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Individual differences in the proneness to have flow experiences are linked to dopamine D2-receptor availability in the dorsal striatum

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ABSTRACT

Flow is a subjective experience of high but effortless attention, enjoyment, and low self-awareness that can occur during the active performance of challenging tasks. The dispositional proneness to experience flow is associated with personality traits that are known to be influenced by dopaminergic neural systems. Here, for the first time, we investigated relations between flow proneness and dopaminergic function. Specifically, we tested the hypothesis that the availability of dopamine D2-receptors in the striatum is positively associated with flow proneness. Striatal D2-receptor availability was measured in a sample of 25 healthy adults using positron emission tomography and [^{11}C]raclopride. Flow proneness was measured using the Swedish Flow Proneness Questionnaire. As hypothesized, there was a significant correlation ($r = .41$) between striatal D2-receptor availability and flow proneness. An exploratory analysis of striatal subregions showed that the relation was mainly driven by the dorsal striatum, with a significantly higher correlation in the putamen than in the ventral striatum. The findings constitute the first demonstration of an association between flow proneness and dopaminergic function. We suggest that the proneness to experience flow is related to personality dimensions that are under dopaminergic control and characterized by low impulsiveness, stable emotion, and positive affect.

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Introduction

The term flow refers to a psychological state of high but subjectively effortless attention, low self-awareness, sense of control and enjoyment that can occur during the performance of tasks that are challenging, but matched in difficulty to the skill level of the person (Csikszentmihalyi and Csikszentmihalyi, 1988; Csikszentmihalyi and Nakamura, 2010). This state has been studied in a wide range of tasks, from chess playing to rock climbing, and is described in remarkably similar terms across activities.

There are large individual differences in how prone people are to experience flow in daily life (Asakawa, 2010; Csikszentmihalyi and Csikszentmihalyi, 1988; Csikszentmihalyi and Schneider, 2000). The differences are to a certain extent associated with personality. When studying relations between flow proneness and broad personality dimensions (McCrae and Costa, 1990), we found a negative association between flow proneness and neuroticism and a positive association with conscientiousness (Ullén et al., 2012). In line with this, other studies have shown negative associations between flow proneness and trait anxiety (Asakawa, 2010; Jackson et al., 1998), as well as positive associations between flow proneness and traits that are related to low neuroticism, e.g. active coping strategies (Asakawa, 2010), psychological well-being (Asakawa, 2004, 2010; Ishimura and Kodama, 2006), and life satisfaction (Asakawa, 2010).

Two lines of evidence implicate the striatal dopamine systems in the neurobiology of flow. The enjoyment associated with flow experiences has often been discussed as a possible reward signal of importance for building task-specific intrinsic motivation (Csikszentmihalyi and Csikszentmihalyi, 1988; Keller and Bless, 2008; Nakamura and Csikszentmihalyi, 2002). Dopaminergic transmission in the striatum, specifically the ventral striatum (nucleus accumbens), has been linked to reward processing in both animal and human studies (Everitt et al., 1999; Leyton et al., 2002; Schultz et al., 1997; Wise, 2004). Secondly, striatal dopamine is also involved in impulse control and positive affect (Buckholtz et al., 2010; Dalley et al., 2007; Oswald et al., 2007; Volkow et al., 2006). High impulsivity is related to high neuroticism as well as low conscientiousness (Whiteside and Lynham, 2001), both of which are, as previously reported, associated with low flow proneness (Ullén et al., 2012). Poor impulse control may make it more difficult to achieve the continuous task focus required to enter and maintain a flow state. Notably, a higher availability of striatal dopamine D2-receptors (D2R)

Abbreviations: D2R BP_{ND}, dopamine D2-receptor binding potential; FP-Leisure, flow proneness in leisure time; FP-Maintenance, flow proneness during household maintenance; FP-Work, flow proneness at work; MR, magnetic resonance; PET, positron emission tomography; ROI, regions-of-interest; SFPQ, Swedish Flow Proneness Questionnaire.

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has been linked to decreased impulsiveness (Lee et al., 2009). Furthermore, a positive relation has been shown between D2R availability, high positive affect and improved emotion regulation (Volkow et al., 2006). These trait tendencies, which may protect against task-related stress and anxiety, are also in line with above mentioned associations between personality and flow proneness.

