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Neurophysiological indicators of internal attention: An fMRI–eye-tracking coregistration study

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Data Availability

Materials, data and analysis scripts are accessible via the Open Science Framework (OSF, <https://osf.io/74vnq/>) and OpenNeuro (<https://doi.org/10.18112/openneuro.ds003176.v1.0.1>).

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Conflict of interest disclosure

The authors declare no conflict of interest.

Ethics approval statement

This study was approved by the local ethics committee.

Abstract

Many goal-directed, as well as spontaneous everyday activities (e.g., planning, mind-wandering), rely on an internal focus of attention. In this fMRI–eye-tracking coregistration study, we investigated brain mechanisms and eye behavior related to internally versus externally directed cognition. Building on an established paradigm, we manipulated internal attention demands within tasks utilizing conditional stimulus masking. Internally directed cognition involved bilateral activation of the lingual gyrus and inferior parietal lobe areas as well as wide-spread deactivation of visual networks. Moreover, internally directed cognition was related to greater pupil diameter, pupil diameter variance, blink duration, fixation disparity variance, and smaller amounts of microsaccades. FMRI–eye-tracking covariation analyses further revealed that larger pupil diameter was related to increased activation of basal ganglia and lingual gyrus. It can be concluded that internally and externally directed cognition are characterized by distinct neurophysiological signatures. The observed neurophysiological differences indicate that internally directed cognition is associated with reduced processing of task-irrelevant information and increased mental load. These findings shed further light on the interplay between neural and perceptual mechanisms contributing to an internal focus of attention.

Keywords

fMRI; eye tracking; internal attention; imagination; divergent thinking

Introduction

We spend an essential part of our days engaged in thoughts that are unrelated to our immediate sensory environment (Kane et al., 2007; Killingsworth & Gilbert, 2010; Song & Wang, 2012). These internally directed cognitions can be either goal-directed, such as in deliberate planning (Spreng et al., 2010), imagination (Benedek, 2018; Zabelina, 2018) and problem-solving (Jung-Beeman et al., 2004; Kounios & Beeman, 2009; Salvi et al., 2015), or spontaneous, such as during mind wandering (Smallwood & Schooler, 2006). As we are limited in our information processing ability (Desimone & Duncan, 1995), internally directed cognition (IDC) and externally directed cognition (EDC) are considered competing states (Chun et al., 2011), sharing a common pool of cognitive resources (Verschooren et al., 2019). Yet, IDC and EDC rely on different neural mechanisms (Dixon et al., 2014) and thus are characterized by distinct neurophysiological signatures as evidenced by research using fMRI (Benedek et al., 2016; Dixon et al., 2018; Kucyi et al., 2017; Margulies et al., 2016; C. Murphy et al., 2018, 2019), EEG (Benedek et al., 2011, 2014; Ceh et al., 2020; Cooper et al., 2003; Ray & Cole, 1985; Vortmann et al., 2019) and eye-tracking (Annerer-Walcher et al., 2018; Benedek et al., 2017; Salvi et al., 2015; Smallwood et al., 2011; Walcher et al., 2017). So far, however, available evidence comes mostly from work that focused on one neurophysiological parameter at a time, which limits our insight on how these parameters relate to each other. Therefore, in the present work we employed fMRI–eye-tracking coregistration to measure brain activation and eye behavior concurrently during an established paradigm that manipulates internal/external attention demands (Benedek et al., 2011, 2016, 2017; Ceh et al., 2020). This study pursues two main goals: First, we tested the robustness of previously reported attention effects on brain activation (and eye behavior), while controlling brain activation effects for attention-related fluctuations in eye behavior. Second, we examined the temporal covariation of brain activation and several oculometric parameters to investigate the neural correlates of attention-related eye behavior changes. Together, these analyses address the question of how neural and perceptual mechanisms interact to support an internal focus of attention.

