $p < 0.05$, corrected for FWE by voxel level. L/R indicates left (L) or right (R) hemisphere.

Cluster size	**MNI coordinate (mm)**			**z-value**		**Location**
(mm^3)	x	y	z		L/R	Anatomical label
3664	10	12	8	5.15	R	Caudate nucleus
	-8	0	-4	5.23	L	Globus pallidus
	10	2	-6	6.43	R	Globus pallidus
	-4	-8	2	4.83	L	Thalamus
	16	-10	8	5.06	R	Thalamus
	8	-10	0	5.49	R	Thalamus
1296	4	36	16	5.86	R	Anterior cingulate cortex
800	-20	-54	-22	6.13	L	Cerebellar vermis
512	8	-64	-24	5.19	R	Cerebellar vermis
336	-10	10	8	5.49	L	Caudate nucleus
144	-2	-70	-34	5.09	L	Cerebellar vermis
96	6	18	14	5.17	R	Anterior cingulate cortex
96	-4	-26	-2	4.93	L	Thalamus
56	22	-44	-26	5.02	R	Cerebellar vermis
16	10	-20	-12	4.68	R	Midbrain
8	10	-80	0	4.64	R	Lingual Gyrus
8	0	-62	-34	4.64		Cerebellar posterior lobule

Table A.2.

Regions showing a significant main effect of outcome. The threshold size of activation was $p < 0.05$, corrected for FWE by voxel level. L/R indicates left (L) or right (R) hemisphere.

