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Original Article

Neural correlates of metacontrol persistence and flexibility induced by creativity and meditation

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The neural mechanisms underlying the cognitive metacontrol states of persistence and flexibility are not yet fully understood but are thought to be modulated by frontal and striatal dopamine, respectively. In this study, we attempted to induce persistence and flexibility states by having participants engage in 2 creativity tasks (remote associates task and alternative uses task) and 2 meditation techniques (focused-attention meditation and open-monitoring meditation), to study the neural correlates of these metacontrol states and test the metacontrol model of creativity (MCC). Results show that brain areas known to be modulated by both frontal and striatal dopamine were activated in conditions that are thought to call for persistence, particularly the prefrontal cortex, anterior cingulate cortex, and basal ganglia, indicating goal-related selective attention and top-down control. In contrast, conditions that call for flexibility showed brain activation in areas of the default mode network, suggesting reduced top-down control. This pattern was much clearer for the creativity tasks than meditation. Notably, we did not find significant effects when contrasting the 2 meditation techniques and when looking at brain activation overlap between meditation and creativity at the whole-brain level. Finally, the examination of the MCC provided partial supporting evidence for the model, but its prediction for the left inferior frontal gyrus showed the exact opposite result, which calls for clarification in future research.

Keywords: creativity; meditation; metacontrol; MRI.

Introduction

In a constantly changing environment, the human brain requires adaptive cognitive control to switch between states of maintaining focus or persistence, and being flexible. For instance, in problem-solving, human beings might first maintain the focus on existing goal-related information to solve the problem; but if existing information proves insufficient, they need to transit into a more flexible state and open up to new information. This mechanism of monitoring and regulation of different cognitive control states has been described as "metacontrol" (Hommel 2015; Eppinger et al. 2021).

The metacontrol states model (MSM) has been proposed (Hommel 2015; Hommel and Colzato 2017a, 2017b; Hommel and Wiers 2017) to refer to the balance between persistence and flexibility in decision-making. It is based on the widely accepted scenario that multiple goal-related representations compete for selection according to a winner-takes-all principle, so that increasing the activation of one alternative reduces the activation of others (Bogacz 2007). However, in the MSM, the degree to which alternatives compete and to which they are biased by the current goal is determined by the present metacontrol state, which varies between persistence and flexibility. Extreme persistence would consist of (i) strong mutual competition between alternatives and (ii) strong top-down bias toward certain alternatives, whereas extreme flexibility would consist of (i) weak competition and (ii) weak top-down bias allowing flexible switching between alternatives (Hommel 2015; Hommel and Colzato 2017b).

As distinct and opposing cognitive control states, persistence and flexibility are likely to involve different neural mechanisms, particularly related to dopamine modulation and its interaction with the prefrontal cortex (PFC) and basal ganglia (BG). Dopamine binds to 5 different dopamine receptors, which fall into 2 main receptor types: the dopamine D1 receptor family (D1R) with subtypes D1 and D5, and the dopamine D2 receptor family with subtypes D2, D3, and D4. In the PFC, D1Rs are expressed in all cortical layers and are approximately 10-fold more abundant than D2Rs (Ott and Nieder 2019). The dual-state theory (Durstewitz and Seamans 2008) proposes that in a D1R-dominated state, dopamine stabilizes prefrontal representations by increasing sustained responses during working memory (Durstewitz et al. 2000; Durstewitz and Seamans 2002), which is likely associated with the persistence. In contrast, a D2R-dominated state renders prefrontal representations unstable, thus enabling switching between representations (flexibility state) via a D2R mechanism, which is opposite to D1R (Durstewitz and Seamans 2008). In addition, dopamine synthesized in the midbrain can transmit not only to the PFC (through the mesocortical pathway) but also to the striatum, which is a part of the BG (through the nigrostriatal pathway), and the D2Rs are omnipresent in the striatum (Beaulieu and Gainetdinov 2011; Gallo 2019). Accumulating evidence reveals

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that striatal dopamine plays a key role in attentional gating or shifting in response to unexpected and behaviorally important stimuli (van Schouwenburg et al. 2010; Cools and D'Esposito 2011) that could be associated with the flexibility. Furthermore, dopamine is thought to modulate its balance in the PFC and striatum to manage the trade-off between cognitive stability and flexibility through a so-called frontostriatal circuit (McNab and Klingberg 2008), and neuroimaging studies have also demonstrated that brain activation in the dorsolateral PFC (DLPFC) is related to working memory and information maintenance (Andrews et al. 2011) which are associated with persistence, while brain activation in the BG is related to task switching (Yehene et al. 2008) which is associated with cognitive flexibility. These mechanisms could underlie stability/persistence and flexibility.

The major aim of the present study was to contribute to a better understanding of how these brain mechanisms could interact, to create or implement particular metacontrol states, that is, to bias metacontrol toward persistence or flexibility, depending on the current task demands. Even though there is evidence of interindividual differences regarding default values of people's metacontrol biases (Hommel and Colzato 2017b), truly adaptive behavior also requires some degree of intraindividual variability of states (Mekern et al. 2019). Previous research has identified several manipulations that seem to robustly induce and alter people's metacontrol states, including creativity tasks and meditation (Lutz et al. 2008; Lippelt et al. 2014; Hommel 2015; Hommel and Colzato 2017a)—the 2 manipulations our study focused on. Both manipulations fall into at least 2 different categories. Regarding creativity tasks, some tasks tap into convergent thinking, which is strongly constrained and searches for one single solution, while other tasks are tapping into divergent thinking, which is loosely constrained and possibly generates many solutions (Guilford 1967). The prototypical convergent thinking task is the remote associates task (RAT; Mednick 1968), in which the participant needs to find the only correct common associate (eg "party") of 3 presented, otherwise unrelated words (eg "cocktail, dress, birthday"). Even though the RAT does need some degree of flexibility in searching through memory for possible solutions, the task requires various processes that rely highly on persistence: potential answers being generated need to be monitored continuously and evaluated immediately (higher top-down bias), and evaluating one potential answer is likely to inhibit other answers (higher competition). Accordingly, it comes as no surprise that engaging in RAT increases goal-related impact and reduces crosstalk in dual-task performance (Fischer and Hommel 2012), and thus requires a high state of persistence. The prototypical divergent thinking task, in turn, is the alternative uses task (AUT; Guilford 1967), in which the participant is presented with a common object (eg brick) and required to generate as many novel uses of this object as possible. Since there is no correct answer in the AUT, the ideas being generated are influenced less by monitoring and evaluating processes (lower top-down bias) and have lower competition between each other, which are the characteristics defined by metacontrol flexibility. Previous studies have found that engaging in AUT can induce positive mood (Akbari Chermahini and Hommel 2012), and AUT performance is related to the spontaneous eyeblink rate, a marker of striatal dopamine (Akbari Chermahini and Hommel 2010), which associates the AUT with flexibility because positive mood could reduce response conflict and suppress competing response (Van der Stigchel et al. 2011).

Regarding meditation, some types have been characterized as focused-attention meditation (FAM) while others are considered open-monitoring meditation (OMM; Lutz et al. 2008). Again, meditation of these 2 types seems to imply a rather different metacontrol state (Hommel and Colzato 2017a). FAM typically calls for sustaining selective attention moment-by-moment on a specific object with a fairly narrow focus, which implies persistence, while OMM calls for the attentive monitoring of anything that occurs in experience without focusing on any explicit object (Lutz et al. 2008; Hommel and Colzato 2017a), which implies flexibility. Interestingly for present purposes, FAM and OMM have been found to facilitate RAT and AUT performance, respectively (Colzato et al. 2012). Considering the connections between the metacontrol states and the processes of creativity and meditation, it thus makes sense to assume that during RAT and FAM, the brain would be more likely to establish a state of persistence, while during AUT and OMM, it would be more likely to establish a state of flexibility. Therefore, we thought that comparing brain activation while performing the RAT vs AUT and comparing brain activation while engaging in FAM vs OMM, could help reveal the neural mechanisms underlying the metacontrol states of persistence and flexibility. If RAT and FAM share a commonality that systematically differs from the commonality shared by AUT and OMM, it would be informative not only to compare RAT to AUT and FAM to OMM but also to consider what one of these comparisons is telling us about the other. A previous study (Manna et al. 2010) has already compared brain activation during FAM vs OMM. However, it did not yield significant results after multiple comparison correction, and only uncorrected results were reported. Furthermore, the direct comparison with brain activation during the creativity tasks was not performed.

