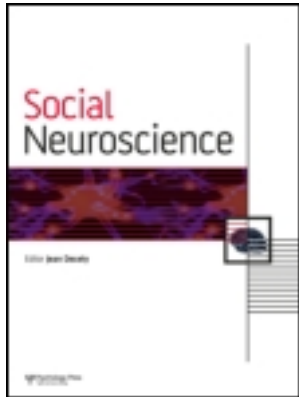


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Positive priming and intentional binding: Eye-blink rate predicts reward information effects on the sense of agency

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Human society is strongly rooted in people's experiences of agency; that is, the pervasive feeling that one engages in voluntary behavior and causes one's own actions and resulting outcomes. Rewards and positive affect play an important role in the control of voluntary action. However, the role of positive reward signals in the sense of agency is poorly understood. This study examined effects of reward-related information on the sense of agency by employing the intentional binding paradigm. This paradigm measures the extent to which actions and their effects subjectively shift together across time, reflecting a crucial component of people's sense of agency. Results showed that intentional binding is stronger when participants are primed with reward-related information via brief exposure to positive pictures. Interestingly, this positive priming effect was moderated by baseline eye-blink rates (an indirect marker of striatal dopaminergic functioning); reward-related information increased intentional binding mainly for participants displaying higher baseline eye-blink rates. These findings suggest a possible role for striatal dopamine activity in the process by which reward-related information shapes the way people see themselves as agents.

Keywords: Sense of agency; Intentional binding; Rewards; Eye-blink rate; Striatal dopaminergic activity.

Humans engage in voluntary action. People direct their behavior toward goals or outcomes they aim to attain, experiencing their movements as coherent and self-caused. Research shows that positive affect plays an important role in voluntary action. Positive affect often derives from reward-related information that is processed by subcortical structures, including the ventral tegmental areas and ventral striatum, and affects voluntary action through dopamine pathways involved in cognitive and motor control (Aston-Jones & Cohen, 2005; Schnitzler & Gross, 2005). The brain's reward circuit responds to stimuli intrinsically related to evolutionarily relevant rewards such as food and sex, but also to stimuli that acquire positive valence by

learning, such as money or a picture of a smiling face (Schultz, 2006). Moreover, positive affective stimuli, such as pictures with a positive connotation, act as reward signals and can influence voluntary action automatically (Custers & Aarts, 2010; Dreisbach & Goschke, 2004). Thus, reward signals are readily picked up by the brain and facilitate voluntary action, such that people are more likely to attain goals.

Although previous research has extensively addressed the link between reward-related information, dopamine functioning, and goal-directed performance, it is still unclear whether and how positive reward signals alter conscious experiences of voluntary action. The present research addresses this

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void in the literature. While addressing the specific role of dopamine functioning, we here examine the effect of positive reward signals, via brief exposure to positive pictures, on a set of key functions that involve both cognitive and motor processes during operant action performance. In this kind of performance, individuals voluntarily execute an action (e.g., a key press) that causes a specific effect (e.g., a tone) to occur. Humans seem to have a distinctive experience of voluntary motor control when their action produces an outcome; that is, the sense of agency or subjective awareness that one initiates and controls one's own actions and resulting events in the external world. A better understanding of the role of reward-related information in the sense of agency is important, because the sense of agency constitutes a fundamental aspect of human self-perception in particular, and societal and legal system in general (Aarts & van den Bos, 2011). Moreover, the sense of agency appears disturbed in individuals with high schizotypal traits (Asai & Tanno, 2008), and in patients with schizophrenia (Brunet & Decety, 2006; Frith, 2005) and obsessive compulsive disorder (Belayachi & Van der Linden, 2010).

Operant action is highly sensitive to reward signals and involves dopamine systems. Dopamine is a key neurotransmitter implicated in incentive motivation (Berridge, 2007), memory formation (Wittmann et al., 2005), and motor function (Volkow et al., 1998). Furthermore, dopaminergic activity in the striatum plays an important role in prediction errors of actual (typically rewarding) outcomes of actions (Schultz & Dickinson, 2000), reinforcement learning (O'Doherty et al., 2004), and executive control (Aston-Jones & Cohen, 2005). Importantly for our study, positive stimuli affect the dopaminergic system in the same way as positive feedback or rewards (Dreischbach & Goschke, 2004). For instance, briefly exposing subjects to positive pictures (compared to neutral or negative pictures) before task performance increases executive control over action, an effect that is also observed in subjects with the *DRD4/7* genotype or high levels of baseline eye-blink rates (EBR), which are both associated with heightened striatal dopamine functioning (Dreischbach et al., 2005).