Neural correlates of internal cognition

While neuroscience has traditionally focused on externally directed cognition, recent research has been increasingly interested in the investigation of internally directed cognition. EDC and IDC are thought to rely on distinct as well as common brain regions (Dixon et al., 2014; Verschooren et al., 2019). EDC is strongly associated with the dorsal attention network (DAN; Corbetta & Shulman, 2002), as the frontal eye fields and intraparietal sulcus are involved in the top-down regulation of external attention. In contrast, IDC has been associated with regions related to the default mode network (DMN; Raichle et al., 2001), including the medial prefrontal cortex, inferior parietal cortex, the posterior cingulate cortex and the medial temporal lobe (Andrews-Hanna, Smallwood, et al., 2014;

Thomas Yeo et al., 2011). Formerly being considered a task-negative network (Fox et al., 2005), recent investigations by means of functional MRI point towards an active role of the DMN in support of internally directed cognition (Andrews-Hanna, Saxe, et al., 2014; Andrews-Hanna, Smallwood, et al., 2014; Axelrod et al., 2017; Benedek et al., 2016; Buckner et al., 2008; Dixon et al., 2018; Konishi et al., 2015; Margulies et al., 2016; C. Murphy et al., 2018, 2019; Poerio et al., 2017; Smallwood et al., 2013; Spreng et al., 2010, 2013, 2016; Stawarczyk & D'Argembeau, 2015). The DMN consists of distinct subsystems (Andrews-Hanna, Smallwood, et al., 2014), which are associated with aspects of self-generated thought that get integrated in the posterior DMN core (Smallwood et al., 2016). Within the DMN, increased functional coupling between the medial-temporal and dorsal-medial subsystem was associated with poor performance on external tasks (Poerio et al., 2017).

Recent studies demonstrate that the DMN is a transmodal region situated at one extreme end of a principal gradient, exhibiting maximum geodesic distance from perceptual and motor areas (Margulies et al., 2016). The spatial distance is assumed to correspond to a functional distance, as an internal focus involves the decoupling of attention from external information (i.e. perceptual decoupling; Smallwood, Brown, et al., 2011). Spanning from uni- to transmodal cortex, this gradient provides a framework to locate cognitive activity on a continuum between two distinct cognitive modes: Activity in unimodal areas is supportive of sensory-based cognition (EDC) and transmodal activity is important for memory-based cognition (IDC; C. Murphy et al., 2019). Indeed, shifts in cognitive demands from perception to memory were observed to correspond to a shift of neural activity from uni- to transmodal regions (C. Murphy et al., 2018). It is proposed that the DMN might contribute to different kinds of thought due to its high flexibility of cortical integration, being able to integrate external information, too (Poerio et al., 2017). This assumption is strengthened by the finding that the DMN and DAN, although associated with IDC and EDC, respectively, are not fundamentally antagonistic (Dixon et al., 2017), but might instead cooperate at times (e.g., when a task requires a combination of internal and external processes; see Dixon et al., 2014). Another important aspect in the differentiation between IDC and EDC states by means of fMRI is the involvement of the frontoparietal control network, whose two distinct subsystems have been identified to support a) the regulation of visuospatial attention via coupling to DAN regions and b) introspective processes via coupling to DMN regions (Dixon et al., 2018), for example regions involved in the self-generative process of creative cognition (Beaty et al., 2014, 2016, 2017, 2018), potentially reflecting the interplay of generative and evaluative processes.

A challenge for studies that compare brain activation between IDC and EDC activities is the unambiguous attribution of activation differences to increased internal attention in contrast to increased self-generated thought. In an attempt to clarify the role of the DMN with respect to attention-related processes, we conducted a study where we manipulated the level of internal

attention demands within two tasks (Benedek et al., 2016). In the convergent thinking task, participants were required to find anagram solutions, while in the divergent thinking task, they needed to generate creative four-word sentences, making for higher levels of self-generated thought. Internal attention demands were manipulated using conditional stimulus masking: In half of the trials, the stimulus was masked after 0.5s, thus increasing the internal attention demands by enforcing the completion of the task in the mind's eye. Indeed, divergent thinking was related to higher activation in DMN regions, indicating that the DMN is responding to the level of self-generated thought of a task. When contrasting the internal task with a more external one (no stimulus masking), IDC was related to increased activation in the right anterior inferior parietal lobe (aIPL), the left cuneus and in bilateral parts of the lingual gyrus, areas associated with visual imagery (Kosslyn et al., 2001), as well as to strong decreases of activation in visual attention networks and the DAN. Since the aIPL is part of the frontoparietal control network (Andrews-Hanna, Smallwood, et al., 2014), IDC was considered to engage a core FPCN region which has previously been associated with internal cognition (Spreng et al., 2010). Importantly, the right aIPL showed increased functional coupling with visual areas during internal attention, while these regions exhibited decreased activity. This suggests that the aIPL might exert top-down control over occipital regions to suppress early visual information processing, which is in line with assumptions that fronto-parietal areas play a crucial role in mediating sustained attention (Sarter et al., 2001). Taken together, the observed differences between internal and external cognition can either be attributed to mechanisms related to sustaining an internal attention focus or to the specific type of internal/external cognitive activity (Benedek, 2018).

