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Neural correlates of experimentally induced flow experiences☆

Martin Ulrich [a,*], Johannes Keller [b], Klaus Hoenig [c], Christiane Waller [c], Georg Grön [a]

[a] Department of Psychiatry, University of Ulm, Leimgrubenweg 12-14, 89075 Ulm, Germany
[b] Department of Psychology and Education, University of Ulm, 89069 Ulm, Germany
[c] Department of Psychosomatic Medicine and Psychotherapy, University of Ulm, Albert-Einstein-Allee 23, 89081 Ulm, Germany

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ABSTRACT

Flow refers to a positive, activity-associated, subjective experience under conditions of a perceived fit between skills and task demands. Using functional magnetic resonance perfusion imaging, we investigated the neural correlates of flow in a sample of 27 human subjects. Experimentally, in the flow condition participants worked on mental arithmetic tasks at challenging task difficulty which was automatically and continuously adjusted to individuals' skill level. Experimental settings of "boredom" and "overload" served as comparison conditions. The experience of flow was associated with relative increases in neural activity in the left anterior inferior frontal gyrus (IFG) and the left putamen. Relative decreases in neural activity were observed in the medial prefrontal cortex (MPFC) and the amygdala (AMY). Subjective ratings of the flow experience were significantly associated with changes in neural activity in the IFG, AMY, and, with trend towards significance, in the MPFC. We conclude that neural activity changes in these brain regions reflect psychological processes that map on the characteristic features of flow: coding of increased outcome probability (putamen), deeper sense of cognitive control (IFG), decreased self-referential processing (MPFC), and decreased negative arousal (AMY).

Introduction

The concept of flow (Csikszentmihalyi, 1975) refers to an activity-associated, subjective experience under conditions of a perceived fit between abilities or skills and task demands in the context of clear goal settings. Characteristic determinants of this psychological state have been conceptualized as high though almost effortless attention, reduced self-referential processing, sense of control, and the feeling that the activity per se is rewarding (Csikszentmihalyi, 2000; Csikszentmihalyi and Nakamura, 2010). Flow experience has been investigated in a wide spectrum of activities from chess playing (e.g., Abuhamdeh and Csikszentmihalyi, 2009, 2012) to skiing or rock climbing (e.g., Delle Fave et al., 2003).

Flow experiences have been studied under modulating conditions including motivational task aspects (Csikszentmihalyi and Csikszentmihalyi, 1988; Keller and Bless, 2008; Nakamura and Csikszentmihalyi, 2002), cognitive aspects (Mosing et al., 2012), and personality traits mediating individual proneness to experience flow (Asakawa, 2004, 2010; Csikszentmihalyi and Csikszentmihalyi, 1988; Csikszentmihalyi and Schneider, 2000; Ishimura and Kodama, 2006; Keller and Bless, 2008; Keller and Blomann, 2008; Ullén et al., 2012). Also physiological correlates of flow experiences have been of interest (de Manzano et al., 2010; Keller et al., 2011). However, the neural correlates of flow experiences have been investigated in only two studies, so far (de Manzano et al., 2013; Klasen et al., 2012). Employing functional magnetic resonance imaging during a video game, brain activation patterns, encompassing reward-related structures as well as cognitive and sensorimotor networks, have been reported to associate with flow factors derived from a content analysis of that video game (Klasen et al., 2012). A recent [11C]raclopride positron-emission-tomography study (de Manzano et al., 2013) showed an association between inter-individually different flow proneness (Ullén et al., 2012) and availability of dopamine D2 receptors in the striatum. The correlation was particularly evident in the putamen and parts of the caudate nucleus extending into the ventral striatum.

To study flow experiences under experimentally controlled conditions at the behavioral level several paradigms have already been tested. A study by Rheinberg and Vollmeyer (2003) used a computer game requiring subjects to keep a spaceship undamaged by approaching rockets. Although three different levels of difficulty had already been implemented, the "optimal" level was adjusted to participants' skills

Abbreviations: AMY, Amygdala; ANOVA, Analysis of variance; B, Boredom (experimental condition); BA, Brodmann area; CASL, Continuous arterial spin labeling; CNR, Contrast-to-noise ratio; DMN, Default-mode network; EPI, Echo-planar imaging; F, Flow (experimental condition); FoV, Field of view; IFG, Inferior frontal gyrus; MNI, Montreal Neurological Institute; MPFC, Medial prefrontal cortex; MRI, Magnetic resonance imaging; O, Overload (experimental condition); R, Rest (experimental condition); rCBF, Regional cerebral blood flow; SPM, Statistical Parametric Mapping; TE, Echo time; TR, Repetition time.

* Corresponding author at: Section Neuropsychology and Functional Imaging, Department of Psychiatry, University of Ulm, Leimgrubenweg 12-14, 89075 Ulm, Germany. Fax: +49 731 500 61402.
E-mail address: martin.ulrich@uni-ulm.de (M. Ulrich).

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only once prior to the experiment but not, critically, continuously and automatically in the course of the experiment to account for possible alterations in participants' performance over time. Our own studies had then implemented a continuous and automatic fit between task demands and subjects' abilities in a modified tetris game (Keller and Bless, 2008), or in a computerized knowledge task (Keller et al., 2011, Experiment 1). However, in neither study a within-subjects design has been employed with repeated blocks of different task demands enabling more systematic comparisons between states of flow and non-flow.

Acknowledging the methodological problems so far, in the present study, we employed a new and innovative approach investigating subjective experiences of flow and associated neural correlates during engagement in mental arithmetic tasks. A mathematical framework has the strong advantage of full experimental control to adjust different levels of task difficulty necessary to realize an almost complete fit between individuals' skills and task demands. Employing a within-subjects study design, addition tasks were used to create three different experimental conditions of "boredom", "flow", and "overload" which were repeatedly presented throughout the entire experiment. In the putative flow condition task difficulty was automatically and continuously adjusted to individuals' skill level. Subjective experiences were assessed after each condition. Perfusion imaging implemented as continuous arterial spin labeling (CASL; e.g., Wang et al., 2005) was performed to measure regional cerebral blood flow (rCBF) as a surrogate marker of energetically demanding neural activity (Logothetis et al., 2001; Wang et al., 2005).