Research on social cognition suggests that people attribute more self-causation to their behavior when it is associated with desired outcomes or positive affect; that is, rewarding events (e.g., Bandura, 1986; Deci & Ryan, 1985; Miller & Ross, 1975). Based on this observation, we propose that positive stimuli may enhance the sense of agency in operant action through the ventral dopaminergic system. Voluntary action is supposed to be controlled by the basal ganglia that transfer signals from the prefrontal cortex

to cortical motor areas, such as the supplementary and pre-supplementary motor areas, to drive currently appropriate actions (Garraux, Peigneux, Carson, & Hallett, 2007; Kuehn & Brass, 2009; Nachev, Kennard, & Husain, 2008). Furthermore, striatal dopamine activity may modulate this drive according to patterns of rewards, thereby facilitating the actual initiation and experience of voluntary action (Sperduti, Delaveau, Fossati, & Nadel, 2011; Watanabe & Munoz, 2010). Reward signals thus can generate an implicit motivation to engage in operant actions (Custers & Aarts, 2010) and augment the sense of agency by amplifying the formation of associations between action and outcome (Pessiglione, Seymour, Flandin, Dolan, & Frith, 2006). Although reward and dopamine are clearly involved in voluntary action, a test of whether reward-related information, such as positive pictures, increases the sense of agency in operant action and the involvement of dopamine functioning in this process still awaits empirical scrutiny.

In an attempt to provide an initial test of this issue, we examined the effects of positive stimuli on the sense of agency by employing the intentional binding paradigm. Based on internal prediction models of sensorimotor control (Frith, Blakemore, & Wolpert, 2000), the intentional binding paradigm assesses the extent to which motor action and sensory outcome are perceived to occur more closely together in time when the person voluntarily performs the action (Haggard, Clark, & Kalogeras, 2002). Typically, when individuals voluntarily (agency condition) press a key that causes 250 ms later a tone, they judge the key press to occur later and/or the tone to occur earlier than when the two events occur alone (single-event baseline condition). This temporal binding effect does not appear when the tone is preceded by an involuntary key press (e.g., resulting from transcranial magnetic stimulation; Haggard et al., 2002) and for actions that we observed in others (Engbert, Wohlschläger, & Haggard, 2008). Thus, temporal binding between action and effect reflects a crucial component in people's feelings of agency of voluntary action.

Based on the line of reasoning discussed above, we hypothesized that the intentional binding between action and outcome might be increased by positive (vs. neutral) stimuli, and we propose that the effect of such positive, reward-related information involves the dopaminergic system. If so, and if the activity of the dopaminergic system can be affected by the presentation of pictures with a positive valence (Dreischbach & Goschke, 2004), we should be able to demonstrate that shifts in perceived time between action and outcome are affected by positive pictures.

Furthermore, to explore the potentially mediating role of dopamine functioning in this process, we

exploited individual differences in baseline eye-blink rate (EBR). EBR is associated with the functional state of the striatal dopamine system (Karson, 1983). For instance, administration of dopamine agonists and antagonists increase and reduce EBR, respectively (Blin, Masson, Azulay, Fondarai, & Serratrice, 1990; Lawrence & Redmond, 1991). Furthermore, additional evidence for the link between striatal dopamine and EBR comes from clinical observations in schizophrenic patients (Freed, 1980), who have hyper-elevated EBR and dopamine functioning in the striatum (Howes & Kapur, 2009; Kegeles et al., 2010), and Parkinson patients, who have reduced EBR likely resulting from losses of nigrostriatal dopaminergic cells (Dauer & Przedborski, 2003).