Eye-tracking correlates of internal cognition

Differences between internal and external cognition are also found at the level of eye behavior. These differences can be attributed to perceptual decoupling and internal coupling mechanisms. For example, during demanding internal tasks, the gaze is commonly averted from irrelevant external stimuli to save cognitive resources for task performance (Abeles & Yuval-Greenberg, 2017; Doherty-Sneddon et al., 2002; Doherty-Sneddon & Phelps, 2005). Besides looking away, closing one's eyes further contributes to reduced visual inflow. Frequent eye closure during IDC tasks has been shown to benefit performance (Ritter et al., 2018; Salvi et al., 2015). Microsaccadic activity, which has been proposed as a mechanism to counteract perceptual fading (Martinez-Conde et al., 2006, 2013), decreases during IDC (Gao et al., 2015; Krueger et al., 2019). Similarly, vergence movements need to be considered: They refer to the rotation of the eyes in opposite direction to obtain single binocular vision. Eye vergence is linked to shifts in visuospatial attention (Solé Puig, Pérez Zapata, et al., 2013; Solé Puig, Puigcerver, et al., 2013) and especially the degree of disparity of the eyes is considered a promising indicator of internal attentional focus (Huang et al., 2019). Both, reduced microsaccadic activity and increasing disparity are assumed to

represent reduced adaptation of eye behavior to needs of visual processing (Annerer-Walcher et al., 2018; McCamy et al., 2012). When engaging in internal cognition, our eyes do not only decouple from external stimulation, but were found to couple to internal events. This is evidenced by changes in pupil diameter (PD) in response to imagined luminance changes (Laeng & Sulutvedt, 2014), as well as by PD and vergence movement changes due to variations of imagined object size and distance (Sulutvedt et al., 2018).

Studies comparing eye behavior between EDC and IDC observed differences in a large range of oculometric parameters (Annerer-Walcher et al., 2018; Benedek et al., 2017; Ceh et al., 2020; Walcher et al., 2017). Some of these parameters showed a very uniform pattern, even across different tasks (e.g. PD, blink behavior), thus appearing to be general indicators of attentional focus. Other eye parameters also differentiated IDC and EDC, but showed strong variability across different tasks (e.g., saccadic activity). Bearing this in mind, we conducted an eye-tracking study (Benedek et al., 2017) that manipulated attentional demands within tasks in order to minimize the role of task effects, using the same design as in the fMRI study by Benedek et al. (2016). We found differences between IDC and EDC in various eye parameters. Specifically, the internal attention condition was associated with fewer, but longer fixations, greater blink duration, fewer saccades and microsaccades, smaller saccade amplitude, greater PD and PD variance as well as smaller AoEV and greater AoEV variance.

The relationship between eye behavior and brain activation in the context of internal cognition

Another important question is how neural and oculomotor processes correspond during EDC/IDC. A few studies have begun to address this question by combining neurophysiological methods and eye tracking in the investigation of internal/external attention. In a recent EEG-eye tracking coregistration study (Ceh et al., 2020) that employed the same paradigm as used in Benedek et al. (2017), we replicated the finding that IDC is associated with relatively higher posterior alpha power (cf. Benedek et al., 2011, 2014; Benedek & Fink, 2014), and, amongst others, with higher PD. Importantly, temporal covariation analyses demonstrated that PD and posterior EEG alpha power were also correlated across time during rest, suggesting a relationship between these neurophysiological indicators of IDC. Since EEG alpha is linked to top-down-inhibition of task-irrelevant brain areas (Benedek, 2018; Fu et al., 2001; Händel et al., 2011; Klimesch, 2012; Rihs et al., 2007) and PD is linked to memory load (Beatty, 1982; Kahneman & Beatty, 1966), such inhibitory processes might be realized by basal ganglia (BG) mediated gating dynamics to aid sustained IDC (Chatham & Badre, 2015): When relevant external information is available, a BG-mediated gate opens to allow for working-memory updating. Otherwise, the gate is closed to support complex forms of sensory-independent cognition. Generally, PD, an indicator associated with the locus-