The present preliminary study is the first to examine the role of the dopamine system in flow proneness. Based on the work summarized above, we expected a positive association between striatal D2R availability and flow proneness. We measured proneness for flow experiences in three domains of everyday life, work (FP-Work), household maintenance (FP-Maintenance), and leisure time (FP-Leisure), using the Swedish Flow Proneness Questionnaire (SFPQ) (Ullén et al., 2012) and dopamine D2R binding potential (BP_{ND}) in the striatum using positron emission tomography (PET) and the radioligand [^{11}C] raclopride.

Materials and methods

Ethics statement

The experimental procedures were undertaken with the understanding and written consent of each participant, conformed to The Code of Ethics of the World Medical Association (Declaration of Helsinki) and were approved ethically by the Regional Ethical Review Board in Stockholm and the Radiation Safety committees of the Karolinska Hospital.

Participants

Twenty-five subjects (17 male) aged between 22 and 68 years (mean = 45, SD = 18) volunteered to participate in the study. They were recruited from two previous studies in which PET examinations had been performed using identical study protocols (Cervenka et al., 2006; McNab et al., 2009). Two participants from each of the previous studies declined to participate in the present study for personal reasons. The included participants were healthy and had no history of neurological or psychiatric illness, as determined by clinical examinations, routine laboratory blood and urine tests, and electrocardiogram (performed in participants above 40 years of age (Cervenka et al., 2006)). No medications were used at the time of the study. No anatomical brain abnormality was detected on MR images in any subject as evaluated by a neuroradiologist at the Karolinska University Hospital. None of the subjects were nicotine users, and the use of caffeine or alcohol was not allowed during the day when the PET examination was performed. All women were menopausal.

Psychological measurements

The psychological tests were administered individually, by investigators blind to the PET data collection and analysis. The psychometric testing was initiated 1 year after the original PET examinations. Also, the average time between measurements for participants in one subsample was longer than for participants in the other; the latter data collection started 1 year after the first. The potential influence of these time lags was investigated and shown not to affect the main findings (see Results).

Flow proneness

Flow proneness was measured using the Swedish Flow Proneness Questionnaire (Ullén et al., 2012). The SFPQ consists of three subscales with 7 items each, and assesses the proneness for flow experiences at work, in leisure activities, and during household maintenance. An example item would be: “When you do something at work, how often does it happen that you feel completely concentrated?” To each item, the respondent answers along a five-point Likert scale: “Never” (1), “Rarely” (2), “Sometimes” (3), “Often” (4), and “Every day, or almost every day” (5). Mean scores were derived for the overall scale as well as for each sub-scale, resulting in one measure each, for overall flow proneness, FP-Total; flow proneness in professional life, FP-Work; leisure time, FP-Leisure; and maintenance work, FP-Maintenance. Construct validity, reliability, and internal consistency have been shown to be adequate for the SFPQ at .96 (comparative fit index), .87 (split-half coefficient), and .83 (Cronbach's α), respectively (Ullén et al., 2012).

General cognitive ability

In order to confirm that general cognitive ability was unrelated to other measures, all subjects were assessed using the Raven's Standard Progressive Matrices Plus (Raven et al., 2000), which mainly reflects psychometric general intelligence (Gustafsson, 1984). The test was administered without time limit.

Image acquisition and analysis

Magnetic resonance (MR) and PET examinations

The MR and PET data were acquired and analyzed by investigators blind to the psychological measurements. T1-weighted MR-images were acquired using a 1.5T GE Signa system (Milwaukee, WI). PET-studies were performed on an ECAT Exact HR-system (CTI Siemens, Knoxville, TN). [^{11}C]raclopride was prepared from [^{11}C]methyl-triflate as described previously (Langer et al., 1999; Sandell et al., 2000). The radioligand was given intravenously as a rapid bolus and the cannula was flushed with saline. Radioactivity in the brain was measured during 51 min, in frames of 3×1 min, 4×3 min and 6×6 min. After correction for attenuation, random and scatter events, images were reconstructed using a Hanning filter of 2.0 mm into a volume of 47 slices, with a center-to-center distance of 3.125 mm and a pixel size of 2.02 mm $\times$ 2.02 mm.