Although it appears that the mentioned creativity tasks (RAT vs AUT) and the meditation techniques (FAM vs OMM) are related to persistence and flexibility, the degree of their relationship and whether they can truly induce the state still requires further discussion. Below, we will link these concepts in a more specific manner: the MSM describes how decision-making is affected by the processing style, which is assumed to vary between extreme persistence and extreme flexibility. The model follows the conclusion of Bogacz (2007), that biologically plausible decision-making models share 2 basic features: they assume that decision-making is competitive, in the sense that alternatives compete for selection and are biased by the current goal, in the sense that alternatives that are more consistent with the current goal receive more top-down support. The MSM characterizes persistence as a processing style in which both competition and top-down support are stronger and flexibility as a processing style where both are weaker. As a consequence, strong forms of persistence should be associated with a strong focus on goal-relevant content and a strong inhibition of goal-irrelevant information, which basically turns the cognitive system into a single-channel mode. Whereas strong forms of flexibility should be associated with the opposite: a lack of focus and openness to nominally irrelevant or unexpected information. Indeed, the review of Hommel and Colzato (2017b) has consolidated evidence for the assumption that conditions that are likely to increase persistence, improve people's performance in tasks that require a strong focus and inhibition of irrelevant information, while the opposite is the case for conditions that are likely to increase flexibility. Engaging in FAM requires meditators to keep a strict focus on their breathing while inhibiting other upcoming thoughts, while OMM requires meditators to be particularly open to any possible thought that may come up. For the creativity tasks, RAT has a well-defined task requirement that demands strong top-down control from the goal and only one correct answer, necessitating the inhibition of irrelevant alternatives. Meanwhile, AUT has a relatively vague task requirement and multiple possible answers, thus requiring weaker top-down control from the goal and less competition among alternatives. Accordingly, we assumed that engaging in FAM and RAT is likely to create a neural state that is similar to the one implied by persistence, whereas engaging in OMM and AUT would be likely to create a neural state that is similar to the one implied by flexibility.

Considering the connection between the processing of creativity tasks and meditation with respect to the metacontrol states they imply, the main research question of this study is to increase our knowledge regarding the neural mechanisms underlying different metacontrol states by comparing the neural correlates during 2 creativity tasks that imply opposite metacontrol states (RAT vs AUT), 2 types of meditation that imply equally opposite metacontrol states (FAM vs OMM), and by analyzing commonalities that emerge in these 2 types of comparisons. Given that the neural states in creativity tasks and during meditation are likely to reflect both task-specific activities and more general brain states, we thought that an analysis of the overlap of brain activations across the 2 types of comparisons would provide a more direct indicator of metacontrol than each of these comparisons alone. First, in the separate comparisons of the brain activations associated with metacontrol states in creativity and meditation, we hypothesized that in the contrasts of RAT > AUT and FAM > OMM, we would find activity in regions related to cognitive control, indicative of stronger top-down control and greater competition between mental representations, particularly related to metacontrol persistence, whereas in the contrasts of AUT > RAT and OMM > FAM, we would find activation in regions related to cognitive control, which would indicate weaker top-down control and reduced competition, related to metacontrol flexibility. Second and more importantly, we were interested in whether and how the brain areas identified in these 2 sets of comparisons (creativity and meditation) would overlap or share common characteristics, which would help us to understand the neural correlates of metacontrol. A third aim was motivated by previous claims that metacontrol is strongly related to frontal and striatal dopaminergic pathways (Durstewitz and Seamans 2008; Cools and D'Esposito 2011; Cools 2016). If so, one would expect the PFC and BG to be involved in metacontrol states and may thus provide natural regions of interest (ROIs) to examine for differences in creativity tasks and meditation routines that can be assumed to induce different metacontrol states. The pattern that one expects from this kind of analysis depends on the scenario one envisions for the interactions between brain systems responsible for balancing metacontrol between the poles of persistence and flexibility. If one considers the frontal dopaminergic pathway a system that promotes persistence and the striatal pathway a system that promotes flexibility, which would fit with the views of Cools (2016) and Cools and D'Esposito (2011), one might expect that RAT and FAM are accompanied by stronger activation of the areas fueled by the frontal dopaminergic pathway, while AUT and OMM are associated with stronger activation of the areas fueled by the striatal dopaminergic pathway. Other scenarios are also conceivable, however. For instance, the approach of Durstewitz and Seamans (2008) implies that both ROIs might be involved in implementing a particular balance between persistence and flexibility, even though the receptor types that are promoting the activities in these regions might differ. Accordingly, visible switches between the dominance of the 2 regions (and PFC vs BG) in RAT/FAM vs AUT/OMM would be more consistent with the first scenario, while the involvement of both regions in all these conditions would rather point to the second scenario.

A fourth and final aim of our study relates to our recent integration of the available literature on convergent and divergent thinking into a working model (Zhang et al. 2020). In the resulting metacontrol of creativity (MCC) model, we proposed that metacontrol biases in creativity tasks might be reflected by task-specific activation patterns of 3 key brain areas: (i) left inferior frontal gyrus (lIFG), (ii) left DLPFC (lDLPFC), and (iii) right temporal and/or parietal cortex (rT/PC), especially the right superior temporal gyrus (rSTG) and posterior parietal cortex (rPPC). The lIFG, which is related to cognitive flexibility (Chávez-Eakle et al. 2007), was frequently found to be active in divergent thinking tasks such as the AUT (Runco and Yoruk 2014). The lDLPFC, which has been related to working memory (Andrews et al. 2011) and facilitates creativity by maintaining focused attention and goals (Beaty and Schacter 2018), is thought to be more associated with persistence. In the regions of the rT/PC, divergent thinking tasks including the AUT induce more alpha synchronization measured with EEG, suggesting a weaker activation of brain areas (Runco and Yoruk 2014) that is thought to facilitate the (re-) combination of semantic information that is normally distantly related (Jung-Beeman 2005), while convergent thinking tasks show more alpha desynchronization suggesting a stronger activation (Mölle et al. 1999; Krug et al. 2003; Shemyakina et al. 2007). Therefore, the MCC model suggests that 2 activation patterns (lIFG+, lDLPFC−, rSTG/rPPC− vs lIFG−, lDLPFC+, rSTG/rPPC+) reflect metacontrol states that are biased toward flexibility and persistence, respectively.

Methods

Participants

The sample size was initially determined based on previous behavioral studies of meditation (ie Colzato et al. 2012), which typically involved 20 to 30 participants. To ensure adequate statistical power and the ability to correct for multiple comparisons in fMRI studies, we set the range of sample size as 40 to 60. In addition, power analysis (paired samples t-test) using a moderate effect size ($d = 0.5$) suggested by G∗Power software (Faul et al. 2007), an α error equal to 0.05, and a power level of 0.9 yielded an adequate sample size of 36 participants. In the data collection, 43 healthy adults participated in this study. Two participants were excluded from data analysis due to mid-study dropout or left-handedness. The final analyzed sample included 41 participants (31 females and 10 males). Their age ranged from 21 to 59 with a mean of 44.10 (SD = 9.43). To make sure that the participants were familiar with the difference between FAM and OMM and were able to successfully implement the corresponding meditation states upon instruction, we only tested experienced meditators (assessed by a questionnaire) with an average meditation experience of 9.4 years, ranging from 5 to 30 years. On average, they engaged in meditation practice 5.76 times per week (SD = 1.84), with each session lasting 25.37 min (SD = 12.77). All participants were Dutch-native, right-handed, non-medicated people recruited through online advertisements and through the social network of the meditation experts involved in this study. The study was approved by the internal review board at the Leiden University Medical Center and conducted in accordance with the Declaration of Helsinki (reference: NL72023.058.19). Informed consent was given by every participant.