Importantly, EBR correlates with personality traits such as impulsivity, novelty seeking, and positive emotionality, which in turn are associated with reward sensitivity (Dagher & Robbins, 2009; Depue, Luciana, Arbisi, Collins, & Leon 1994; Huang, Stanford, & Barratt, 1994; Martin & Potts, 2004). For instance, impulsive individuals tend to prefer immediate rewards, and choosing immediate rewards is associated with greater activity in areas innervated by the mesolimbic dopamine system, including the ventral striatum (Hariri et al., 2006; McClure, Laibson, Loewenstein, & Cohen, 2004). In addition, increasing levels of dopamine functioning (by administration of levodopa) renders subjects more sensitive to reward learning (Pleger et al., 2009). Taken together, then, these findings support the prediction that if pictures with positive valence enhance intentional binding by modulating dopamine functioning, then the positive priming effect on intentional binding should be more pronounced in participants with higher EBR. The present experiment was designed to test this novel prediction.

METHOD

Participants

Twenty-eight healthy young adults (mean age = 22.07; $SD = 2.96$) participated in the experiment in return for a small payment. Informed consent was given in written format.

Task and materials

To assess intentional binding of action and outcome, we employed the method of Haggard et al. (2002), with one important modification. In our experiment,

participants were presented with either a positive or a neutral picture just before a trial started. In this way, we could examine the effect of reward-related information on intentional binding. Twenty neutral and 20 positive pictures were selected from the IAPS (Lang, Bradley, & Cuthbert, 2005). The selected IAPS picture numbers of the neutral condition were as follows: 7002, 7004, 7009, 7010, 7020, 7025, 7030, 7031, 7035, 7040, 7050, 7080, 7090, 7100, 7140, 7150, 7175, 7224, 7233, and 7235; the selected picture numbers of the positive condition were as follows: 1440, 1460, 1463, 1604, 1710, 1750, 1920, 1999, 2040, 2057, 2091, 2311, 2340, 2352, 2530, 2550, 7325, 7410, 7470, and 8540. According to the IAPS, the mean valence ratings (9-point scale) for the neutral and positive pictures were 4.93 and 7.66, respectively. Baseline EBR was recorded by infrared videography technology (Tobii X120 Eye Tracker Danderyd, Sweden).

Intentional binding procedure

The experimental task is displayed in Figure 1. In a series of trials, participants attended to a clock (diameter = 2 cm) with a clock hand (2 mm) rotating clockwise with a period of 2,560 ms. The clock face (presented on the computer screen) was marked with conventional intervals (5, 10, 15, etc.). Each trial started with a fixation cross (1500 ms) and the text 'Pay attention' (1000 ms), to ensure that participants would focus on the pictures. Next, a pre-mask was presented for 100 ms, and then a (neutral or positive) picture was presented for 150 ms, followed by a post-mask (100 ms). For both masks, a gray square with the same size of the picture was used. After this picture-presentation procedure, the clock hand started moving from a random position. Depending on the trial type, participants freely pressed a key that caused a tone to occur (1000 Hz, presented for 100 ms on a headphone), pressed the key and heard no tone, or only heard the tone. At the end of each trial, participants reported the position of the clock hand at the moment they pressed the key or heard the tone, using the numbers 0 through 60 in intervals of 1.

The task consisted of four types of trials. In one trial type (1), participants made a voluntary key press with their index finger, at a time of their own free choice during the second cycle of the minute hand's rotation. Pressing the key caused the auditory tone to occur 250 ms later. After the tone, participants judged the onset of their key press. In a second trial type (2), participants also pressed the key that produced the tone, but in this case they were asked to judge the onset of