We predicted subjective experiences of flow to result in higher rating scores relative to control conditions. Particularly, items testing for relative enjoyment and for subjectively experienced task-skill balances should yield significantly higher positive ratings. Functionally, from previous evidence (de Manzano et al., 2013) we hypothesized stronger involvement of the striatum during the flow relative to control conditions. Since flow has been characterized by reduced self-awareness (Csikszentmihalyi, 2000; Csikszentmihalyi and Nakamura, 2010), we also expected regions in the medial prefrontal cortex mediating self-referential processing (Brewer et al., 2011; D'Argembeau et al., 2007; Goldberg et al., 2006; Gusnard et al., 2001; Jenkins and Mitchell, 2011; Johnson et al., 2009; van Buuren et al., 2010; Whitfield-Gabrieli et al., 2011; Zysset et al., 2003) to be down-regulated during flow.

Material and methods

Participants

Twenty-seven male, right-handed German native speakers (average age: 23.0, standard deviation: 2.3) were recruited from the local university and were paid 20 EUR for participation. Due to the novelty of the present experimental approach only men were included, in order to control for putative sex differences as possible source of variation (particularly, hormonal alterations during the menstrual cycle possibly affecting magnitude and local distribution of cerebral hemodynamics, e.g., Dietrich et al., 2001; Fernández et al., 2003; Hausmann et al., 2002). Structured interviews were conducted during recruitment of the volunteers. None of the participants reported to have any psychiatric/neurological diseases or contraindications regarding the magnetic resonance imaging (MRI) procedure. The study was in accordance with the Declaration of Helsinki and the local ethical committee at Ulm University. Written informed consent was obtained prior to the experiment.

Experimental design

Participants had to perform mental arithmetic tasks varying in difficulty. There were three conditions, a boredom condition (B) with low task demands, an adaptive or "flow" condition (F) where challenging task difficulty was dynamically adjusted to participants' individual level of skill, and an overload condition (O) with very high task difficulty.

In all conditions, the participants were asked to sum two or more numbers in their mind and to enter the result as accurately and as fast as possible using an on-screen keyboard in combination with a trackball (see Fig. 1). The result which always consisted of three digits had to be entered digit by digit and submitted by pressing an "Enter" button. Mistakes could be corrected using a "Delete" button. Input was immediately displayed in the result box which initially had the default value "000" until a result was entered. After submitting the result, there was a break of 4 s (indicated by the expression "xxx + x") before the next calculation was presented. Each calculation remained on the screen for a maximum duration of 18 s or until subjects submitted the result. Different degrees of task difficulty associated with the B, F, and O conditions were achieved as follows.

In the boredom condition, only two numbers were to be summed, with the first summand randomly drawn from the interval 100 to 109, and the second summand from the interval 1 to 9. Also, the result of summation was confined to numbers between 101 and 110, so that the participants did not have to break up the second summand to obtain the result. As a consequence, task demands were constantly low.

In the flow condition, task demands adapted automatically and continuously to the participants' level of skill which had been estimated beforehand in a preparation phase (see below), and used as starting level. After an evaluation period consisting of two completed calculations, the results were analyzed with respect to accuracy. When two out of the last two results were correct task difficulty increased by one level which was achieved using two distinct mechanisms. In case the last summand had only one digit, the level increased by changing the last summand to a two-digit number in the upcoming calculations (e.g., Level 5: 23 + 45 + 59 + 3 changed to Level 6: 73 + 46 + 54 + 17). For a further up-level change, an additional one-digit number was added to the mathematical expression (e.g., Level 6: 89 + 38 + 65 + 15 changed to Level 7: 26 + 24 + 33 + 60 + 8). Both mechanisms were applied alternately. Analogously, when two results were incorrect in succession, task difficulty decreased by one level, and this was achieved by the two mechanisms outlined above but in reverse order. Otherwise, task demands remained unchanged.

In the overload condition, the starting level of task difficulty was set three levels higher than the starting level of the flow condition. A level-up adjustment occurred when at least three out of the last five results were correct. Task demands decreased when at least four out of five results were wrong. However, task difficulty did never fall below the starting level. This algorithm was applied to ensure that task demands were always higher than the participants' level of skill, thus "overloading" subjects but also minimizing the probability to permanently frustrate participants.

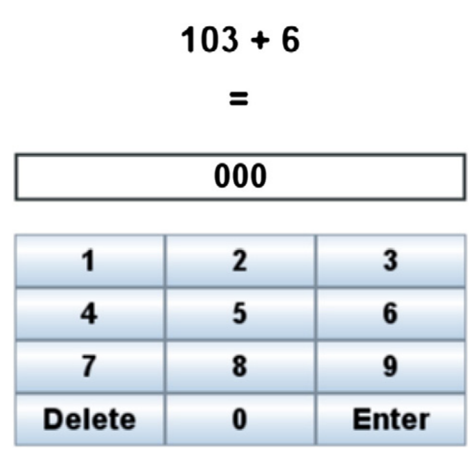

Fig. 1. Experimental design. Depicted is the relevant middle section of a screen shot taken from the boredom condition. Subjects had to sum the numbers and to enter the result using the on-screen keyboard operated by a trackball.

Feedback about accuracy of subjects' responses was not presented in order to rule out any activation differences between the three conditions to be motivated by different frequencies of positive or negative feedbacks.