General procedure

Participants visited the laboratory twice, once for a creativity scanning session while performing the RAT and AUT, and once for a meditation scanning session while undergoing FAM and OMM. The order between these sessions and the order of creativity task and meditation within sessions were counterbalanced. Before entering the scanner, participants were thoroughly instructed and practiced the upcoming meditation and creativity task. Once adequately prepared, participants proceeded to the scanner. Each session in the scanner lasted less than 60 min. Before and after the scan, participants filled in an affect grid (Russell et al. 1989) to assess subjective feelings of pleasure and arousal. After the experiment, participants were thanked for their participation and received a compensation of 40 Euros.

Experimental tasks

Creativity tasks

In the RAT (Mednick 1968), participants were to find the only correct common associate (eg "party") of the presented 3 unrelated words (eg "cocktail, dress, birthday"). There were 40 Dutch items of the RAT used in this study, which were selected during a validation test from a pool of 144 items created by Dutch-native researchers. After a jittered fixation of 4 to 6 s, the item was presented for maximally 30 s (see Fig. 1A). Once participants came up with the solution, they pressed a button. After the button press, the item was no longer presented, and the participant could speak out the answer within 5 s. Next, participants were to press another button within 5 s to indicate whether they solved the item with a feeling of insight, or "aha! feeling." The instruction to explain insight was taken from a previous study (Jung-Beeman et al. 2004) and translated into Dutch. Note that the assessment of insight served purposes that are unrelated to this study, which is why we will not consider these data in the present report.

In the AUT (Guilford 1967), participants were to generate as many creative uses as possible for a given object (eg cup's alternative uses can be flowerpot, making art, fishbowl, ...). The items of AUT were taken from a previous study (Abraham et al. 2012) and translated into Dutch. There were 18 items, and each was presented for 30 s after a jittered fixation of 4 to 6 s, similar to the RAT. During the 30 s, the participants could press the button immediately (no verbal response was required in this period) when they had one idea. After the 30 s, they had 5 s to verbally report the most creative idea they had generated (see Fig. 1A).

Due to the noise generated by the MRI scanner, and difficulties timing the verbal responses with possible breaks in scanning, we only recorded the button presses for fMRI analysis, but the verbal responses were not recorded. However, participants were informed their voices would be recorded before entering the scanner, to ensure they performed the task in a serious way. The fact and reasons behind this were disclosed to the participants at the end of the experiment.

Meditation

For FAM, participants were instructed to gently engage in sustaining the focus of their attention on breathing sensations, such as at the nostrils, noticing with acceptance and tolerance of any arising distraction, like toward stimuli or thoughts, and return gently to focus attention on the breath after having noticed the distracting source (Manna et al. 2010). For OMM, participants were asked to observe and recognize any experiential or mental content as it arises from moment to moment, without restrictions and judgment, including breathing and body sensations, percepts of external stimuli, arising thoughts and feelings (Manna et al. 2010).

The fMRI protocol of meditation followed a common procedure for both FAM and OMM (see Fig. 1B). First, a 2-min audio was played to guide participants into a specific meditation state. Subsequently, the scanning began, and participants were instructed to maintain the meditation state until the end of the scan, which lasted approximately 13 to 14 min. Once the scanning and meditation started, every 45 s, a 30-s audio guidance was provided to encourage them to keep meditating as instructed. The meditation instructions and audios were created by professional meditation trainers.

fMRI data acquisition

fMRI data were acquired using a standard whole-head coil on a 3-Tesla Philips Achieva MRI system (Best, the Netherlands) at the Leiden Institute for Brain and Cognition, in Leiden University Medical Center (Leiden, the Netherlands). A headphone and foam inserted around the headphone were used to minimize head movement. Prior to the functional scans, a high-resolution 3DT1-weighed anatomical scan was obtained for registration purposes (repetition time [TR] = 7.9 ms; echo time [TE] = 3.5 ms, flip angle = 8°, 155 transverse slices, field of view = $250 \times 195.83 \times 170.5$ mm, 0 mm slice gap and voxel size = $1.1 \times 1.1 \times 1.1$ mm). For fMRI, T2∗-weighed whole-brain Echo-Planar Images were acquired with the following parameters: TR = 2.2 s, TE = 30 ms, flip angle = 80°, 40 transverse slices, 0.275 mm slice gap, and voxel size = $2.75 \times 2.75 \times 2.75$ mm. Five dummy scans preceded each fMRI scan to allow for equilibration of T1 saturation effect. Stimuli were projected using E-prime 3.0 software (Psychology Software Tools, Pittsburgh, PA) onto a screen at the head of the scanner bore which participants viewed through a mirror attached to the head-coil. Moreover, for additional research purposes, resting-state fMRI data, diffusion tensor image data, and magnetization transfer contrast MRI data were also scanned, which were not used for the analysis of this study.

fMRI data analysis

fMRI data were preprocessed and analyzed using SPM12 (Statistical Parametric Mapping; Wellcome Center for Human Neuroimaging, London, UK). EPI (echo planar imaging) images were corrected for slice-timing differences and motion. Segmentation of the individual subject's structural image provided normalization parameters that were used to normalize the functional images to the Montreal Neurological Institute (MNI) template reference brain. Finally, images were smoothed with a 6 mm full-width-at-half-maximum Gaussian kernel.

The preprocessed fMRI data from the creativity (RAT and AUT) and meditation (FAM and OMM) sessions were separately subjected to first-level general linear model (GLM) analyses, incorporating the effects of time and dispersion, to investigate the neural correlates of metacontrol states in creativity and in meditation, respectively. For the creativity tasks, the period of 2 s preceding the button press in both RAT and AUT was considered as the thinking processes related to the metacontrol states and used for the fMRI analysis. The average amount of the 2-s periods around a button press used for fMRI analysis were 25.80 (SD = 7.19) for RAT, and 67.05 (SD = 14.48) for AUT. For the meditation tasks, the fMRI analysis focused on the 45-s period (total of 11 trials, which is 495 s) without audio in both FAM and OMM. The GLM analysis involved modeling the hemodynamic response function during the mentioned periods in each condition for each participant's data. To account for potential confounds, especially head motion