Image processing and analysis

PET-images were coregistered to MR images using SPM2. Regions-of-interest (ROIs) for the striatum, including ventral striatum, caudate and putamen were manually delineated on the MR image of each subject individually using the Human Brain Atlas software (Roland and Zilles, 1994). Delineation was performed in the coronal projection and included the entire structures, while keeping a margin towards CSF and white matter in order to avoid partial volume effects. A ROI for cerebellum was drawn below the petrosal bone in 5–7 slices. The investigator was blind towards the scores on SFPQ. The ROIs were transferred to the series of PET-images to generate time–activity curves, pooling data for the entire ROIs and for left and right side. The striatal D2R BP_{ND} was calculated using the simplified reference tissue model with the cerebellum as reference region (Lammertsma and Hume, 1996). In this context, D2R BP_{ND} represents the ratio at equilibrium of specifically bound radioligand to that of non-displaceable radioligand in tissue (Innis et al., 2007). The simplified reference tissue model has previously been validated for [^{11}C]raclopride (Lammertsma and Hume, 1996).

Data analysis

Data were analyzed using Statistica 10.0 (StatSoft). Pearson product moment partial correlations between striatal D2R BP_{ND} and flow measures were performed, controlling for participant age. One-tailed significance tests were used since we predicted a positive association between striatal D2R BP_{ND} and flow measures. To statistically test whether the correlation between flow proneness and D2R BP_{ND} differed between anatomical subregions of the striatum, we employed the Hotelling–Williams test for dependent overlapping correlations (Williams, 1959). This test was implemented in Matlab 7.1 (The MathWorks, Inc.). To determine the effect of participant age on flow proneness and striatal D2R BP_{ND}, we performed a multiple linear regression with striatal D2R BP_{ND} as dependent variable and FP-Total and Age as independent variables.

Results

Descriptive statistics illustrating the mean, range and standard deviation of the analyzed variables are shown in Table 1. Six participants, who were university students, were not employed and therefore had no scores for FP-Work. Consequently, analyses including FP-Work were based on nineteen participants.

Since cross-sectional studies have shown an effect of age on D2R binding (Ishibashi et al., 2009; Volkow et al., 1996), we tested our hypothesis controlling for participant age. A significant correlation between striatal D2R BP_{ND} and FP-Total was found ($r=.41$; $p=.022$; $n=25$) (Fig. 1, Table 2), thus confirming our hypothesis. Given this main finding, we performed two supplementary exploratory analyses. Firstly, we examined relations between striatal D2R BP_{ND} and the individual flow scales. Correlations were significant for FP-Work ($r=.50$; $p=.018$; $n=19$) and FP-Maintenance ($r=.38$; $p=.033$; $n=25$), and for FP-Leisure ($r=.36$; $p=.044$; $n=25$). All flow measures were highly intercorrelated (r-values ranging between .74 and .96; see Supplementary data, Table S1). Secondly, we explored striatal subregions. These analyses indicated that the relationship between D2R binding and flow proneness was essentially limited to the dorsal striatum, i.e. the caudate nucleus and putamen (Table 2). We therefore investigated whether the correlations between FP-Total and D2R BP_{ND} differed between the striatal subregions. The correlation for putamen ($r=.55$) was significantly higher ($t(22)=2.61$; $p=.016$) than the correlation for ventral striatum ($r=.17$). The corresponding difference between the caudate nucleus ($r=.46$) and the ventral striatum did not reach statistical significance ($t(22)=1.45$; $p=.16$). General cognitive ability was unrelated to both FP-Total ($r=.08$; $p=.70$; $n=25$) and striatal D2R BP_{ND} ($r=.23$; $p=.28$; $n=25$). Age was found to have an effect on striatal D2R BP_{ND} ($r=-.69$, $p<.0001$) but not on flow proneness (FP-Total: $r=.14$, $p=.50$). To determine the influence of age on the relation between flow proneness and D2R, we also performed a multiple linear regression with striatal D2R BP_{ND} as dependent variable and FP-Total and Age as independent variables. Both independent variables were found to contribute to striatal D2R BP_{ND} (FP-Total: $\beta=.30$, $t(22)=2.14$, $p=.044$; Age: $\beta=-.73$, $t(22)=-5.19$, $p=.002$), together explaining about 57% of the variance. The interaction was non-significant ($\beta=.02$, $p=.90$).