coeruleus–noradrenergic system (Laeng et al., 2012), seems to be a promising indicator for this study, as it is also linked to the DAN (Alnæs et al., 2014), which is associated with EDC and thus sensitive to changes of attentional focus. In their study, Alnæs et al. used PD to index attentional effort in a multiple object tracking task that manipulated levels of visual attention. They found increases of PD with increasing numbers of objects to be tracked. In a follow-up session, they employed the same task in an fMRI setting, where PD changes correlated with FEF and superior parietal lobe (SPL) activity, regions within the DAN. The study also found a correlation between PD and locus coeruleus (LC) activity, as also reported in other work (P. R. Murphy et al., 2014). Since the LC is implicated in attentional dynamics (Aston-Jones et al., 1999), the covariation further strengthens the notion that pupil diameter is indicative of attentional focus.

Similarly, the investigation of blink activity has yielded promising results: While watching videos, spontaneous blinks led to momentarily decreases in DAN activity but to increased activation in DMN regions (Nakano et al., 2013). Interestingly, blackening the screen did not lead to such changes, suggesting that blinks are actively involved in attentional disengagement from external stimulation. In an MEG study, spontaneous blinks were also related to increased precuneus activity (C. C. Liu et al., 2017), an area within the DMN (Fransson & Marrelec, 2008) that is especially important in the context of spontaneous IDC (Dixon et al., 2014). Importantly, blinks are associated with active top-down-modulation of visual processing, as evidenced by suppressed activity in visual cortex (Bristow et al., 2005). Therefore, we assume that similar (de)activation patterns can be observed during goal-directed tasks.

Regarding saccadic activity, both microsaccades and small visually-guided saccades have been linked to BOLD signal changes in areas of the visual cortex (Martinez-Conde et al., 2013; Tse et al., 2010). Saccade frequency, but not saccade amplitude has been associated with BOLD signal changes in FEF, supplementary eye fields, parietal and striate cortex, as well as motion-sensitive areas of the parieto-occipital cortex (Kimmig et al., 2001). Taken together, attention-related brain processes can refer to sensory gating at the neural level as well as at the oculomotor level via control of relevant ocular mechanisms.

Aims of this study

So far, it has been established that neurophysiological indicators (e.g., fMRI, EEG) and eye behavior are sensitive to attentional focus; however, little is known about their mutual relationship. We have taken a first step in investigating the connection between EEG alpha activity and eye behavior in a previous study (Ceh et al., 2020). In the present study, using the same paradigm, we examined how brain activity as measured by functional MRI and eye behavior relate to each other in the context of IDC vs. EDC: First, we tested whether brain activation patterns and eye behavior

differences occur between states of EDC vs. IDC by replicating a well-established manipulation of internal attentional demands. Specifically, we expected that IDC compared to EDC is associated with stronger brain activation in areas of the aIPL, lingual gyrus and cuneus as well as decreased brain activation in visual networks including the occipital gyrus and SPL (Benedek et al., 2016). Additionally, we expected increases of PD, saccade amplitude, fixation duration and fixation disparity variance, as well as decreases of saccade and microsaccade count during IDC (Benedek et al., 2017; Ceh et al., 2020). Second, we investigated which brain areas activate as a function of eye behavior changes over time. Together, these findings are expected to shed further light on neurophysiological dynamics underlying sustained internally directed cognition.

Methods

Materials, data and analysis scripts are accessible via the Open Science Framework (OSF, <https://osf.io/74vnq/>) and OpenNeuro (<https://doi.org/10.18112/openneuro.ds003176.v1.0.1>).

Participants

34 subjects participated in this study. They gave written informed consent prior to the start of the MR-session and completed a questionnaire to verify MRI safety. Four subjects were excluded, either because of missing eye-tracking data ($n = 3$; e.g. excessive blinks) or due to technical problems ($n = 1$). The final sample thus consisted of 30 participants (20 female), with an average age of 22.7 years ($SD = 3.50$). Participants were right-handed, had normal ($n = 23$) or corrected-to-normal (soft contact lenses; $n = 7$) vision and reported no history of ocular, psychiatric or neurological conditions. They were financially compensated or received partial course credit for participation. The local ethics committee had approved the procedure of this study.