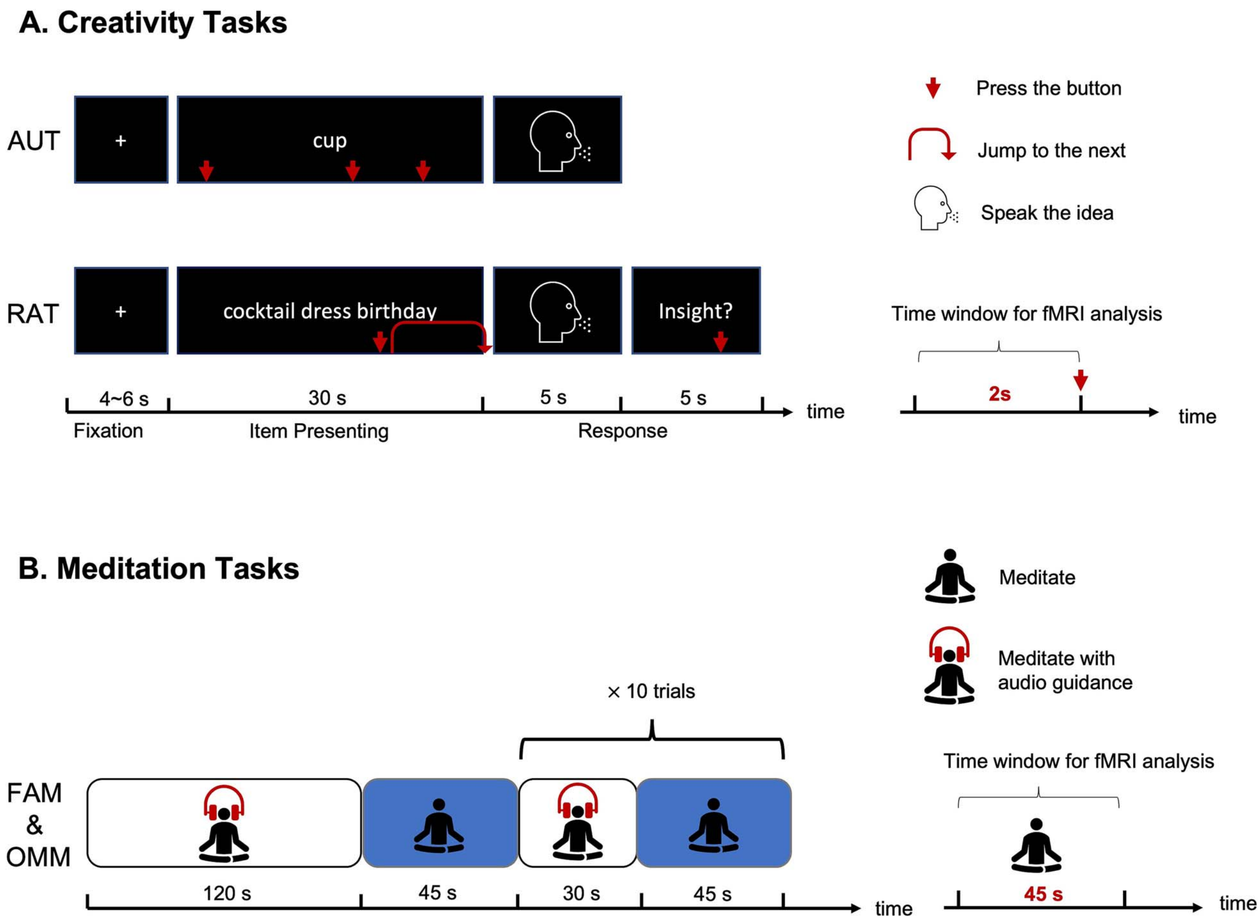

Fig. 1. Schematic time course of the experimental tasks. (A) Creativity tasks: all the trials of the tasks started with a jittered fixation of 4 to 6 s. In the AUT, the item was presented for 30 s during which the participants could press the button when they had an idea, after which they had 5 s to speak the most creative idea they had generated. In the RAT, the item was presented for maximally 30 s. Once the participants pressed the button, the item-presenting phase would be over, and they could speak the answer and press the button for the insight feeling. During item presentation, the time window (2 s) prior to pressing the button would be used for fMRI analysis. (B) Meditation: the FAM and OMM shared the same procedure. First, a 2-min audio was played to guide participants into a specific meditation state. Subsequently, the scanning began, and participants were instructed to maintain the meditation state until the end of the scan, which lasted approximately 13 to 14 min. Once the scanning and meditation started, every 45 s, a 30-s audio guidance was provided to prevent participants from becoming distracted and to encourage them to meditate as instructed. The time window of the 45 s would be used for fMRI analysis.

induced by speaking during creativity tasks, 6 motion parameters as additional regressors were included in the GLM analysis.

To address our 4 research aims, we statistically analyzed the data as follows at the second level. First, an ANOVA with 2 within-subject factors, condition (creativity vs meditation) and metacontrol (persistence vs flexibility), was analyzed at the whole-brain level. We primarily focused on the main effect of metacontrol (RAT and FAM vs AUT and OMM) in line with our research objectives. Correction for multiple comparisons in the f-contrasts was applied using family-wise error (FWE) correction ($P < 0.05$). Based on the results from the previous step, follow-up t-contrasts (voxel-wise FWE correction and Bonferroni correction for multiple t-contrasts, $P < 0.05$) were conducted to compare brain activations in the 2 creativity tasks (RAT vs AUT) and in the 2 meditation conditions (FAM vs OMM) at the whole-brain level through voxel-wise group-level analyses.

Second, to identify possible metacontrol-related brain activation overlap between creativity and meditation, we used the activation maps of the creativity contrasts as masks for the contrasts of meditation (RAT > AUT for FAM > OMM, AUT > RAT for OMM > FAM) where we conducted small volume correction (SVC) analysis with FWE correction ($P < 0.05$) to determine whether the meditation contrasts had significant activations within the areas activated in the contrasts of creativity.

Third, to examine the role of the brain areas modulated by dopamine, an ROI analysis was performed. The ROIs modulated by frontal dopamine were selected as DLPFC and ACC, because dopamine neurons mainly project to these 2 areas through the mesocortical pathway (Mark Williams and Goldman-Rakic 1998; Petrides 2005; Wise 2008; Ott and Nieder 2019). Throughout the nigrostriatal pathway, dopamine is transmitted to the caudate nuclei and putamen of the striatum (Hull and Rodríguez-Manzo 2009), which is a component of the BG and also the main ROIs that we selected associated with striatal dopamine. From a previous fMRI study on "stability and flexibility" (Armbruster et al. 2012), we selected the areas of DLPFC and ACC activated during the stability condition, as well as the BG (including putamen and caudate) activated during the flexibility condition as the ROIs. These ROIs were created using MarsBaR toolbox (Brett et al. 2022) to generate spherical masks with a radius of 7 mm, centered on the MNI coordinates of the peak voxels based on Armbruster et al. (2012). The selected ROIs and their corresponding MNI coordinates (x, y, z) were as follows: lDLPFC (−48, 4, 36), rDLPFC (40, 4, 30), lACC (−6, 16, 46), lBG (−20, 0, 14), and rBG (18, 2, 14). Following this, we integrated the ROIs to form 2 larger ROIs: PFC (including lDLPFC, rDLPFC, and lACC) and BG (including lBG and rBG). The brain activations in these 2 ROIs were compared between the states of persistence and flexibility during meditation and creativity.

Fourth and finally, the MCC model (Zhang et al. 2020) was evaluated by using the WFU PickAtlas toolbox (Maldjian et al. 2003, 2004) to extract the ROIs based on Brodmann's areas (BAs). The primary reason for using the BA template was that the brain areas from the MCC are summarized from various previous studies, and there have been no similar studies providing MNI coordinates. The following BA-based brain areas were selected as ROIs: the lDLPFC (BA9 and BA46; Hoshi 2006; Mylius et al. 2013), the lIFG (BA44; Ivancovsky et al. 2018), the rSTG (BA41; Vartanian et al. 2018), and the rPPC (BA40; Sohn et al. 2000). In this analysis, we compared the brain activations in these ROIs between RAT vs AUT, as well as between FAM vs OMM.

Results

Behavioral results

In the creativity session, the average number of RAT button presses for fMRI analysis was 25.80 (SD = 7.19) and the number of AUT button presses was 67.05 (SD = 14.48) during each task.

Neuroimaging results

Main effect of metacontrol by comparing activation during creativity tasks and meditation types at whole brain level.