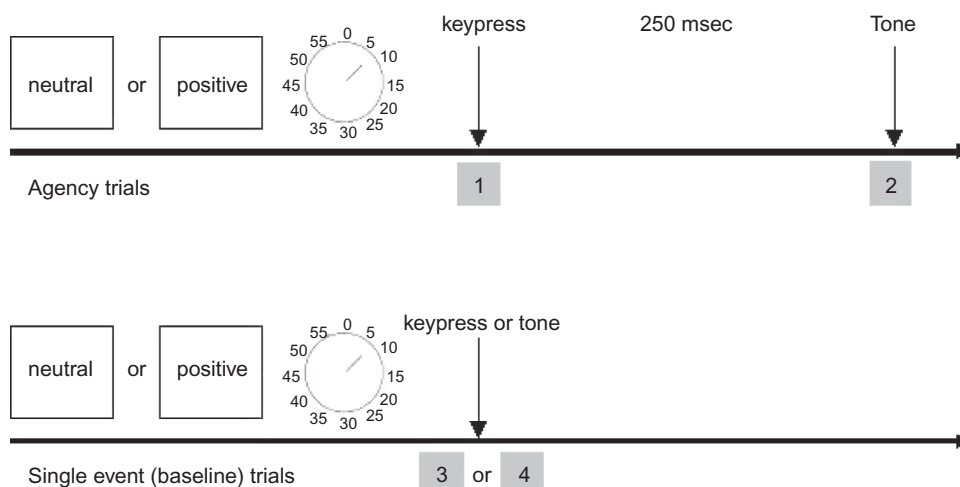


Figure 1. The procedure of the task. Each trial started with the brief presentation of a neutral or positive picture. Next, subjects attended to a clock with a hand rotating clockwise with a period of 2,560 ms. Depending on the trial type, subjects freely pressed a key that caused a tone to occur 250 ms later, pressed the key and heard no tone, or only heard the tone. At the end of each trial, they reported the position of the clock hand at the moment they pressed the key or heard the tone. The task consisted of two types of *agency* trials in which (1) subjects pressed the key that was followed by a tone, and judged the onset of their action, and (2) subjects pressed the key that was followed by a tone, and judged the onset of the tone; and two types of *single-event* trials in which (3) subjects pressed the key, but a tone did not follow, and judged the onset of their action, and (4) no key presses were made, and only a tone sounded, and participants judged the onset of the tone.

the tone. We refer to these first two types of trials as agency trials. In a third trial type (3), key presses were performed, but a tone did not follow, and participants judged the onset of their action. In a fourth trial type (4), no key presses were made, and a tone sounded at a random time during the display of the running clock; on these trials, participants judged the onset of the tone. We refer to these last two types of trials as single-event trials. The task was divided into four blocks; each included one type of trial. Each block contained 40 trials, and in each block the neutral (20 trials) and positive pictures (20 trials) were presented in a random order, corresponding to a separate condition in a 2 (judgment: key press vs. tone) \times 2 (agency: single event vs. agency) \times 2 (valence of picture: neutral vs. positive) within-subjects design. The order of blocks was randomized.

For each trial, judgment error (in ms) was calculated as the difference between the perceived time of an event and its actual time of occurrence. A positive judgment error corresponds to delayed awareness of the event, and a negative judgment error corresponds to anticipatory awareness.

EBR measurement

The eye tracker recorded light reflections from the open eye. Accordingly, eye blinks can be measured when participants close their eye and no light is

reflected. During the measurement, participants were comfortably seated in front of a computer screen with a cross in the center, and asked to look at the cross in a relaxed state for about 5 min (due to recalibration of the eye tracker during this task, the time could vary a bit between participants). This duration was chosen, because a shorter observation period is likely to be compromised by natural fluctuations in endogenous eye blinks (Doughty, 2001). All recordings took place between 10 am and 5 pm, since EBR are most stable during this period (Barbato et al., 2000). In addition, both temperature and lighting were held constant in the experimental room during all measurements, since these are thought to influence eye-blink ratings (Doughty, 2001). An eye blink was defined as missing data from 100 to 500 ms, and the number of eye blinks corrected for the total amount of recorded time served as the EBR score (Tobii Technology; Product Description, 2009 Danderyd, Sweden). In line with other studies measuring EBR in healthy individuals (e.g., Doughty, 2001), the mean EBR/min in our sample was 15.77 ($SD = 10.58$).

RESULTS

The mean judgment errors were subjected to ANCOVA, with judgment (key press vs. tone), agency

(single event vs. agency) and valence (neutral vs. positive) as within-subjects variables, and the subject's baseline EBR score as a continuous variable. This analysis revealed a significant interaction between judgment and agency, $F(1, 26) = 32.42, p < .001, \eta_p^2 = .56$. We replicated the standard intentional binding effect (Haggard et al., 2002): Judging the onset of the action when it was followed by the tone (vs. not followed by the tone) produced a positive judgment error (mean shift = +41.77 ms, $SE = 9.07$). In addition, judging the onset of the tone when it was preceded by the action (vs. not preceded by the action) produced a negative judgment error (mean shift = -48.04 ms, $SE = 15.80$). This interaction effect corresponds to an *intentional binding effect* of 89.81 ms (i.e., the difference between the shift in action and tone).