We found no sex differences in FP-Total ($t(23)=.90$; $p=.38$) or striatal D2R BP_{ND} ($t(23)=.46$; $p=.65$), controlling for participant age. The slope of the correlation between FP-Total and striatal D2R BP_{ND} in females was not significantly different from that in males ($r=.43$ and $r=.44$, respectively). We also performed a general linear model analysis with striatal D2R BP_{ND} as dependent variable, and age, sex and FP-Total as independent variables. This analysis confirmed a significant effect of age ($F(1,21)=15.2$; $p<.0001$) and FP-Total ($F(1,21)=3.8$; $p=.03$), but not of sex ($F(1,21)=.11$; $p=.74$). The interaction was non-significant ($F(1,20)=.4$; $p=.52$).

In order to assess the potential influence of the time lag between PET examinations and psychological testing on the results, we performed two GLM analyses. In the first analysis we used striatal D2R BP_{ND} as dependent variable and sub-sample (from which previous study the participant was recruited), age and FP-Total as independent variables. Flow-FP remained significant ($F(1,21)=3.4$, $p=.04$), while there was no effect of sub-sample ($F(1,21)=.8$, $p=.39$). In the second analysis we used striatal D2R BP_{ND} as dependent variable and time lag (in months), age and FP-Total as independent variables. Flow-FP remained significant ($F(1,21)=3.2$, $p=.04$), while there was no effect of time lag ($F(1,21)=.4$, $p=.53$). Thus, the individual time lags between PET examinations and flow proneness measurements did not have a significant effect on the present findings. Furthermore, these results show that there was no additional effect of belonging to either sub-sample.

Table 1
Descriptive statistics of variables included in the data analysis. Age, participant age. Striatum, striatal D2-dopamine receptor binding potential (D2R BP_{ND}). FP-Total, mean flow proneness across domains. FP-Work, flow proneness during work. FP-Maintenance, flow proneness during household maintenance. FP-Leisure, flow proneness in leisure time. Raven, Raven's Standard Progressive Matrices Plus scores.

	Age	Striatum	FP-Total	FP-Work	FP-Maintenance	FP-Leisure	Raven
n	25	25	25	19	25	25	25
Mean	45	2.83	3.69	3.31	3.65	3.73	41
Max	68	3.56	2.52	4.14	4.57	5.00	55
Min	22	2.27	4.62	2.43	2.17	2.43	10
SD	18	0.31	0.61	0.54	0.62	0.69	10

Discussion

Here we demonstrate, for the first time, that individual differences in the proneness to have flow experiences are associated with brain biochemistry. Specifically, the availability of D2R in the striatum was, as hypothesized, positively associated with overall flow proneness (FP-Total) after controlling for age. Similar associations were seen also for the different flow proneness subscales (FP-Work, FP-Maintenance and FP-Leisure), which measure flow proneness in different domains of life. In line with this, we have earlier found that relations between flow proneness and personality are similar across flow proneness subscales (Ullén et al., 2012) and, recently, that genetic effects on flow proneness overlap across the different flow subscales (Mosing et al., 2012a). Flow proneness may thus be influenced by biological mechanisms that involve dopamine, independently of the specific tasks and contexts in which people generally experience flow.

As discussed, it appears plausible that dopaminergic influences on flow proneness could be related to both impulse control and reward processing. The positive associations between D2R binding in dorsal striatum and flow proneness are consistent with the previously discussed model, where high striatal D2R availability is related to low impulsivity, which in turn facilitates flow proneness. A negative association between D2R availability and impulsivity has been demonstrated for both dorsal and ventral striatal regions in human as well as animal research (Dalley et al., 2007; Lee et al., 2009). Relations between dopamine systems and impulsivity are complex, and dopamine can presumably influence impulse control in multiple ways, e.g. by modulating behavioral inhibition, reward learning, and temporal discounting of rewards (Dalley et al., 2007, 2008; Pine et al., 2010).