F-test: main effect of metacontrol

The main effect of Metacontrol (F-contrast: RAT and FAM vs AUT and OMM) from the ANOVA is presented in Table 1, where the PFC and the BG (the areas of most interest) are both activated. The source of the main effect of metacontrol was further examined using follow-up t-contrasts, see the paragraphs below.

T-test: creativity—RAT vs AUT

The results of the follow-up t-contrasts between RAT and AUT are presented in Table 2 and Fig. 2. In the t-contrast of RAT > AUT, regions in PFC (inferior, middle, and superior frontal gyrus) and ACC, which are thought to be modulated by frontal dopamine, as well as BG (caudate and putamen), thought to be modulated by striatal dopamine, were activated. In addition, anterior insula and superior parietal lobule were also activated. In the t-contrast of AUT > RAT, regions related to the default mode network (DMN) were activated, such as angular gyrus, posterior cingulate cortex, and precuneus. Furthermore, lingual gyrus and middle cingulate cortex were also activated.

T-test: meditation—FAM vs OMM

The comparison between FAM and OMM did not yield significant results after performing whole-brain FWE-correction (both the contrasts of FAM > OMM and OMM > FAM). The whole-brain uncorrected effects are not presented and discussed, due to the overly high probability of false positives.

The overlap of brain activations between creativity and meditation

The activation maps obtained from the RAT > AUT and AUT > RAT comparisons were utilized as masks for conducting SVC analyses on the FAM > OMM and OMM > FAM comparisons, respectively. However, both the SVC analyses did not reveal any significant activations.

Analysis of dopamine-related ROIs

Again, paired-sample t-tests were performed to examine the differences in all the selected ROIs between RAT vs AUT and between FAM vs OMM, respectively.

In the comparison of the brain states related to creative thinking (see Fig. 3A), RAT showed higher activation than AUT in PFC (t [40] = 3.66, $P < 0.001$, $d = 0.57$), but yielded no significant difference in BG. However, RAT showed higher activation than AUT in all ROI masks (lDLPFC: t [40] = 7.34, $P < 0.001$, $d = 1.15$; rDLPFC: t [40] = 4.95, $P < 0.001$, $d = 0.77$; lACC: t [40] = 6.83, $P < 0.001$, $d = 1.07$; lBG: t [40] = 4.49, $P < 0.001$, $d = 0.70$; rBG: t [40] = 5.00, $P < 0.001$, $d = 0.78$).

In the comparison of the meditation states (see Fig. 3B), FAM showed higher activation than OMM in lACC (t [40] = 2.07, $P = 0.04$, $d = 0.32$) and rBG (t [40] = 2.17, $P = 0.04$, $d = 0.34$), while no other significant differences were found.

Testing the MCC model

Paired-sample t-test was performed to examine the differences in the selected ROIs of lDLPFC, lIFG, rSTG, and rPPC between RAT vs AUT, as well as between FAM vs OMM. The results are presented in Fig. 4. In the comparison between RAT vs AUT, RAT showed higher activations than AUT in the ROIs including lDLPFC (t [40] = 2.41, $P = 0.02$, $d = 0.38$), lIFG (t [40] = 3.03, $P = 0.004$, $d = 0.47$), and rPPC (t [40] = 2.48, $P = 0.02$, $d = 0.39$), while the difference was not significant in the rSTG (t [40] = 0.42, ns). In the comparison between FAM vs OMM, FAM showed higher activations than OMM in the lIFG (t [40] = 2.19, $P = 0.03$, $d = 0.34$) and the rPPC (t [40] = 2.06, $P = 0.046$, $d = 0.32$), while the differences were not significant in the lDLPFC (t [40] = 0.76, ns) and the rSTG (t [40] = 1.06, ns).

Discussion

The main aim of this study was to investigate the neural mechanisms underlying metacontrol states (persistence vs flexibility) induced by creativity tasks (RAT vs AUT) and meditation techniques (FAM vs OMM). Results from the 2 creativity tasks showed that brain areas modulated by both frontal and striatal dopamine were activated more by the task that was hypothesized to induce a strong bias of metacontrol toward persistence (RAT) than by the task thought to induce a flexibility bias (AUT). Whole-brain and ROI analyses indicated that the RAT strongly activated areas in the PFC (including inferior, middle, and superior frontal gyrus; DLPFC), ACC, and the BG (including caudate and putamen). The AUT, in turn, activated the DMN regions. Since it is widely recognized that the PFC is associated with executive function and goal-contingent top-down control (Funahashi and Andreau 2013; Friedman and Robbins 2021), its activation under conditions that are likely to rely on persistence meets the expectation from metacontrol theory (Hommel 2015; Hommel and Colzato 2017b; Hommel and Wiers 2017). Of higher theoretical diagnosticity is the activation of the BG, however. In previous studies on stability and flexibility (Armbruster et al. 2012) and neuroanatomic considerations regarding metacontrol (Cools 2016; Cools and D'Esposito 2011), striatal structures including the BG have commonly been thought to be associated with flexibility, rather than persistence. If so, our findings do not support a scenario of the interaction between frontal and striatal structures in which the activation of frontal structures promotes persistence, and the activation of striatal structures promotes flexibility. Rather, it seems that both kinds of structures continuously interact to negotiate the current degree of persistence versus flexibility. In other words,

Table 1. Brain activations of the main effect of metacontrol (RAT and FAM vs AUT and OMM) using an F-contrast (FWE-corrected at whole-brain level, $P < 0.05$).

		MNI coordinates					
Area	**L/R**	**X**	**Y**	**Z**	**K**	**F**	**P**
Lingual gyrus	R	8	−74	−2	2,475	136.93	<0.001
Lingual gyrus	L	−4	−78	−2		96.43	<0.001
Superior occipital gyrus	L	−18	−94	16		56.91	<0.001
Caudate	R	10	12	0	1,389	96.71	<0.001
Anterior insula	L	−28	28	2		70.4	<0.001
Caudate	L	−8	12	−2		66.69	<0.001
Inferior frontal gyrus	L	−50	10	24	704	71.13	<0.001
Inferior frontal gyrus	L	−48	30	18		57.08	<0.001
Superior parietal lobule	R	32	−54	54	803	61.44	<0.001
Superior parietal lobule	R	26	−60	64		55.33	<0.001
Superior parietal lobule	R	36	−42	44		51.06	<0.001
Precentral gyrus	L	−8	−24	56	261	60.71	<0.001
Precentral gyrus	R	4	−28	64		46.33	<0.001
Precentral gyrus	R	6	−24	54		34.29	0.006
Superior frontal gyrus	L	−22	2	50	256	58.14	<0.001
Superior frontal gyrus	L	−22	−6	60		52.53	<0.001
Superior parietal lobule	L	−24	−72	52	1,071	56.69	<0.001
Superior parietal lobule	L	−30	−56	64		54.76	<0.001
Superior parietal lobule	L	−40	−42	50		53.69	<0.001
Inferior occipital gyrus	R	32	−94	−4	36	43.2	<0.001
Superior frontal gyrus	R	12	26	60	15	41.64	<0.001
Angular gyrus	R	58	−50	32	46	41.21	<0.001
Superior frontal gyrus	R	26	0	56	58	41.02	<0.001
Precentral gyrus	L	−38	−6	48	10	34	0.007
Precentral gyrus	L	−50	−8	42	13	33.41	0.009
Inferior temporal gyrus	L	−48	−52	−16	11	33.16	0.01

Table 2. Brain activations for the contrasts of RAT > AUT and AUT > RAT. Voxel-wise FWE correction was applied at the whole-brain level ($P < 0.05$, FWE-corrected), followed by Bonferroni correction ($P < 0.05$) for multiple t-contrasts.