Each condition lasted for 184 s. After each block, eight Likert-scaled statements were presented and subjects' responses could range from 1 (“I do not agree at all”) to 7 (“I completely agree”). These items were used to assess participants' subjective experiences during the preceding task block with respect to involvement, enjoyment, perceived fit between skills and task demands, and feeling of control (for a full list of items used, see legends of Table 1 or Fig. 2). A ninth item assessed participants' subjective sense of time (“I experienced the preceding task phase as …”) on a continuous visual scale ranging from 0 (“very short”) to 100 (“very long”). Subjects were told that the experimenter could not see their ratings. Present items have already been used in two previous studies on flow experiences (Keller and Bless, 2008; Keller et al., 2011), however within entirely different experimental tasks. Internal consistencies of the present scale were therefore estimated from the present data and were consistently high around Cronbach's alpha of 0.80 (B: $\alpha = 0.81$; F: $\alpha = 0.82$; O: $\alpha = 0.80$).

Besides the three task conditions (B, F, O) there was a rest condition (R) with only a white screen. The participants were asked to leave their eyes open and to avoid unnecessary movements. Here, no subjective ratings had to be given afterwards.

The main experiment consisted of three blocks per each task condition as well as three rest blocks. Two sequences (“R-B-F-O-F-R-O-B-O-B-F-R” and “R-B-O-F-O-R-F-B-F-B-O-R”) were used, counterbalanced across participants. The first task condition was always of the type “boredom” to get subjects familiar with the experiment under MRI scanning conditions. After each task block and ensuing subjective ratings there was a break of 25 s during which subjects could get prepared for the next task block. Perfusion imaging was only performed during the calculations.

In the preparation phase, the participants underwent two practice blocks (5 min each). The first block (boredom condition) served to make the participants familiar with the trackball. The second block featured the flow condition to determine the participants' level of skill. Starting at the lowest possible level, task demands continuously adapted to the participants' skills. The average task level pertaining to the last 25% of results was used as the starting level for the flow condition in the experiment.

After scanning, participants' preferences for mental arithmetic and reading (for comparison) were determined by asking the following three questions: “How much do you like performing mental arithmetic?”, “How much do you like reading?”, and “To what extent do you prefer reading over mental arithmetic?”. The participants gave their responses on visual analog scales ranging from “not at all” to “as much as possible” (items 1 and 2) and “much less than mental arithmetic” to “much more than mental arithmetic” (item 3), respectively. The scales were implemented digitally with response scales ranging from 0 to 10 and a step width of 0.1.

The computer algorithms used for generating the math calculations, analysis of the results, level adjustments and presenting and recording the ratings were programmed in Scala version 2.9.01 and run in Java Runtime Environment version 6.0.05 on a standard PC with Windows XP Professional version 2002 Service Pack 3. Stimuli appeared on MRI compatible video goggles (VisuaStim Digital, Resonance Technology Inc., Northridge, CA, USA) at a resolution of 800 × 600 pixels. If necessary, correction lenses were provided to ensure sufficient visual acuity.

MRI data acquisition

Magnetic resonance imaging data were acquired on a 3.0 T Magnetom Allegra (Siemens AG, Erlangen, Germany) head-only MRI system using a single channel transmit-receive head coil. Perfusion imaging was performed using continuous arterial spin labeling (CASL, Wang et al., 2005; for details on the sequence used, see also Adolph et al., 2010; Groen et al., 2011). T2*-weighted interleaved (labeled, control) images with and without labeling were acquired using a gradient echo echo-planar imaging (EPI) sequence with the following parameters: repetition time (TR) = 4000 ms, echo time (TE) = 16 ms, flip angle = 12°, field of view (FoV) = 220 mm, matrix size = 64 × 64, number of slices = 18, slice thickness = 5.0 mm, interslice gap = 1.5 mm, and voxel size = 3.44 × 3.44 × 6.5 mm^3. Orientation of transversal slices was parallel to the bicommissural line. One perfusion block comprised 23 acquisitions of labeled and control images each. Scan time for one perfusion block was 184 s. At the end of scanning, a high resolution T1-weighted structural image was obtained by administering a magnetization prepared rapid acquisition gradient echo sequence (TR = 2300 ms, TE = 3.93 ms, inversion time = 1100 ms, flip angle = 12°, FoV = 256 mm, matrix size: 256 × 256, voxel volume = 1 mm^3, slice orientation: sagittal; scan time = 517 s).

Data analysis

Performance data and reports on subjective experiences

Individual subjective ratings were averaged across the three repetitions of each condition. Repeated measurement analyses of variance (ANOVA) were computed separately for each of the nine items to test for significant differences between boredom, flow, and overload conditions. Significant differences were further investigated using post-hoc Newman–Keuls tests. Since items 1 (“I would love to solve math

Table 1
Behavioral results from the subjective ratings associated with the boredom (B), flow (F), and overload (O) conditions.

Item	ANOVA		Linear trend			Quadratic trend			Newman–Keuls post-hoc		
									F vs. B	F vs. O	B vs. O
	$F(2, 52)$	p	$F(1, 26)$	p	R^2 (%)[a]	$F(1, 26)$	p	R^2 (%)[a]	p	p	p
1: Solve again	6.28	0.004	0.80	0.380	3.0	**44.61**	**0.001**	**63.2**	0.025	0.003	0.243
2: Involved	64.17	0.001	75.23	0.001	74.3	33.50	0.001	56.3	0.001	0.114	0.001
3: Thrilled	5.34	0.008	0.09	0.769	0.3	**42.25**	**0.001**	**61.9**	0.012	0.011	0.697
4: Boring	94.15	0.001	106.87	0.001	80.4	62.48	0.001	70.6	0.001	0.326	0.001
5: Skills	55.18	0.001	66.01	0.001	71.7	1.81	0.190	6.5	0.001	0.001	0.001
6: Ability match	4.27	0.019	0.77	0.387	2.9	**17.97**	**0.001**	**40.9**	0.080	0.015	0.272
7: Task-relevance	50.31	0.001	48.72	0.001	65.2	57.25	0.001	68.8	0.001	0.654	0.001
8: Focused	45.59	0.001	44.62	0.001	63.2	48.70	0.001	65.2	0.001	0.954	0.001
9: Time experience	15.05	0.001	13.35	0.001	33.9	23.53	0.001	47.5	0.001	0.943	0.001
Sum (I1, I3, I6) [b]	6.17	0.004	0.55	0.463	2.1	47.56	0.001	64.7	0.019	0.004	0.328

Item description: 1: “I would love to solve math calculations of that kind again”, 2: “I was strongly involved in the task”, 3: “I was thrilled”, 4: “The task was boring”, 5: “I had the necessary skill to solve the calculations successfully”, 6: “Task demands were well matched to my ability”, 7: “During the task all thoughts on task-irrelevant issues that I am personally concerned with were extinguished”, 8: “During the task my consciousness was completely focused on solving the math calculations”, 9: Subjective experience of time [0 = “very short”].