Experimental Design, Tasks & Procedure

The experimental tasks and design were closely adapted from previous research (Benedek et al., 2011, 2016, 2017; Ceh et al., 2020). Following a 3x2-within-subjects-design, participants performed a convergent thinking task (anagram generation; Conv), a divergent thinking task (sentence generation; Div), and a simple memory task (i.e. baseline condition; BL) each under low and high internal attention demands. In each trial, a meaningful German four-letter-word was presented. In the Conv task, participants were required to rearrange the four letters to build another meaningful four-letter word (e.g., “ROBE” is transformed to “BORE”). In the Div task, participants were asked to generate a meaningful, original four-word-sentence, using each letter as an initial letter of one word (e.g., “ROBE” is transformed to “Robert observes eye behavior”); each letter had to be used once, but not necessarily in the original order. This sentence generation task makes for higher levels of self-generated thought as it asks to create an individual solution within a large solution space, whereas the anagram task only asks to find predefined correct solutions within a very

limited solution space. Both tasks generally benefit from externally directed attention, but can also be performed reasonably well without continuous access to the stimulus (see previous studies from our lab). In the BL task, participants were asked to memorize the stimulus word. This undemanding task was used as null trials to form a baseline for subsequent analyses.

The sequence of a trial is outlined in Figure 1. Each trial started with a temporally variable fixation cross, ranging from three to five seconds, followed by the stimulus word presented in white capital letters on the center of a black screen (Arial, size 40). In half of all trials (IDC condition), the stimulus word was masked ("XXXX") after a brief initial encoding period (0.5s), enforcing higher internal attention demands in the subsequent task performance, which lasted for 18.5 s. In the other half of trials (EDC condition), the stimulus word remained visible for the entire trial. When the stimulus word (question mark in the baseline condition) reappeared in green color, participants were instructed to vocalize their solutions, which were recorded by means of an MRI-compatible noise cancelling microphone (FOMRI-III; Optoacoustics, Mazor, Israel). In case participants came up with solutions prior to the vocalization phase, we instructed them to keep thinking of further (Conv task) or more original solutions (Div task) to ensure continuous on-task effort. An item was treated as correctly solved, when at least one anagram solution was found (Conv task), a grammatically correct sentence using all four letters had been produced (Div task), or the stimulus was remembered correctly (BL task).

The experiment included a total of 48 trials (18 Conv, 18 Div & 12 BL), half of which were masked. Trials were grouped into 8 blocks of 6 trials, which were organized in an ABCBACAB or BACABCBA fashion. Each block started with an initial task cue, indicating, which task was to be performed. It was randomly determined within each block, which three of the six trials were masked. Trials were separated by an inter-trial-interval (black screen; 1.5 s). The trial order was identical for each subject, meaning that the same sequence of trials was used in different tasks for different participants.

Before entering the scanner, participants received a task introduction, explaining the tasks and conditions and using six practice trials. In the scanner, eye positions were calibrated and validated before performing a structural scan followed by the acquisition of fMRI data during task performance (~ 30 min). After the scanner session, participants were asked to rate the task difficulty of both the Conv and Div task under each attention demand on a 5-point Likert scale (very easy – very difficult).

Figure 1.

Trial sequence. Each trial started with an initial fixation period lasting between three and five seconds. Then, the stimulus word was shown for a) the full course of 20 seconds (EDC condition) or b) 0.5 seconds and then replaced by a mask (“XXXX”) for the remaining 19.5s (IDC condition). In the convergent thinking task (Conv task) participants had to find anagram solutions, and in the divergent thinking task (Div task) participants had to generate meaningful four-word sentences with the presented initial letters. Participants were instructed to vocalize their answer(s) when the stimulus word (or a question mark in the baseline condition) would appear in green color for 6s. Trials were separated by a black screen shown for 1.5s.

Data collection, preprocessing and analysis

fMRI

Whole brain imaging was performed on a 3T Siemens *Skyra* MRI system (Siemens Medical Systems, Erlangen, Germany) using a 20-channel head coil. Structural brain images were obtained using a T1-weighted MPRAGE sequence (TR = 1680 ms, TI = 1000 ms, TE = 1.88 ms, FA = 8°, 192 slabs, voxel size = 0.88 mm isotropic, FoV = 256 x 256 mm). BOLD-sensitive T2*-weighted functional images were acquired using the CMRR-multiband (<https://www.cmrr.umn.edu/multiband/>) EPI pulse sequence (TR = 1000 ms, TE = 38.4 ms, multiband acceleration factor = 4, flip angle = 60°, 48 slices, voxel size = 3 mm isotropic, FoV = 80 x 80 mm). Additionally, ten functional images with opposite phase encoding were acquired to correct for susceptibility induced distortions.