			MNI coordinates					
Contrast	**Area**	**L/R**	**X**	**Y**	**Z**	**K**	**T**	**P**
RAT > AUT	Caudate	R	10	10	0	2,203	11.89	<0.001
	Putamen	L	−20	12	−8		10.53	<0.001
	Caudate	L	−10	8	4		9.78	<0.001
	Precentral gyrus	L	−42	4	32	1,137	9.79	<0.001
	Inferior frontal gyrus	L	−48	36	14		9.39	<0.001
	Middle frontal gyrus	L	−42	26	22		8.56	<0.001
	Precentral gyrus	R	8	−26	56	1,543	9.45	<0.001
	Middle frontal gyrus	R	28	0	58		9	<0.001
	Precentral gyrus	R	26	−10	60		8.04	<0.001
	Superior parietal lobule	L	−18	−64	54	635	8.39	<0.001
	Superior parietal lobule	R	28	−52	54	868	8.08	<0.001
	Superior frontal gyrus	L	−22	−4	62	319	7.84	<0.001
	Middle frontal gyrus	L	−24	12	48		7.39	<0.001
	Middle frontal gyrus	L	−24	0	50		7.08	<0.001
	Anterior cingulate gyrus	L	−10	28	26	25	7.02	0.002
	Anterior cingulate gyrus	R	10	28	26	15	6.46	0.006
	Anterior insula	R	34	24	−4	49	6.41	0.006
AUT > RAT	Lingual gyrus	R	8	−74	−2	2,844	13.39	<0.001
	Lingual gyrus	R	22	−62	−8		9.47	<0.001
	Angular gyrus	R	56	−54	26	185	8.54	<0.001
	Angular gyrus	L	−56	−58	32	43	7.64	<0.001
	Posterior cingulate gyrus	L	0	−42	24	46	6.97	0.002
	Precuneus	R	2	−70	38	94	6.74	0.002

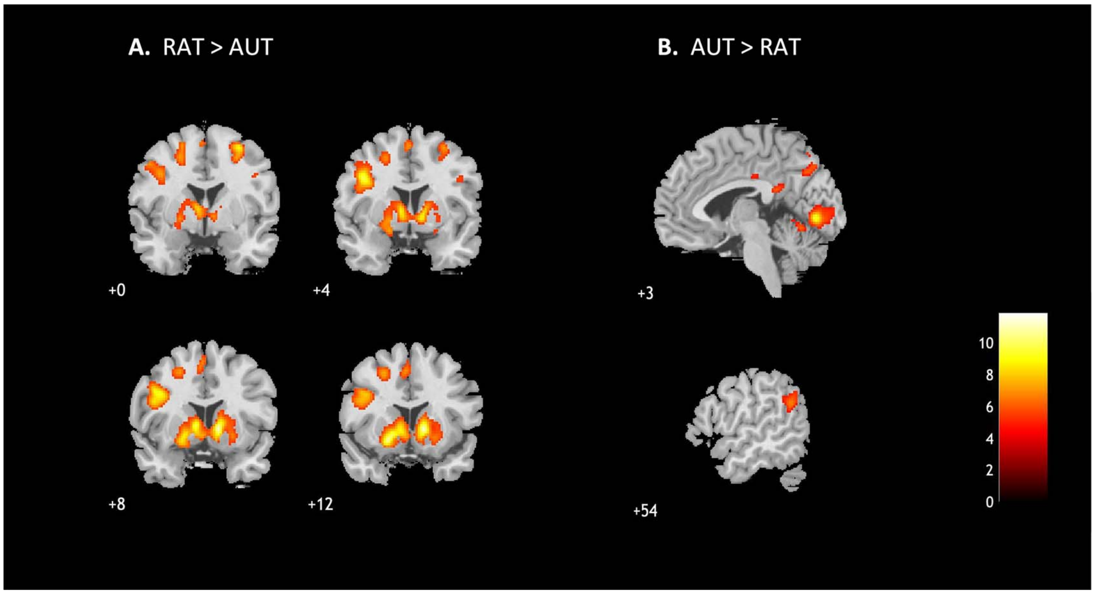

Fig. 2. Brain activations revealed by the t-contrasts of A) RAT > AUT and B) AUT > RAT. Voxel-wise FWE correction was applied at the whole-brain level ($P < 0.05$, FWE-corrected), followed by Bonferroni correction ($P < 0.05$) for multiple t-contrasts.

persistence and flexibility do not reflect the isolated activation of a corresponding neural structure but, rather, emerge from the continuous interactions between frontal and striatal components of a distributed but well-integrated metacontrol system. This integrated system may operate along the lines of Durstewitz and Seamans (2008), who have claimed that D1 and D2 receptors in both kinds of structures are biasing metacontrol toward persistence or flexibility, respectively. But other scenarios are possible. For instance, the interaction between frontal and striatal structures might be steered by tuning the productivity of the VTA and the substantia nigra, which are fueling the frontal and the striatal dopaminergic system. Another, not mutually exclusive possibility is that the balance between the frontal and the striatal dopaminergic pathway is moderated by serotonergic input (Prochazkova et al. 2018), which has been demonstrated to have that ability (De Deurwaerdère et al. 2021). In addition, the process of updating information from long-term memory to working memory in RAT requires some "top-down flexibility" which is not the same as the "metacontrol flexibility" but it has been shown to recruit the striatal structures (Frank et al. 2001; Nir-Cohen et al. 2020).

Our findings align well with the triple network model which provides a unifying framework for understanding how large-scale networks coordinate during cognitive tasks (Menon 2011; Das and Menon 2024), particularly in terms of the interplay between the frontoparietal network (FPN, corresponding to PFC activation in RAT), the DMN (activated in AUT), and potentially the salience network (SN, given the role of ACC in conflict monitoring). In the present study, all 3 areas that RAT activated more strongly than AUT (PFC, ACC, and BG) are commonly assumed to create selectivity in attention and action control: the PFC is key in providing goal-contingent top-down support for goal-related representations (Miller and Cohen 2001), the ACC is assumed to be a crucial hub in monitoring internal conflict and signaling the need for stronger goal-support from the PFC (Botvinick et al. 2004), and the BG are considered to bias stimulus and response selection according to expected rewards (Johnston et al. 2007; Yehene et al. 2008; Richter and Yeung 2015). Accordingly, the joint activation of these 3 components, aligning with the FPN and SN of the triple network model (Menon and Uddin 2010; Das and Menon 2020), is likely to reflect the degree of selectivity of information processing, which according to metacontrol theory corresponds to a strong persistence bias (Hommel and Colzato 2017b). The AUT, in turn, activated areas commonly associated with the DMN in the triple network model (Das et al. 2022; Menon 2023), including the angular gyrus, posterior cingulate cortex, and precuneus. The DMN, a task-negative or resting-state network, is known to be negatively correlated with executive control function and cognitive control (Raichle 2015), and positively associated with cognitive flexibility (Vatansever et al. 2016). Hence, the DMN is activated by the absence of concrete task constraints and in the absence of the need to be selective with respect to stimuli or responses. This is exactly the state that metacontrol envisions for strong biases toward flexibility, which means that our AUT findings are fully in line with our theoretical expectations. Notably, the triple network model posits that dynamic SN–FPN–DMN interactions underlie cognitive shifts (Menon 2011; Das and Menon 2024), and our findings extend this to metacontrol states, suggesting that persistence/flexibility biases may arise from SN-mediated switching between FPN and DMN dominance.