Importantly, the interaction effect between judgment and agency was qualified by a significant three-way interaction involving valence of picture, $F(1, 26) = 4.50, p = .04, \eta_p^2 = .15$. In line with our prediction, the intentional binding effect was stronger in the positive valence condition (96.21 ms, $SE = 16.35$) than in the neutral valence condition (83.40 ms, $SE = 15.77$). Figure 2 displays mean judgment errors as a function of judgment, agency, and valence. Note that the significant difference in intentional binding between the neutral versus positive valence condition was driven mainly by enhanced anticipatory awareness of the outcome (tone) in the positive valence condition. This stronger shift for the outcome suggests that the positive reward signal caused a stronger prediction of the outcome.

Furthermore, apart from the significant three-way interaction effect between judgment, agency, and valence reported above, the analysis revealed a significant three-way interaction effect of judgment, agency and EBR, $F(1, 26) = 4.33, p = .05, \eta_p^2 = .14$; the intentional binding effect was larger for participants with a high EBR score compared to those with a

low EBR score. However, the analysis also yielded a significant four-way interaction involving valence of picture, $F(1, 26) = 6.69, p = .02, \eta_p^2 = .21$.

To examine this four-way interaction and to test our specific hypothesis concerning the moderating role of EBR in positive priming effects on intentional binding, we conducted further analyses. First, whereas the intentional binding effect in the neutral condition tended to increase with higher EBR scores, $F(1, 26) = 2.52, p = .12, \eta_p^2 = .09$, this relation between EBR and intentional binding was stronger and significant in the positive condition, $F(1, 26) = 6.18, p = .02, \eta_p^2 = .19$. Furthermore, we estimated the effect of valence on intentional binding strength for participants with low EBR scores (1 *SD* below the mean EBR score) and for participants with high EBR scores (1 *SD* above the mean EBR score; see Aiken & West, 1991). These analyses showed no effect of valence on the intentional binding strength for participants with a low EBR score, $F < 1, ns$. However, valence had a significant effect on the intentional binding strength for participants with a high EBR score, $F(1, 26) = 10.89, p = .003, \eta_p^2 = .30$. This latter pattern of data suggests that positive priming of reward-related information is more likely to facilitate intentional binding when EBR is high. Figure 3 displays the mean intentional binding effect as a function of valence and EBR.

DISCUSSION

Research in neuroscience and decision making indicates that the brain is keen on processing reward-related information to control a wide range of overt behaviors, including voluntary movement and operant action, which is likely to involve dopaminergic mediation (Bromberg-Martin, Matsumoto, & Hikosaka, 2010; Schultz, 2006). An emerging new question, both in health and in disease, is whether reward-related

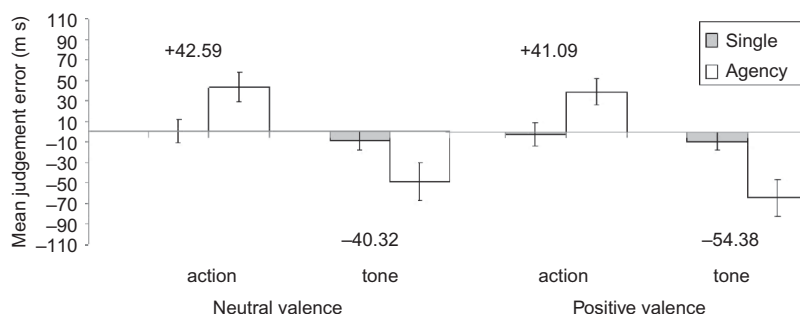


Figure 2. Mean judgment error as a function of the event judged (action vs. tone), whether the event took place in a single-event or agency trial, and when participants were primed with a neutral or positive picture. Positive numbers indicate that an event was perceived as happening after it actually happened, and negative numbers that it happened before it actually happened. The numbers above the bars indicate the mean shifts (in ms) between single-event and agency trials. Error bars represent *SE*.