MRI data were converted to BIDS format ensuring standardization and anonymization of data (Gorgolewski et al., 2016). Data were preprocessed with the preprocessing pipeline *fMRIPrep* 1.5.0 (Esteban et al., 2018, 2019), which is based on *Nipype* 1.2.2 (Gorgolewski et al., 2011, 2018). In summary, each structural image was corrected for intensity non-uniformity, skull-stripped and normalized to standard space through nonlinear registration with *antsRegistration* (ANTs 2.2.0). Functional data was corrected for susceptibility distortions via estimation of a deformation field, based on two EPI references with opposing phase-coding directions using *3dQwarp* (Cox & Hyde, 1997). Slice-timing correction was performed using *3dTshift* (Cox & Hyde, 1997). Based on the

estimated susceptibility distortion, an unwarped BOLD reference was calculated for a more accurate coregistration with the anatomical reference. The BOLD reference was then coregistered to the T1w reference using flirt (FSL 5.0.9, Jenkinson & Smith, 2001) and resampled to *MNI152NLin6Asym* standard space. Then, a high-pass filter (128s cut-off) was applied. Several time-series of potential confounds were calculated including framewise displacement, global signals and physiological regressors to allow for component-based noise correction (*CompCor*, Behzadi et al., 2007). In a final step, functional data were smoothed with a 6 mm full-width at half-maximum Gaussian kernel in SPM 12 (Wellcome Centre for Human Neuroimaging, London, UK).

Effects were estimated using the General Linear Model (GLM) as implemented in SPM 12. At the first level, six task regressors were included, consisting of the convergent (Conv; i.e., AN task), divergent thinking task (Div; i.e., SG task), and the baseline task (BL), each for the internal (IDC) and external attention condition (EDC; i.e., Conv-IDC, Conv-EDC, Div-IDC, Div-EDC, BL-IDC, BL-EDC). The task regressors were modelled with boxcar functions starting 0.5 s after stimulus onset (i.e., corresponding to the onset of actual task performance after stimulus encoding, and also corresponding to the onset of stimulus masking in EDC conditions) and with durations of 19.5 s, convolved with the canonical hemodynamic response function (HRF). Additionally, 6 eye parameters were entered as regressors (i.e., PD, fixation disparity, saccade count, microsaccade count, blink count and fixation count, sliced at the TR rate of 1.0 s; for further details see also, fMRI-eye-tracking covariation analyses). These eye parameters were treated as regressors of no interest in the task analyses, thus controlling for any effects related to variation in eye behaviors. Finally, nine standard motion parameters derived during preprocessing were entered as regressors of no interest to control for susceptibility effects related to response generation and head motion. Linear contrasts were used to obtain subject-specific estimates for each effect, which were entered into a second-level analysis treating subjects as a random effect with a one-sample t-test against a contrast value of zero at each voxel.

In a first step, we analyzed the task-general brain activation pattern reflecting the brain activation that is common across tasks and conditions (i.e., Conv-EDC + Conv-IDC + Div-EDC + Div-IDC vs. BL-EDC + BL-IDC). The effect of internal attention was analyzed with a contrast of internal vs. external attention conditions across tasks (i.e., Conv-IDC + Div-IDC vs. Conv-EDC + Div-EDC). Finally, the effect of divergent thinking was analyzed with a contrast of divergent vs. convergent thinking across attention conditions (Div-IDC + Div-EDC vs. Conv-IDC + Conv-EDC). In these analyses eye parameters and motion parameters were treated as regressors of no interest. Findings of the whole-brain analyses are reported when they are significant at voxel-level ($p < .05$, FWE-corrected for multiple comparisons) and cluster size ($k \geq 3$). Attention effects were further explored using a slightly

less conservative criterion by correcting for multiple comparison with FWE at cluster level (cluster-forming threshold; $p < .001$, $k \geq 111$).

Eye Tracking

Binocular eye tracking data were acquired using an MRI-compatible EyeLink 1000 eye tracker (SR Research Ltd.) with a temporal resolution of 500 Hz. The eye tracker was mounted on a tray within the scanner bore between the participant's head and a 32" screen (res. 1920 x 1080; NordicNeuroLab, Inc.) at the end of the scanner bore. A mirror was attached to the head coil allowing the participant unrestricted view of the display and continuous tracking of the eyes. The participant's eyes were located approx. 125 cm from the screen. The experiment was run in full-screen mode using the EyeLink Experiment Builder software (version 2.1.512; SR Research Ltd.). We conducted a 9-point calibration and validation at the beginning of the experiment.