Much less in line with our theoretical expectations are the findings from the meditation parts of the sessions. In the ROI analysis of FAM, the lACC and the rBG were found to be activated, which is in line with the findings for the RAT and with the assumption that both FAM and RAT are associated with comparable metacontrol (ie persistence) states. However, the remaining findings failed to show a clear difference between the 2 meditation modes, which is in line with previous observations of Manna et al. (2010). This lack of significant differences also rendered the SVC analysis for the overlap between the contrasts of RAT vs AUT with the contrasts of FAM vs OMM uninformative. While our data do not provide any hint as to why we failed to find any differences, it is possible that the different structure of creativity tasks on the one hand and meditation on the other are responsible. In creativity tasks, participants are presented with particular stimuli that they need to process in particular ways. Even though we assume that this requires or promotes the establishment of a particular metacontrol bias,

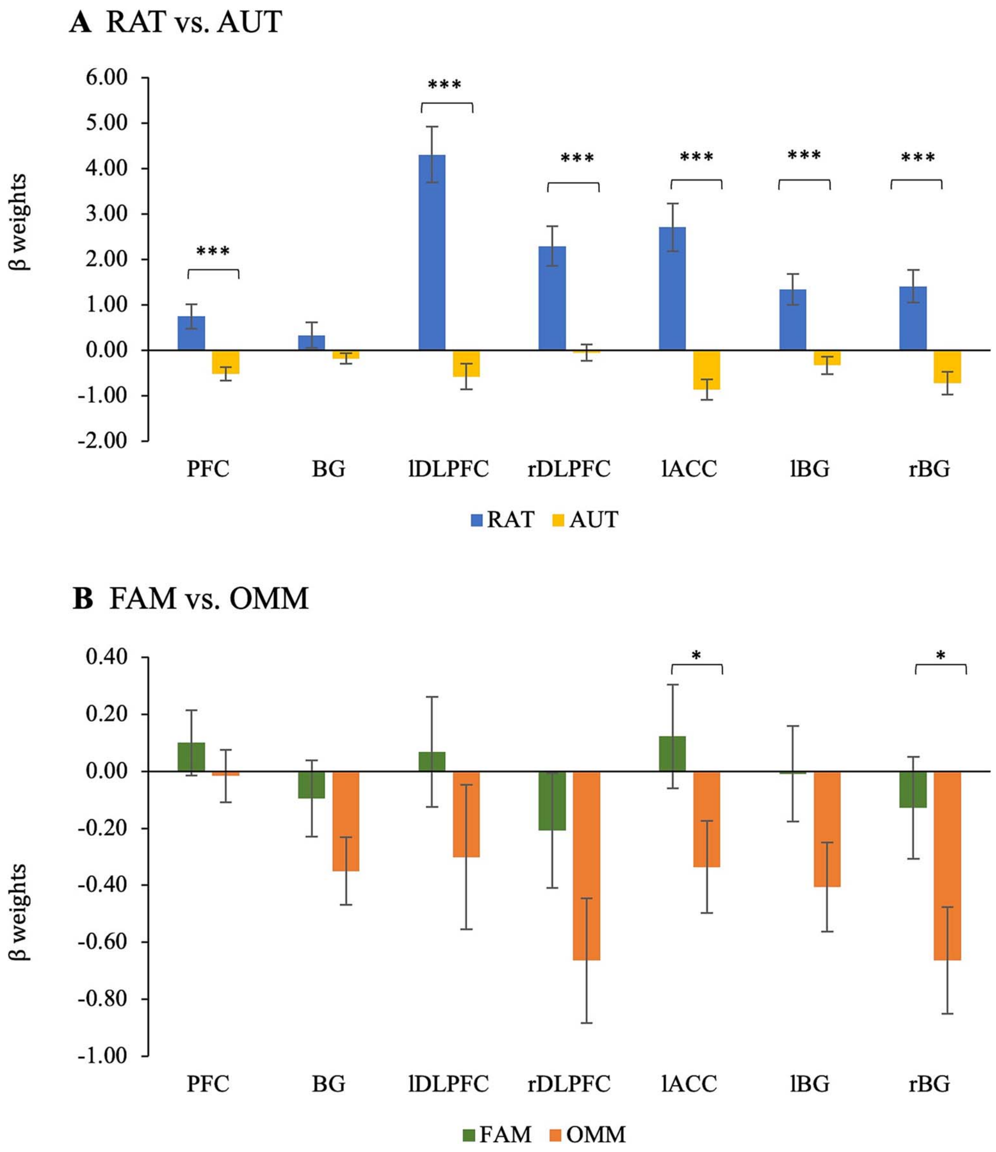

Fig. 3. β weights extracted from the masks of PFC, BG, lDLPFC, rDLPFC, lACC, lBG, and rBG in the comparisons between (A) RAT vs AUT and (B) FAM vs OMM. Vertical bars indicate ±1 standard error of the mean. One asterisk (*) indicates that the difference is significant at the $P < 0.05$ level; 3 asterisks (***) indicate that the difference is significant at the $P < 0.001$ level.

the activation patterns we obtained might not so much tap into the mechanisms underlying this establishment but, rather, reflect how the established state changes information processing. Meditation, in turn, may be taken to mainly consist in the establishment of a state, which does not necessarily require any further processing after it has been successfully established. Had we also presented the meditating individuals with a particular task, we may thus have obtained activation differences indicative of the underlying metacontrol bias. For example, in a recent EEG study, participants were required to perform FAM/OMM first and then complete the flanker task. During this task, brain activity was studied after different meditation sessions, revealing significant differences (Lin et al. 2024). Indeed, we obtained some evidence for the activation of persistence-related structures in the FAM condition. One may speculate that this is because in this condition, participants are required to concentrate on their breath and ignore other distractions. It could be this mini-task that induced activation of the ACC, which would be needed to detect distractions, and the BG, which could be functional in inhibiting these distractions, so to switch the focus back to the breath. If so, it is possible that not all meditation processes are sufficiently "active" to generate measurable differences that can be picked up by fMRI. In addition, in a recent review, Laukkonen and Slagter (2021) noted that even though the participants distinguish between FAM and OMM, they recognize it is a continuum and, in practice, there is a lot of back and forth. For instance, during OMM, participants may utilize the breath as an anchor to focus on the present moment, which could involve FAM. This fluctuation might also potentially account for the lack of significant differences observed between FAM and OMM at the whole brain level. Accordingly, future studies should not just require participants to engage in meditation but also confront them with some kind of task that is likely to generate recognizable BOLD activity.

As explained in the introduction, the fourth aim of this study was to test the MCC model suggested by Zhang et al. (2020). For this purpose, we conducted ROI analyses for both creativity tasks (RAT vs AUT) and meditation types (FAM vs OMM) on the theoretically implicated brain areas (lDLPFC, lIFG, and rSTG/PPC). The