[a] R^2: determination coefficient describing the explained variance by linear and quadratic trend tests.

[b] The condition effect on subjective experiences was not qualified by condition sequence (see Material and methods section) [$F(2, 50) = 0.39$, $p = 0.678$].

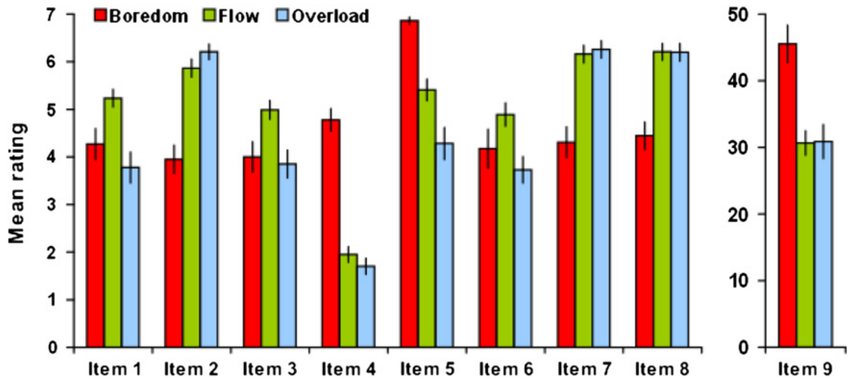

Fig. 2. Ratings associated with the boredom, flow, and overload conditions. Error bars indicate standard error of the mean (27 participants). Item description: 1: "I would love to solve math calculations of that kind again", 2: "I was strongly involved in the task", 3: "I was thrilled", 4: "The task was boring", 5: "I had the necessary skill to solve the calculations successfully", 6: "Task demands were well matched to my ability", 7: "During the task all thoughts on task-irrelevant issues that I am personally concerned with were extinguished", 8: "During the task my consciousness was completely focused on solving the math calculations", 9: Subjective experience of time [0 = "very short"]. For statistical results, see Table 1.

calculations of that kind again"), 3 ("I was thrilled"), and 6 ("Task demands were in very good match with my ability") are closely related to the definition of flow, we expected the corresponding ratings to be highest for the flow condition and to be comparatively low for B and O. We therefore defined a negative quadratic relationship between B, F, and O as an "inverted U shaped effect" and a positive quadratic trend as a "U shaped effect". For all nine items, the existence of invU or U shaped trends was tested using corresponding trend tests. For the purpose of discriminant validity, further F-tests examined whether the relationship between B, F, and O followed a linear trend.

Additionally, an index hereafter referred to as "flow index" was computed to represent the individually experienced level of flow. It was obtained by condition-wise summation of the ratings associated with items 1, 3, and 6, and subsequent subtraction of the boredom and overload conditions from the flow condition (flow index $= -B_{1+3+6} + 2 * F_{1+3+6} - O_{1+3+6}$). As will be shown in the Results section, selection of these items was based on an empirical item-by-item analysis with these items discriminating best between the flow and both control conditions (see also the Discussion section). The flow index as derived above was used for ensuing analyses testing for correlations with the participants' preference for mental arithmetic, and also with neuroimaging results (see next section).

All self-report results were assessed at a significance level of 0.05.

MRI data

Imaging data preprocessing and statistical analyses were performed with Statistical Parametric Mapping (SPM8, Wellcome Department of Cognitive Neurology, London, UK) as previously described (Adolph et al., 2010; Groen et al., 2011). Briefly, labeled and control images were block-wise realigned and then coregistered across blocks. Afterwards the difference between labeled and control images was computed and converted into absolute rCBF images (unit: mL/100 g tissue/min). For normalization, a segmented version of the T1 image was coregistered onto the mean EPI of block 1. Data were spatially normalized using the DARTEL process stream (Ashburner, 2007), transformed into standard Montreal Neurological Institute (MNI) space, resliced to a resolution of isotropic 2 mm^3, and finally smoothed using a Gaussian kernel with 10 mm full width at half maximum.

For each subject, a general linear model was used for voxel-wise averaging of the rCBF data, including the realignment parameters and the volume mean over time as a covariate to reduce the effect of spatially coherent noise (Wang et al., 2003). Upon model estimation, one-sided t-contrasts were created representing the average rCBF across the three blocks pertaining to each condition. The obtained three contrast images (B, F, and O) from each subject were submitted to a random-effects analysis, implemented as flexible factorial design, with the factors Condition and Subject (to remove subjects' related variability). After estimation, two one-sided t-contrasts were computed to test for invU and U shaped relationships between B, F, and O. The resulting statistical parametric maps from this "categorical analysis" were thresholded at $p < 0.005$ at the voxel level in combination with a cluster extent threshold that required cluster sizes of 78 contiguously significant voxels (= expected cluster size).

Since the categorical analysis revealed significant invU and U shaped effects (see the Results section), additional correlation analyses were performed. First, at the single subject level two further contrast images were created testing for invU shaped and U shaped relationships between B, F, and O (contrast weights: $[-1\ +2\ -1]$ and $[+1\ -2\ +1]$, respectively). Then, two separate SPM8 regression analyses were conducted to test for significant correlations of the subjective flow index with the invU shaped and U shaped neural rCBF patterns. Correlation analyses were inclusively masked with the corresponding contrast of the categorical analysis (thresholded at $p < 0.005$, uncorrected, extent threshold = 78 voxels).