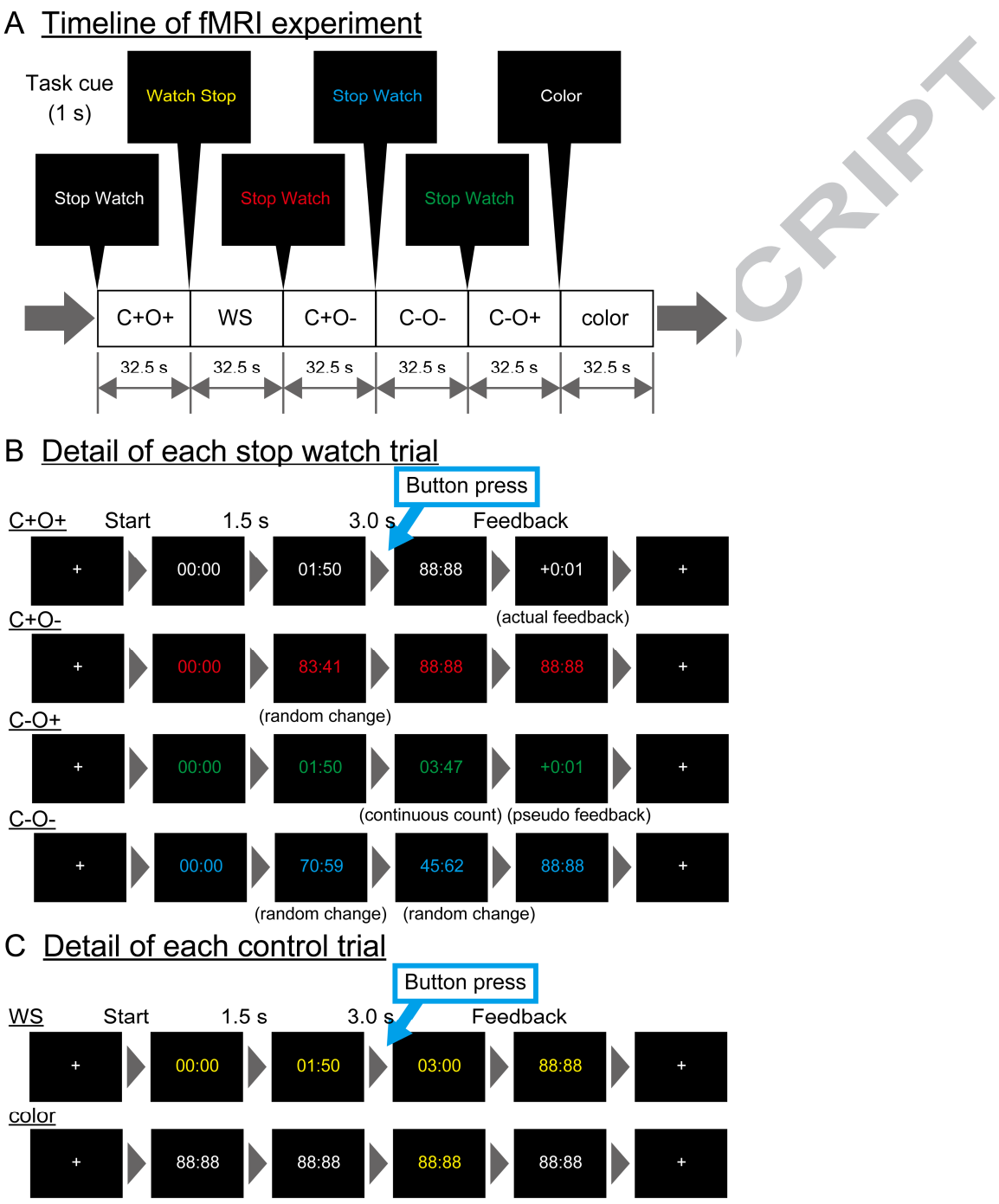
Cluster size (mm^3)	**MNI coordinate (mm)**			**z-value**	**Location**	
	x	y	z		L/R	Anatomical label
68360	44	50	-4	6.99	R	Middle frontal gyrus
	42	34	12	7.67	R	Middle frontal gyrus
	46	28	20	> 8	R	Middle frontal gyrus
	30	22	-8	> 8	R	Claustrum
	-30	18	-6	> 8	L	Claustrum
	46	8	24	> 8	R	Inferior frontal gyrus
	12	6	0	7.75	R	Caudate nucleus
	22	2	-12	6.38	R	Globus pallidus
	-12	2	4	7.59	L	Putamen
	32	0	46	> 8	R	Middle frontal gyrus
	-22	0	-12	6.52	L	Putamen
	8	-12	4	> 8	R	Thalamus
	10	-18	10	> 8	R	Thalamus
	-8	-18	8	6.85	L	Thalamus
	8	-26	-8	7.22	R	Midbrain
	-6	-26	-6	6.01	L	Midbrain
29360	46	-40	46	7.63	R	Inferior parietal lobule
	32	-60	42	> 8	R	Precuneus
	16	-66	40	7.72	R	Precuneus
	12	-70	54	6.57	R	Precuneus
21728	-46	-36	40	> 8	L	Supramarginal gyrus
	-34	-50	48	> 8	L	Inferior parietal lobule
	-24	-60	44	> 8	L	Precuneus
	-28	-68	32	> 8	L	Precuneus