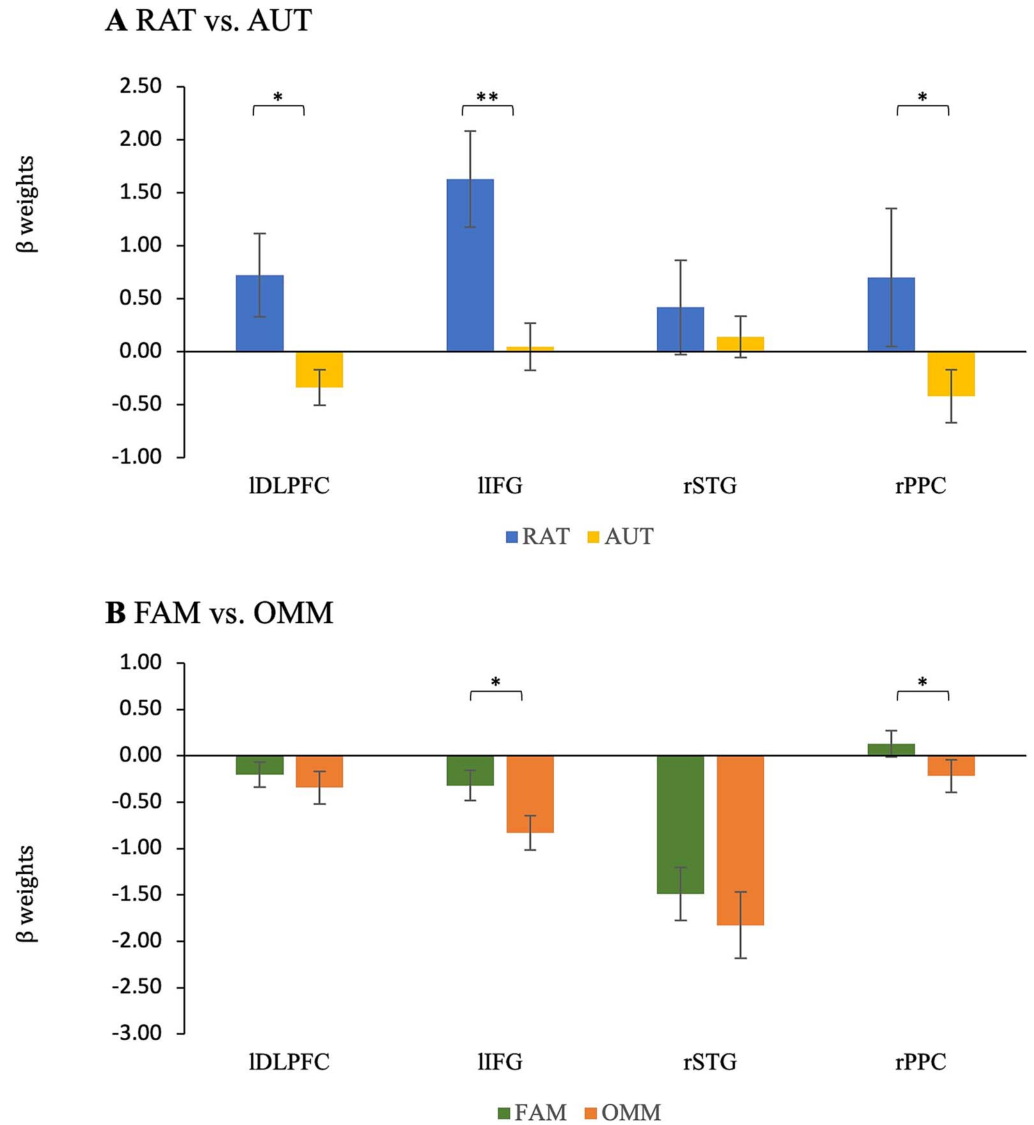

Fig. 4. β weights extracted from the masks of lDLPFC, lIFG, rSTG, and rPPC in the comparisons (A) between RAT vs AUT as well as (B) between FAM vs OMM. Vertical bars indicate ±1 standard error of the mean. One asterisk (*) indicates that the difference is significant at the $P < 0.05$ level; 2 asterisks (**) indicate that the difference is significant at the $P < 0.01$ level.

MCC predicts 2 distinct activation patterns to reflect metacontrol biases toward persistence (lIFG−, lDLPFC+, and rSTG/PPC+) and flexibility (lIFG+, lDLPFC−, rSTG/PPC−), respectively—where + means more, and − means less activation than in the task or mediation type associated with the opposite metacontrol bias. The degree to which our findings fit with the model varies with the respective brain structure. For PPC, the results are exactly as expected: rPPC was more activated during RAT than during AUT, and during FAM than during OMM. For lDLPFC, the predicted pattern was confirmed for the creativity tasks, but not for meditation type. However, given that meditation was a less potent factor in this study anyway, we do not consider this pattern as inconsistent with our model. The same holds for rSTG, which did not produce any significant differences. However, results for lIFG were exactly opposite as predicted—which calls for an explanation.

The reasons for why MCC predicted less lIFG activation under persistence than under flexibility were previous studies demonstrating lIFG activation during tasks involving divergent thinking, which is commonly associated with flexibility (Zhang et al. 2020). However, it is important to note that the neural contrasts in those studies involved comparisons like divergent thinking vs control tasks or baseline (Runco and Yoruk 2014), rather than comparisons between RAT and AUT. This suggests that the role of lIFG in the MCC model might be specific for divergent thinking tasks (compared with control tasks), rather than pointing to a differential role of the lIFG in flexibility versus persistence.

Another possible explanation may derive from the fact that the MCC model has considered the possibility that it is not the absolute activation level of the left IFG that determines the metacontrol states but, rather, the balance between the left and right IFG. In a study that employed transcranial direct current stimulation (tDCS) to modulate the balance between the left and right IFG (Mayseless and Shamay-Tsoory 2015), it was discovered that increased cortical excitability in the left IFG through anodal tDCS, combined with reduced cortical excitability the right IFG from cathodal tDCS, can enhance performance in divergent thinking tasks. This suggests that a relatively deactivated left IFG can boost divergent thinking or flexibility, which actually aligns with the current finding for lIFG.

In any case, the role of lIFG in creativity tasks, meditation, and metacontrol in general needs further exploration in future studies, which may call for a revision of the MCC model. One reason why such a revision could be necessary is the fact that the lIFG is a part of the PFC, which is modulated by the frontal dopaminergic pathway and thus associated with persistence. In particular, the lIFG is critical for response inhibition (Swick et al. 2008) and semantic selection (Grindrod et al. 2008), which are likely to play an important role in persistence-heavy tasks.

Limitations

Although creativity tasks and meditation techniques have been shown to induce metacontrol states, they are not direct measurements of these states, and their brain activations might also involve other cognitive functions unrelated to metacontrol. Furthermore, due to our inability to record the verbal responses during the AUT and RAT tasks, we were unable to conduct detailed behavioral analysis to gain a deeper understanding of the metacontrol states induced by these tasks. Moreover, while we used dopamine-related theorizing and the MCC theory for a goal-related, focused analysis of metacontrol, this approach may overlook some metacontrol-related areas beyond this scope. In validating the relevant brain regions for the dopamine theory and the MCC model, we did not apply multiple comparison corrections because we had very clear and specific research hypotheses. Compared to purely exploratory analyses, hypothesis-driven confirmatory analyses typically have a lower risk of false positives, making the use of uncorrected t-tests a relatively reasonable approach. However, it is also important to note that, even in confirmatory analyses, more stringent multiple comparison corrections could still benefit the study by enhancing the credibility of the findings. However, in our research, the brain activity differences between the 2 meditation conditions, FAM and OMM, were relatively small as detected by the fMRI scan. Therefore, applying stricter corrections might potentially obscure some findings that could be valuable for further research and exploration.

Conclusion

Our findings suggest that metacontrol persistence is associated with activation in the PFC, ACC, and the BG, while metacontrol flexibility is linked to activation of the DMN. However, this pattern was much clearer in the analysis of brain activation related to the 2 creativity tasks than in the brain activation associated with the 2 types of meditation. Meditation may be a good method to induce particular metacontrol states, but to assess the impact of these states on information processing, it would need to be associated with a particular task. With regard to the MCC model, we found supporting evidence with regard to predictions related to PPC and, partially, PFC, but no significant findings were observed for STG and the findings for lIFG where exactly opposite of what was predicted. More research will be necessary to determine whether it is absolute or relative activation of lIFG that matters for metacontrol, and whether lIFG is really part of the flexibility network, as suggested by the MCC model, or rather part of the persistence network.

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Author contributions

Weitao Zhang (Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Writing—original draft, Writing—review & editing), Zsuzsika Sjoerds (Conceptualization, Methodology, Project administration, Supervision, Writing—review & editing), Rebecca Mourits (Methodology, Writing—review & editing), and Bernhard Hommel (Conceptualization, Funding acquisition, Supervision, Writing—original draft, Writing—review & editing).

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Conflict of interest statement. The authors declare no conflicts of interest.

Data availability

Materials, data, and analysis script will be made available upon request to the lead author.

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