Results

Performance data

Task performance, expressed by the percentage of correctly solved math calculations across the three blocks for each condition, decreased from 98.4% in the boredom condition to 63.2% in the flow condition, and to 31.0% in the overload condition. Differences between conditions were significant ($F(2, 52) = 321.04$, $p < 0.001$), and post-hoc Newman–Keuls tests showed pair-wise differences between all conditions (all $p < 0.001$).

Due to the constant, maximum available time of 18 s per calculation irrespective of condition type, the absolute number of processed math problems decreased from 21.2 (B) to 10.5 (F) to 9.26 (O), with the main effect of condition being significant ($F(2, 52) = 367.98$, $p < 0.001$). The pair-wise differences between all conditions were also significant, as revealed by post-hoc Newman–Keuls tests (B vs. F: $p < 0.001$, B vs. O: $p < 0.001$, F vs. O: $p = 0.013$). To address the question whether the number of processed calculations had an influence on the subjective experiences of flow, correlation analyses were performed: For each of the nine Likert-scaled items participants' ratings obtained from the flow condition were correlated with the number of processed calculations. It turned out that there was no significant correlation for any one item (maximum, absolute $r = 0.32$, maximum $t(25) = 1.71$, minimum $p = 0.099$).

Subjective experiences

Participants' average ratings regarding subjective experiences during the task blocks are summarized in Fig. 2 and Table 1. The ANOVAs testing for differences between B, F, and O were significant for all nine items and also for the sum of items 1, 3, and 6 representing the flow index (for detailed statistics, see Table 1). The relationship between B, F, and O can be classified as follows: items 1, 3, and 6, as well as their sum, showed a significant inverted U shape (see Fig. 2); that is, the relationship between B, F, and O followed a significant quadratic trend (minimum $F(1, 26) > 17.96$, $p < 0.001$) but not a linear trend (all $F(1, 26) < 0.80$, $p > 0.380$). Conversely, ratings associated with item 5 significantly decreased linearly ($F(1, 26) = 66.01$, $p < 0.001$) from B to F to O while the quadratic trend was not significant ($F(1, 26) = 1.81$, $p = 0.190$). This was supported by the post-hoc tests which revealed significant differences between all three conditions (all $p < 0.001$). For items 2, 7, and 8, the ratings associated with F and O were each significantly higher than ratings in B (all $p < 0.001$), while not significantly differing between F and O (all $p > 0.114$). Consequently the trend of effects was indifferent, reflected by significant linear as well as quadratic trends (all $F(1, 26) > 33.50$, $p < 0.001$). Similarly, the relationship between B, F, and O of items 4 and 9 also significantly followed both linear and quadratic trends (all $F(1, 26) > 13.34$, $p < 0.001$). Here, however, the boredom condition was associated with higher ratings than the F and O conditions (all $p < 0.001$), with the F and O ratings not being significantly different from each other (all $p > 0.325$).

The analyses testing whether subjects' preference for mental arithmetic or reading correlated with the degree of experienced flow, represented by the flow index, did not reveal any significant results: “How much do you like performing mental arithmetic?”: $r = 0.30$, $t(25) = 1.56$, $p = 0.130$; “How much do you like reading?”: $r = 0.03$, $t(25) = 0.17$, $p = 0.865$; and “To what extent do you prefer reading over mental arithmetic?”: $r = -0.03$, $t(25) = 0.15$, $p = 0.883$. This suggests that individuals can experience flow mostly independent of their general attitude regarding the task they are involved in.

Perfusion data

Categorical analysis

The contrast testing for significantly greater rCBF levels during flow compared to boredom and overload conditions yielded a set of brain regions, summarized in Fig. 3A and Table 2. All clusters appeared exclusively in the left hemisphere. One cluster emerged in the putamen, spreading into the vicinity of the ventral striatum. Another cluster was found in the anterior inferior frontal gyrus (IFG, Brodmann area (BA) 45). Further clusters covered portions of the superior (BA 7) and inferior (BA 40) parietal lobules, the cuneus (BA 18), and lingual gyrus (BA 18/19).

Table 2
Brain regions showing a categorical invU effect, i.e., greater rCBF during the flow condition than during the boredom and overload conditions.

	Region	BA	Number of voxels	Peak voxel (MNI space)			
				x	y	z	z-score
L	Putamen	–	108	−20	12	−4	4.20
L	Inferior frontal gyrus	45	130	−46	36	10	3.87
L	Superior parietal lobule	7	98	−20	−58	40	3.15
L	Inferior parietal lobule	40		−26	−48	36	2.98
L	Cuneus	18		−12	−68	28	2.96
L	Lingual gyrus	18/19	118	−14	−50	−4	3.10

As depicted in Fig. 3B and Table 3, the opposite effect, that is, lower rCBF levels associated with the flow condition than with the boredom and overload conditions, was observed in the left amygdala, posteriorly extending into the hippocampus and parahippocampal gyrus. A second cluster included the left and the right anterior cingulate gyrus (BA 32) and adjacent right-sided ventral and dorsal portions of the medial superior frontal gyrus (BA 10), hereafter referred to as medial prefrontal cortex (MPFC). The contrast also revealed significant clusters in the bilateral angular gyri (BA 39) and the right supramarginal gyrus (BA 40). Further clusters were found in the supplementary motor area (BA 6) and right precentral gyrus (BA 4/6).