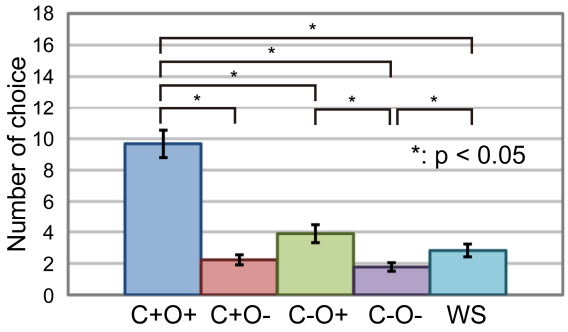
	-10	-72	44	6.77	L	Precuneus
11296	-42	36	6	5.27	L	Middle frontal gyrus
	-44	0	26	> 8	L	Precentral gyrus
6672	8	34	20	4.88	R	Anterior cingulate cortex
	6	28	42	> 8	R	Medial frontal gyrus
4968	6	2	28	5.77	R	Posterior cingulate cortex
	2	-26	26	7.54	R	Posterior cingulate cortex
4488	-26	-68	-28	6.52	L	Cerebellar vermis
	-10	-80	-26	7.55	L	Cerebellar vermis
3376	-48	-64	-10	> 8	L	Fusiform gyrus
1936	54	-52	-12	> 8	R	Fusiform gyrus
1776	0	-60	-36	6.74		Cerebellar posterior lobule
1160	12	-76	-24	6.62	R	Cerebellar vermis
1112	-28	4	50	5.87	L	Middle frontal gyrus
1088	-32	-76	-50	6.25	L	Cerebellar posterior lobule
256	-24	-36	-42	5.58	L	Cerebellar posterior lobule
160	26	-66	-28	5.56	R	Cerebellar vermis
80	26	38	-20	5.05	R	Middle Frontal Gyrus
40	22	-42	-44	4.83	R	Cerebellar posterior lobule
32	6	-34	-30	4.72	R	Cerebellar vermis
8	24	56	-12	4.66	R	Superior Frontal Gyrus

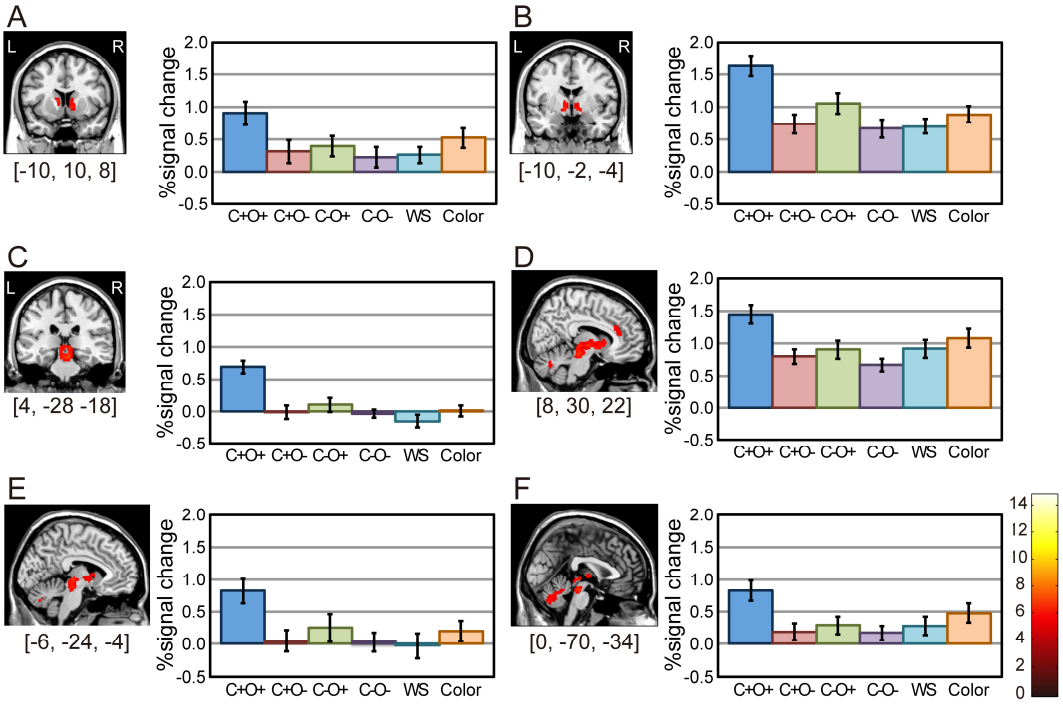
Table A.3.