Data Viewer (SR Research Ltd.) was used to output relevant eye information (i.e. pupil, blink and gaze position data). Eye parameters were computed from raw data using R scripts (R Core Team, 2020; v.4.0.2). Pupil diameter (PD) was defined as the average across both eyes and was z-transformed. To compute fixation disparity, we transformed gaze coordinates from pixels to mm, and subtracted the horizontal gaze coordinates of the left eye from the right eye. Fixation disparity is similar to the angle of eye vergence reported in previous studies (Benedek et al., 2017; Ceh et al., 2020; Walcher et al., 2017), but can be interpreted more easily: A focus on screen refers to zero disparity; values greater than zero reflect that subjects focus at a more distant point (i.e., divergence), while negative values reflect focus at a closer location (i.e., convergence). Saccades and microsaccades were determined using the Microsaccade Toolbox for R (Engbert et al., 2015) deviating from threshold settings as in previous studies (Benedek et al., 2017; Ceh et al., 2020; Walcher et al., 2017b) to account for relatively smaller stimulus size because of increased distance to the screen, with microsaccades being defined as saccades with an amplitude below 0.633° visual angle, lasting for at least 6 ms and $\lambda = 4$. Saccades, as well as additional 20 ms periods before and after each saccade were removed from pupil and gaze position data. Blink periods, as well as additional 200 ms periods before and after each blink were removed as well, to eliminate phases where the pupil was partially occluded (McCamy et al., 2012).

Task-based analyses relied on eye tracking data in the 18.5 s activation interval starting 1.5 s after stimulus onset to account for possible influences related to stimulus presentation (Nikolaev et al., 2016). For continuous eye parameters (PD, fixation disparity), we computed average and variance within each trial and then computed the median across trials. For discrete parameters (fixations, saccades, microsaccades, blinks) we counted the number of events and then computed the median across trials. As in previous studies (Benedek et al., 2017; Ceh et al., 2020), attention effects

(ATTENTION: IDC vs. EDC) and potential task effects (TASK: Conv vs. Div) were analyzed with 2x2 within-subject ANOVAs for each eye parameter. The main analyses included both correctly and incorrectly solved trials as we assume that the latter involved similar cognitive processes that simply were not fully terminated in time. Bonferroni-correction was applied to 2x2 ANOVAs (i.e., critical alpha was set to $.05/12 = .004167$).

fMRI-eye-tracking covariation analyses

Eye tracking data of each parameter were sliced in 1 s segments on the subject level to match the scanner's repetition time (TR = 1.0 s). To ensure the continuity of data, continuous eye parameters (i.e., PD, fixation disparity) were interpolated during periods of blinks (or other potential artifact periods; e.g., saccades) by means of linear approximation using the *na.approx* function of the *zoo* package in R. For every 1 s interval, we computed count scores for all discrete eye parameters (i.e., blinks, fixations, saccades, microsaccades) and mean scores for all continuous eye parameters (for an illustration of the resulting data structure, see Figure 2). To investigate the effect of eye movements on brain activity, we entered eye parameters in the first-level model and treated them as regressors of interest. Additionally, we modelled the main tasks (Conv and Div) and the baseline task (BL) as two regressors of no interest (note that attention direction was not modelled separately in this analysis, to avoid removing attention-related variance from the covariation analysis). This approach enabled us to investigate the relationship of brain activation with each eye parameter over time. Findings of the whole-brain analyses are reported when they are significant at voxel-level ($p < .05$, FWE-corrected for multiple comparisons) and cluster size $k \geq 3$. Significant effects were further explored using a slightly less conservative criterion by correcting for multiple comparison with FWE at cluster level (cluster-forming threshold; $p < .001$, $k \geq 111$).

Figure 2.

Visualization of a dataset for one exemplary participant, including BOLD act for 4 selected regions and frequency / z-scores for the six eye parameters. The data are presented in 1 s segments across the duration of the entire data acquisition (eight consecutive blocks). EDC = externally directed cognition, IDC = internally directed cognition, SOG = superior occipital gyrus, LG = lingual gyrus, R = right, L = left.