Correlational analyses

Correlation analyses investigated the relationship between subjects' experienced degree of flow (flow index) and corresponding effects at the neural level (Fig. 4). The first correlation tested the relationship between the invU shaped flow index and similarly shaped differences at the neural level of each participant. A positive correlation was evident in 124 out of those 130 voxels in the left inferior frontal gyrus that had been identified in the categorical group analysis using the invU contrast. Significance at the peak voxel ([−44, 36, 6], $r = 0.62$, $t(26) = 3.97$) was $p < 0.001$, one-sided. After averaging across the 124 voxels the

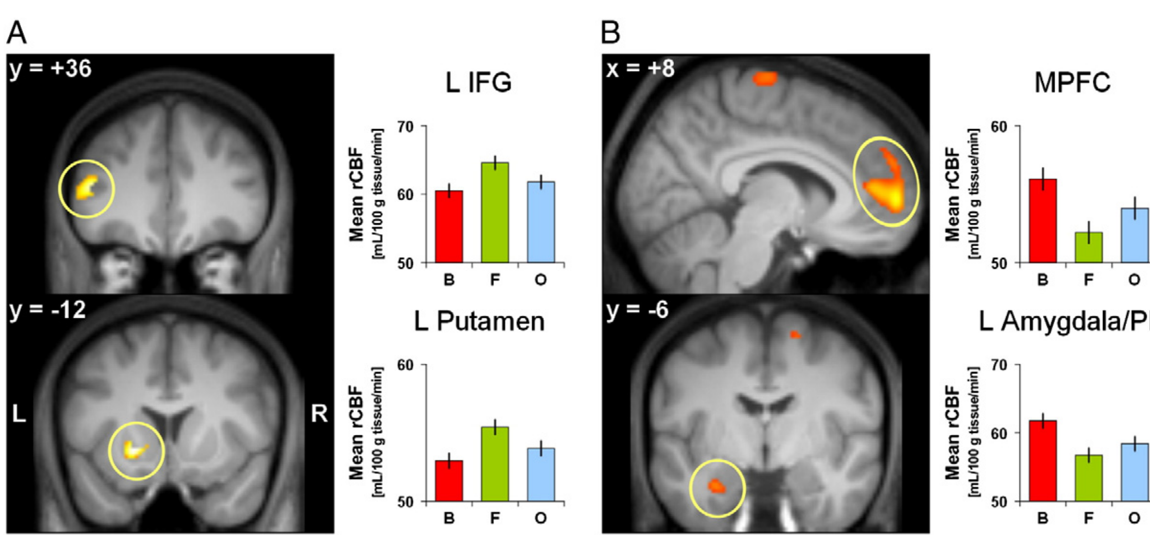

Fig. 3. Perfusion results from the categorical group analysis. A) The inverted U shaped contrast revealed higher rCBF levels during the flow condition (F) than during the boredom (B) and overload (O) conditions in the left anterior inferior frontal gyrus (IFG) and left putamen. B) The inverted U shaped effect was evident in the medial prefrontal cortex (MPFC) and in a cluster including the left amygdala, hippocampus and parahippocampal gyrus (PH). Statistical parametric maps were overlaid on the group averaged T1 image. Coordinates refer to MNI space. The bar chart on the right next to each brain section depicts the mean rCBF levels associated with conditions B, F, and O, averaged across all voxels of a significant cluster. Error bars represent standard error of the mean (27 participants). L: left, R: right. rCBF: regional cerebral blood flow.

Table 3
Brain regions showing a categorical U effect, i.e., lower rCBF during the flow condition than during the boredom and overload conditions.

	Region	BA	Number of voxels	Peak voxel (MNI space)			
				x	y	z	z-score
R	Angular gyrus	39	403	48	−58	32	5.16
R	Medial superior frontal gyrus	10	684	8	58	4	4.12
R	Anterior cingulate gyrus	32		6	46	10	3.85
R	Medial superior frontal gyrus	10		12	56	26	3.22
L	Angular gyrus	39	113	−40	−60	24	3.61
R	Precentral gyrus	6	109	22	−12	64	3.41
L	Parahippocampal gyrus	–	162	−28	−18	−26	3.12
L	Amygdala	–		−28	−6	−26	3.07
R	Supramarginal gyrus	40	94	52	−34	32	3.09
R	Supramarginal gyrus	40		60	−26	26	3.08
R	Supplementary motor area	6	232	6	−18	74	3.02
R	Precentral gyrus	4		16	−24	70	2.89

mean correlation coefficient was $r = 0.47$ ($t(26) = 2.64$, $p = 0.007$, one-sided). No correlation was observed for the left putamen.

The flow index also showed a correlation with the neural U shaped effect, that is, the higher the flow index, the lower was the rCBF during the flow condition as compared to the boredom and overload conditions. That effect was observed in 13 voxels within the amygdala cluster bearing a categorical U effect from the group analysis. Peak voxel: [−22, −8, −28]: $r = 0.50$, $t(26) = 2.88$, $p = 0.004$ (one-sided); cluster-averaged $r = 0.40$, $t(26) = 2.21$, $p < 0.018$ (one-sided). With a trend toward significance 36 voxels in the medial prefrontal cortex also showed a positive correlation with this U shaped effect. Peak voxel: [6, 60, 20]: $r = 0.36$; $t(26) = 1.95$, $p = 0.031$ (one-sided); cluster-averaged $r = 0.29$; $t(26) = 1.53$, $p = 0.069$ (one-sided).

Discussion

We investigated subjective experiences and neural correlates of flow during arithmetic calculations using MR-based perfusion imaging in a sample of 27 healthy, male participants. Following the definition of flow, corresponding experiences were experimentally induced by automatically and continuously adjusting task demands relative to the individual skill level. This condition was contrasted against conditions of boredom and overload. Subjective ratings for items directly expressing characteristics of flow were significantly higher for the flow condition than for the control conditions. Notably, the experience of flow did not depend on the number of calculations processed and was not reliably correlated with individual levels of mathematical preferences. Relative to control conditions, neural activity as indexed by changes in regional cerebral blood flow (rCBF) increased during the flow condition in the left putamen, the left inferior frontal gyrus (IFG) and posterior cortical regions. Significantly decreased neural activity during flow was observed in the medial prefrontal cortex (MPFC) and left amygdala. In left IFG and left amygdala changes in neural activity were significantly correlated with subjectively experienced flow. In the MPFC rCBF changes were correlated with the flow index at trend level significance.