Dopaminergic projections to the ventral striatum, which arise mainly from the ventral tegmental area (Fallon and Moore, 1978), play an important role for the processing of reward and motivation (Voorn et al., 2004; Wise, 2004). This has been demonstrated using a variety of techniques, such as dopamine-selective lesions (Roberts et al., 1977), single-cell recordings (Schultz et al., 1997) and human neuroimaging (D'Ardenne et al., 2008; Klein-Flugge et al., 2011). We found lower correlations between dopamine D2R availability and flow proneness in the ventral than in the dorsal striatum. The difference was significant for the putamen and a non-significant trend in the same direction was seen for the caudate nucleus. This pattern indicates that flow proneness is more dependent on the nigrostriatal than the mesolimbic dopamine system, and thus that flow proneness is not specifically related to dopaminergic systems processing reward and intrinsic motivation. However, the findings have to be interpreted carefully. First, with regard to the ventral striatum, the smaller effect size could partly be caused by the generally lower signal-to-noise ratio for D2R BP_{ND} measurements in that region (Mawlawi et al., 2001). Second, both anatomical and physiological data suggest that differences between the dorsal and the ventral striatum typically appear as gradients rather than distinct boundaries (Voorn et al., 2004), and some studies have implied also the dorsal striatum in processing of reward (Kelley and Delfs, 1991; Phillips et al., 1981; Voorn et al., 2004). It can also be noted that the limbic corticostriatal loop is heavily interconnected with other corticostriatal systems (Haber et al., 2000; Wise, 2004).

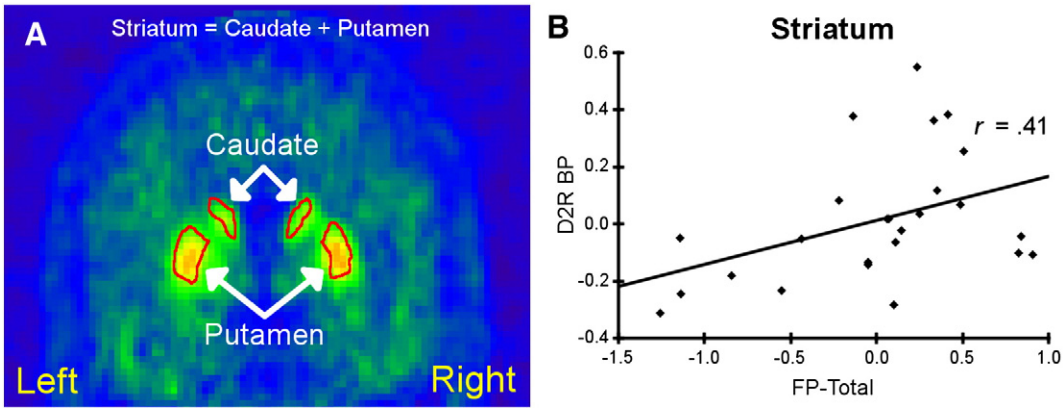

Fig. 1. Availability of dopamine D2-receptors in the striatum correlates with flow proneness. (A) Coronal image of regional radioactivity at rest in one participant, after intravenous injection of [^{11}C]raclopride, as measured by PET. Striatal ROIs, derived from the corresponding MR-image, are delineated in red (lines thicker than original). Left = left hemisphere; Right = right hemisphere. (B) Scatterplot depicting participant data points and the relationship between residual flow proneness scores (FP-Total) and striatal dopamine D2-receptor availability (D2R BP_{ND}), after controlling for participant age (one-tailed Pearson product moment partial correlation, $n = 25$; $r = .41$; $p = .022$).

Generally, the findings are in line with the broader picture suggested by a number of earlier studies. We have recently shown that flow proneness is associated with low neuroticism and high conscientiousness (Ullén et al., 2012). Neuroticism is related to D2R polymorphisms (Wacker et al., 2005) and other dopamine related genes (Badcock et al., 2011; Hess et al., 2009; Kazantseva et al., 2011). The trait harm avoidance, which is strongly related to neuroticism (de Fruyt et al., 2000), has been shown to be negatively related to striatal D2R availability (Kim et al., 2011). Relations with dopamine related genes have been found also for conscientiousness (Dragan and Oniszczenko, 2007; Hess et al., 2009). Recent data from our group (Mosing et al., 2012b) show a relationship between flow proneness, behavioral inhibition and locus of control that is almost entirely explained by shared genetic influences. Importantly, both these latter traits are related to low impulsivity (Dalley et al., 2008; Wiehe, 1987) and dopaminergic function (Dalley et al., 2008; De Brabander and Declerck, 2004). Finally, several studies have found links between flow proneness and traits associated with positive affect, i.e. self-esteem, life satisfaction and psychological well-being (Asakawa, 2004, 2010; Ishimura and Kodama, 2006; Jackson et al., 1998), traits for which positive associations with striatal D2R availability have been demonstrated (Martinez et al., 2010; Volkow et al., 2006).