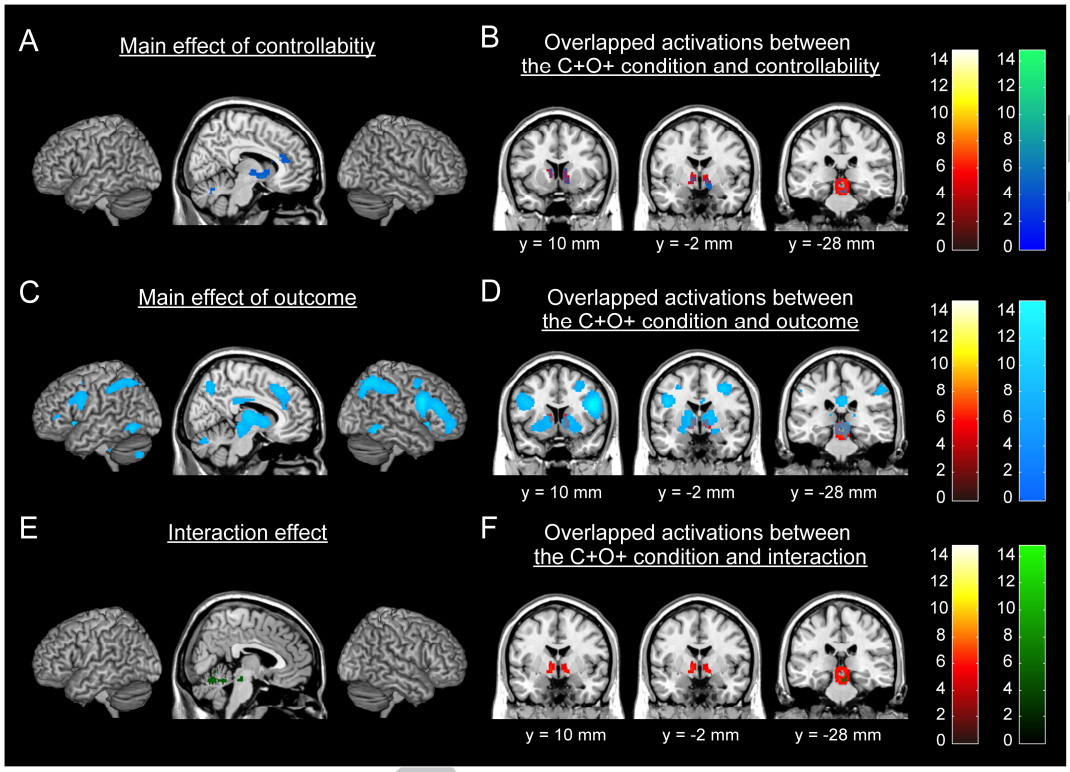
Regions showing a significant interaction effect between the controllability and outcome. The threshold size of activation was $p < 0.05$, corrected for FWE by voxel level. L/R indicates left (L) or right (R) hemisphere.

Cluster size (mm^3)	**MNI coordinate (mm)**			**z-value**	**Location**	
	x	y	z		L/R	Anatomical label
1136	2	-64	-18	5.49	R	Cerebellar vermis
	4	-50	-18	4.99	R	Cerebellar vermis
304	4	-28	-18	4.95	R	Midbrain
136	16	-46	-32	4.94	R	Cerebellar anterior lobule
32	-22	-24	68	4.94	L	Postcentral gyrus
64	2	-60	-6	4.92	R	Cerebellar vermis
32	6	-70	-36	4.82	R	Cerebellar vermis
40	28	-42	-30	4.79	R	Cerebellar vermis
8	10	-42	-28	4.79	R	Cerebellar vermis
8	-6	-24	-4	4.73	L	Thalamus
8	24	-44	-32	4.72	R	Cerebellar anterior lobule









Title: Neural evidence for the intrinsic value of action as motivation for behavior
Authors: Miura et al.

Highlights

- We investigated how the intrinsic value of action is neurally represented by fMRI.
- Existence of controllability and outcome was manipulated as task conditions.
- A task with the both controllability and outcome evoked greater enjoyment.
- The reward network was activated when both of controllability and outcome existed.
- The intrinsic value of action is processed in a way similar to an extrinsic reward.