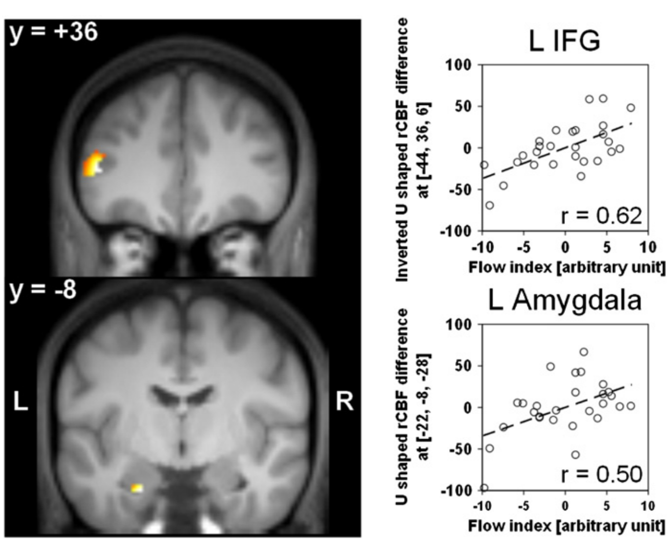

Fig. 4. Correlations between the behavioral flow index and corresponding neural effects. In the left anterior inferior frontal gyrus (IFG) the degree of experienced flow (flow index) showed a significant positive correlation with the inverted U shaped relationship between the boredom, flow, and overload conditions at the neural level (rCBF). In the left amygdala the flow index correlated positively with the opposite, U shaped rCBF difference. Statistical parametric maps were superimposed on the group averaged T1 image in MNI space. Scatter plots were derived from the voxel with the highest correlation coefficient. L: left, R: right.

Relative increases in neural activity during flow

Involvement of the putamen is in line with a previously reported significant correlation of individual flow proneness and D2 receptor binding (de Manzano et al., 2013) in the striatum. Although extending into the ventral parts of the caudate nucleus, the maximum peak of the present rCBF increase was in the putamen proper supporting the previous study's conclusion that experiencing flow may be more dependent on the nigrostriatal than the mesolimbic dopamine system. This also supports the notion that flow proneness is not specifically related to those parts of the dopaminergic system that process extrinsic rewards. This is further corroborated by a previous study on neuronal encoding of reward value and direction of actions in the primate putamen (Hori et al., 2009). It has been shown that the putamen is particularly involved in the guidance of goal-directed behavior by coding outcome probability in relation to effort (Hori et al., 2009). From that perspective, flow experiences, although often described as rewarding, cannot be reduced to the mere activity of the human dopaminergic reward system. Instead, the pleasant aspect of this peculiar experience may be mediated by the expectation of a rather high outcome probability in the context of an effortful task of high difficulty.

The relative increase of neural activation in the left inferior frontal gyrus may align with another feature of the definition of flow, that is, a sense of control. This interpretation is supported by two recent studies demonstrating that specific adaptation to task goals was correlated with activation of this structure (De Baene et al., 2012; Fincham et al., 2002). Involvement of the IFG has also repeatedly been reported to serve mental arithmetic (Arsalidou and Taylor, 2011; Baldo and Dronkers, 2007; Zago et al., 2008) and to be especially recruited in tasks of greater difficulty (Gruber et al., 2001; Kong et al., 2005). Therefore greater activity of the IFG in the flow condition might indicate an inverted U shaped response level, with its peak at an almost optimal level of task difficulty but decreased activity at the left and right ends of the curve where recruitment is not yet necessary (boredom) or no longer of use due to task difficulty being too high (overload). Since the optimally perceived level of task difficulty may associate with a deeper feeling of cognitive control in presence of rather high positive outcome probability, both interpretations are possibly not mutually exclusive but complementary. This aspect is further corroborated by the significant positive correlation between increased neural activity in the left IFG and the flow index, which is difficult to explain by the neural recruitment hypothesis alone.

Relative decreases in neural activity during flow

One of the most prominent results of the present study was decreased rCBF in the medial prefrontal cortex during the flow condition compared to control conditions. This observation is in line with the concept of the so called brain's "default-mode network" (DMN) which usually shows greater activity during passive states ("at rest") than during goal-directed behaviors, when DMN activity is deactivated by the functional challenge (Andrews-Hanna, 2012; Buckner et al., 2008; Raichle et al., 2001; Shulman et al., 1997). The DMN comprises several brain regions four of which showed U shaped rCBF effects in the present study (MPFC, angular gyrus, supramarginal gyrus, parahippocampal cortex). One prominent function commonly attributed to the DMN is self-referential processing (e.g., Gusnard et al., 2001), which has been particularly linked with the MPFC (Brewer et al., 2011; D'Argembeau et al., 2007; Gusnard et al., 2001; Jenkins and Mitchell, 2011; Johnson et al., 2009; Northoff et al., 2006; van Buuren et al., 2010; Whitfield-Gabrieli et al., 2011; Zysset et al., 2003). A previous lesion study could even demonstrate that damage to the MPFC abolished self-referential processing (Philippi et al., 2012). Moreover, from healthy controls and from patients with major depression it has been reported that increased metabolic activity of the MPFC correlates positively with unhappiness (Brewer et al., 2011), negative affectivity (Lemogne et al., 2011), and increased depressive self-focus, associated with increased attribution of negative emotions to oneself (Grimm et al., 2009; Lemogne et al., 2009; Lemogne et al., 2012). Medial prefrontal cortices were also relatively deactivated in experienced meditators consistent with decreased self-referential processing during meditation (Brewer et al., 2011; Farb et al., 2007). Given these previous results we therefore conclude that the present flow-associated decrease in MPFC activity represents one of the main features of flow experiences, that is, a reduction in self-referential processing together with a putative reduction of negative affectivity that may contribute to the feeling that flow activity per se is enjoying.