A potential limitation of the present study is the time interval between the PET examinations and the acquisition of behavioral data. Among the factors which may influence D2R levels over time is age, supported by cross-sectional studies demonstrating a decrease in striatal D2 binding of 5–8% per decade (Ishibashi et al., 2009; Volkow et al., 1996). In addition, short term factors may also play a role, as shown by pharmacological and behavioral challenges leading to reductions in D2R BP_{ND}, which is thought to reflect changes in endogenous dopamine levels (Laruelle, 2000). However, given the above parameters, the overall age effect induced by the time interval in this study is expected to be minor, and there were no systematic interventions between the PET examinations and behavioral testing. Moreover, the expected age-related D2R BP_{ND} changes should have been fairly similar across participants and are thus unlikely to have introduced changes in rank order between participants which could have influenced the association between D2R binding and flow proneness. Lastly, there was no influence of individual time lags on the present findings.

Table 2
Associations between flow proneness and striatal dopamine D2-receptor availability. Numbers are *r* values for partial correlations between the different SFPQ flow measures and striatal dopamine D2-receptor availability, controlling for participant age. Results are shown for the striatum as well as for its anatomical subregions (Caudate, Putamen, Ventral striatum). Significant correlations (one-tailed) are indicated with one ($.01 \le p < .05$) or two ($p < .01$) asterisks. Non-significant trends ($.05 \le p < .10$) are indicated with $^{+}$. L, left side; R, right side; L + R, left and right together.

Region	Laterality	FP-Total	FP-Work	FP-Maintenance	FP-Leisure
		$n = 25$	$n = 19$	$n = 25$	$n = 25$
Striatum	L + R	$.41^{*}$	$.50^{*}$	$.38^{*}$	$.36^{*}$
	L	$.35^{*}$	$.44^{*}$	$.31^{+}$	$.30^{+}$
	R	$.46^{*}$	$.53^{*}$	$.43^{*}$	$.40^{*}$
Caudate	L + R	$.46^{*}$	$.75^{**}$	$.40^{*}$	$.35^{*}$
	L	$.39^{*}$	$.57^{**}$	$.34^{+}$	$.30^{+}$
	R	$.44^{*}$	$.78^{**}$	$.38^{*}$	$.33^{+}$
Putamen	L + R	$.55^{**}$	$.56^{**}$	$.46^{*}$	$.53^{**}$
	L	$.49^{**}$	$.51^{*}$	$.39^{*}$	$.46^{*}$
	R	$.56^{**}$	$.55^{**}$	$.48^{**}$	$.54^{**}$
Ventral striatum	L + R	.17	.26	.22	.10
	L	.10	.22	.17	.05
	R	.21	.25	.24	.14

Conclusions

In summary, we found that higher flow proneness is associated with greater dopamine D2R availability, which in previous studies has been linked to low impulsivity, emotional stability, and positive affect, i.e. traits conducive to flow proneness. While further work is needed to analyze the precise role of dopamine in flow and flow proneness, the present results are of importance as a first direct demonstration of an association between flow proneness and dopaminergic function. The present findings are also in line with previous studies showing that general cognitive ability is unrelated to both flow proneness (Ullén et al., 2012) and density of dopamine D2-receptors (Ball et al., 1998; Moises et al., 2001). This is somewhat intriguing because it suggests a parallel mechanism for sustained effortless attention that is essentially unrelated to the mentally effortful top-down regulated processes which are exerted and typically described in relation to high levels of cognitive performance (Bruya, 2010). We have earlier suggested, based on studies of physiological correlates of flow experiences (de Manzano et al., 2010), that the subjective experience of high but effortless concentration during a flow state occurs through an interaction between attentional circuits, on the one hand, and emotional and motivational systems that mediate positive affect and intrinsic motivation for task performance, on the other hand. This statement finds some support in findings by Klasen et al. (2011) who were able to demonstrate, using functional MR, that flow was associated with neural activity in various brain regions involved in cognition, motivation as well as emotion. The present results indicate that our proneness to experience such states depends on individual differences in dopaminergic neurotransmission.

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.neuroimage.2012.10.072.

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