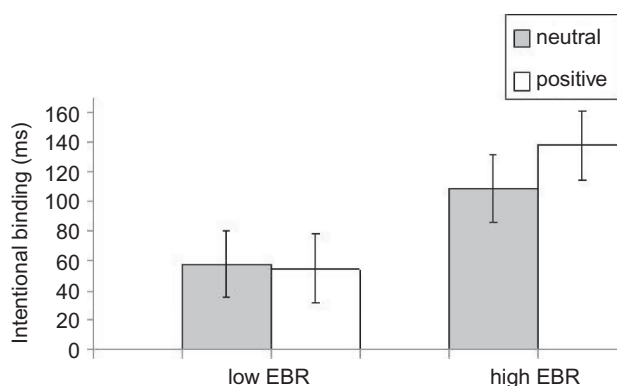


Figure 3. Mean intentional binding effect (i.e., difference between shift in action and tone, in ms) as a function of the valence of picture (neutral vs. positive) and EBR score (1 *SD* below vs. above the mean score). Error bars represent *SE*.

information may influence the experience of voluntary action, and, if so, whether these influences are dopaminergically mediated as well (Aarts, Custers, & Marien, 2009; Heinz & Schlagenhauf, 2010; Corlett, Taylor, Wang, Fletcher, & Krystal, 2010; Redgrave, Gurney, & Reynolds, 2008). For example, a recent proposal on the etiology of schizophrenia (Whitford, Ford, Mathalon, Kubicki, & Shenton, in press) suggests that prediction errors during the performance of self-generated actions and thoughts in schizophrenia patients lead to increased phasic activity of midbrain dopaminergic neurons.

Here we examined and established that positive reward-related information augments intentional binding between motor action and sensory effects in creating the sense of agency in healthy adults. Importantly, this effect of positive reward signals occurred on overall binding, but not on the temporal shifts of the individual action or tone. This indicates that positive reward-related information causes voluntary action and outcome to be experienced as bound together in time, rather than changing the experience of the action or effect alone. Thus, reward-related information automatically facilitates not only the control of voluntary behavior (Aston-Jones & Cohen, 2005; Custers & Aarts, 2010; Dreisbach & Goschke, 2004) but also the sense of agency in performing the behavior.

Furthermore, we found that the effects of reward-related information on intentional binding were moderated by individual differences in baseline spontaneous EBR. The priming of reward signals was more likely to facilitate intentional binding when EBR was high. Given that EBR is thought to be a reflection of striatal dopaminergic functioning (e.g., Karson, 1983), our data suggest that the effects of reward-related information on the sense of agency in operant action are mediated by dopamine pathways. These findings are in line with other recent suggestions that dopamine

plays a role in intentional binding and the sense of agency (Haggard et al., 2003; Redgrave et al., 2008). The present findings offer an important extension of this research by indicating that striatal dopaminergic functioning may be involved in the effects of reward-related information on the sense of agency during voluntary action performance. Specifically, striatal dopamine activity may enhance the temporal binding between action and outcome in response to positive reward signals, thereby facilitating the sense of action coherence and self-causation.

The interactive effect of positive stimuli and EBR on intentional binding in the present study provides indirect evidence of a possible role of dopamine in creating perceptions of action coherence and control in response to reward-related information. A more direct test showing that striatal dopaminergic activity mediates the effects of reward-related information on the sense of agency thus requires further empirical examination. Such a test may be especially relevant to understanding the role of rewards in the sense of agency in psychiatric and neurological conditions that exhibit hyper-activation of dopamine, such as schizophrenia (apparent in exaggerated levels of EBR), or reduced activation of dopamine, such as Parkinson's disease (apparently reflected in low levels of EBR). Interestingly, recent research shows greater levels of intentional binding in patients with a putative psychotic prodrome (i.e., initial symptoms pointing to a psychotic disorder) that may be attributed to stronger (yet valid) predictive influences of external effects of one's own action (Hauser et al., 2010; Danderyd, Sweden). However, in schizophrenia (i.e., in patients who suffer from full-blown psychotic disorder), intentional binding seems to rely on retrospection, rather than prediction, of the actual occurrence of the effects of one's own action (Voss et al., 2010). One could propose that predictive influences should improve in

the presence of positive priming (which increases dopamine synthesis) and thus contribute to the sense of agency that is otherwise disturbed in patients with schizophrenia.

We do not know yet how reward signals impinge on the sense of agency in the context of an illness, but our data suggest that people do not benefit from reward signals when their level of dopamine functioning is too low. Accordingly, future research, both in healthy and diseased individuals, should explore whether, and how, reward-related information causally interacts with levels of striatal dopamine activity (e.g., by using dopamine agonists and antagonists) in modulating experiences of voluntary action, in order to further our understanding of the neurocognitive processes that shape the way people perceive themselves as agents.

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