In this context the prominent U shaped rCBF pattern in the MPFC also suggests a specific conditional aspect of experiencing flow. It has been reported that DMN activity usually decreases with almost any increase in task engagement (e.g., McKiernan et al., 2003). This is well reflected by the present data with decrease in neural activity from the boredom to the flow condition. Notably though, the increase in activity from flow to overload does not fit with this observation since task difficulty was further increased and should have induced some further decrease in the DMN activity. However, already by definition the overload condition has been implemented to clearly exceed participants' skills. The increase in neural activity during overload may therefore reflect some extra, though task-related, self-referential processing in terms of rumination, meta-cognitive deliberations in order to better compensate the cognitive overload, or even complaints. From that perspective, present results suggest that down-regulation of DMN regions may go beyond the issue of mere task difficulty. The extra amount of task-induced DMN deactivation associated with flow is obviously only achieved when skills and task demands are optimally balanced while mere engagement in a task lacking this specific balance between skills and demands does not seem sufficient to down-regulate DMN activity associated with the experience of flow.

A second brain region for which neural activity was significantly decreased during flow was the left amygdala. Across participants, this decrease was also correlated with the flow index. The higher the subjective experience of flow, the greater the decrease in neural activity in this structure. Previous studies (Anders et al., 2008; Colibazzi et al., 2010; Duvarci and Pare, 2007; Gallagher and Schoenbaum, 1999; Garavan et al., 2001; Lewis et al., 2007; McGaugh, 2004; McReynolds and McIntyre, 2012) have shown that coding of arousal may represent the least common denominator of the amygdala's functional specialization. Hence, the most parsimonious interpretation of our result is that the decrease most likely reflected a decrease in arousal associated with the experience of flow. However, one might also speculate that the amygdala's reduced activity during flow may indicate more positive emotions compared to both controls conditions. Previous studies with direct emotional challenges could show that negative emotions were associated with increased activation of the amygdala while positive emotions aligned with relatively reduced activity (Kim et al., 2004; Morris et al., 1996; Straube et al., 2008; Whalen et al., 1998).

Another open issue is whether this decrease in the amygdala's activity may associate with the decrease of rCBF in the MPFC or even with the rCBF increase in the putamen coding for outcome probability of increased task effort. The idea behind this speculation is that reduced processing of self-referential information and associated negative affectivity may align with decreased arousal. Similarly, a feeling of higher outcome probability despite increased task effort may also associate with decreased arousal experienced in the flow condition in the presence of an almost complete fit between individual levels of skill and task demands.

Limitations

A limitation of the present study was recruitment of solely male volunteers for reasons described in the Material and methods section. This not only reduces generalizability of the present results but also motivates to run the same experiment in a comparably large all-females sample to investigate sex-related commonalities and differences in the neural correlates of flow.

Also, the present significances were not corrected for multiple comparisons. Generally, contrast-to-noise-ratio (CNR) in brain activation studies is lower for perfusion than BOLD imaging (Detre et al., 2012; Donahue and Jezzard, 2013; Liu and Brown, 2007; Viviani et al., 2011; Wang et al., 2011; Yang et al., 2005). This is caused by rather small signal differences between label and control images (around less than 1%), and implies that application of correction for multiple comparisons as used in BOLD statistics cannot easily be transferred to perfusion statistics. We strongly hope that the present results may stipulate further research within the same experimental framework to replicate present findings and to support their robustness. So far, present significances should be treated as exploratory rather than confirmatory.

Another issue for future research is construction of items to still better map subjective experiences of flow, particularly in context of this specific paradigm. Unfortunately, some of the present items, though advantageous in previous studies (Keller and Bless, 2008; Keller et al., 2011), did not possess the discriminatory power to clearly distinguish present flow state from *both* boredom and overload. While all items responded rather sensitive to different condition effects, most likely unforeseen semantic ambiguity may have contributed to this lack of discriminatory power. For example, task involvement can increase under both the flow and the overload condition, since aspects of involvement were not further qualified for the subjects. Involvement in a task not only can be a pleasurable experience due to increased outcome probability of correct solution, but can also describe an effortful, less pleasurable experience in the overload condition. Therefore, the present flow index based on a subset of items may not exhaustively represent the full flow spectrum. Still, an overall index including all of the items would have been inappropriate given the lack of discriminatory power.

Although flow is a rather well defined psychological construct, the defining features are most likely not independent of each other but may interact in a sense of mutual contribution to the overall flow experience. Likewise, present observations of increased and decreased neural activation during flow may also interact to contribute to the final subjective experience. The temporal resolution of perfusion imaging, though advantageous for low frequency paradigms, does not permit testing for interactions in the sense of effective functional connectivity. Future research should investigate whether it is possible to induce experiences of flow by using tasks of shorter duration, e.g., in typical functional MRI block designs with durations of around 30 s. If these tests are positive then it may become possible to investigate the different flow dependent modulations of neural activity with respect to effective interaction, to still better delineate the neural mechanisms that contribute to the experience of flow.

Conclusions

In the present study we investigated subjective experiences and neural correlates of flow during mental arithmetic. Subjective flow was expressed as the experienced balance between individual skill levels and task difficulty combined with an increased experience of pleasure and an increased propensity to repeat the mathematical tasks under flow conditions. Functionally, the flow condition was associated with an increase of neural activity in the putamen possibly reflecting increased outcome probability, and in the left inferior frontal gyrus which might reflect a deeper sense of cognitive control. Reductions in neural activity were observed in the medial prefrontal cortex suggesting decreased self-referential processing that has previously been shown to associate with negative affectivity. Decrease of rCBF was also evident in the amygdala which might mirror a decrease in arousal contributing to or reflecting the positive emotional experiences during flow. Experimental induction of flow experiences appears to be, much like meditation, a promising tool for stress reduction programs for persons suffering from chronic stress syndromes including increased arousal and increased self-reflection with associated negative affectivity.

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Conflict of interest

The authors declare no competing financial interests.

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