Results

Behavioral results

Participants were able to solve 76.67% ($SE = 1.91$) of all trials. A 2x2 repeated measures ANOVA regarding the within-subject factors ATTENTION (IDC vs. EDC) and TASK (Conv vs. Div) was conducted in order to further investigate task performance. Significant main effects were found for ATTENTION ($F_{1,29} = 5.11$, $p = .031$, $\eta_p^2 = .15$), showing that the internal attention condition resulted in lower performance ($M = 74.45\%$, $SE = 2.70$) compared to task performance when stimuli were continuously available ($M = 78.90\%$, $SE = 2.70$); a significant main effect TASK ($F_{1,29} = 18.57$, $p < .001$, $\eta_p^2 = .39$) indicated that the convergent thinking task ($M = 82.78\%$, $SE = 2.43$) was easier than the divergent thinking task ($M = 70.56\%$, $SE = 2.76$). There was no significant interaction between ATTENTION and TASK ($F_{1,29} = 0.02$, $p = .88$).

These effects were also reflected in subjective difficulty ratings. A repeated measures ANOVA revealed significant main effects for both ATTENTION ($F_{1,29} = 70.46$, $p < .001$, $\eta_p^2 = .71$) and TASK ($F_{1,29} = 17.20$, $p < .001$, $\eta_p^2 = .37$), but no significant interaction between ATTENTION and TASK ($F_{1,29} = 1.33$, $p = .26$). Task performance in the internal attention condition ($M = 2.43$, $SE = 0.13$) was rated more

difficult than task performance in the external attention condition ($M = 1.72$, $SE = 0.13$) and the convergent thinking task ($M = 1.67$, $SE = 0.13$) was found to be easier than the divergent thinking task ($M = 2.48$, $SE = 0.13$). These results are consistent with previous studies using the same paradigm in showing that task performance in the mind's eye is more difficult due to the increased memory load (Benedek et al., 2011, 2017; Ceh et al., 2020).

fMRI results

We first computed task-general brain activation effects, reflecting the brain activation that is common across tasks and conditions (see Table S1 in Supplementary materials). Convergent and divergent thinking across attention conditions was associated with a frontal-parietal brain activation pattern, involving the left-lateralized inferior frontal gyrus (IFG), bilateral supplementary motor cortex (SMC), supramarginal gyrus (SMG) and superior parietal lobe (SPL), as well as cerebellar, thalamic and hippocampal areas. Moreover, the tasks generally showed reduced brain activation in DMN-related regions, such as middle cingulate gyrus (MCG), angular gyrus (AG) and middle and superior temporal gyrus (MTG, STG).

Effects of internal versus external attention are shown in Table 1. IDC involved increased activation in bilateral parts of the lingual gyrus (LG), bilateral precuneus, right cuneus and left posterior cingulate (PC). IDC further resulted in lower brain activation compared to EDC in widespread areas of visual networks including bilateral parts of the superior parietal lobe (SPL), occipital areas (inferior and middle occipital gyrus), and in bilateral precentral gyrus, bilateral inferior temporal gyrus (ITG), left-lateralized parts of the basal ganglia (BG; i.e., putamen) brainstem and thalamus, as well as bilateral cerebellar areas.

Complimentary analyses applying FWE correction at cluster-level revealed that IDC was additionally associated with activation in bilateral parts of the inferior parietal lobe (IPL) and further show decreased activation in right-lateralized parts of the basal ganglia (i.e., caudate nucleus) (see Table S2 and Figure 3).

Brain activation effects associated with the convergent vs. divergent thinking are shown in Table 2. Divergent thinking was associated with relatively stronger activation in areas of the left IFG and SFG, the left middle and superior temporal gyrus (MTG, STG), bilateral parts of the caudate, the left-sided insula and right-lateralized cerebellar regions. Convergent thinking was associated with higher brain activation in right lateralized regions of the brain, involving the SPL, SMG, AG, MTG, STG and precuneus.

Figure 3.

Brain activation results for internally vs. externally directed cognition (Whole brain T-map, $p < .001$, FWE-corrected at cluster level; neurological display convention). Internal attention is associated with increased activation at bilateral lingual gyrus ($z = -8$), bilateral inferior parietal lobe ($z = 24$ to 40), bilateral (pre-)cuneus ($z = 24$ to 40) and with reduced activation at precentral gyrus ($z = 24$ to 56) and occipital and superior parietal cortex ($z = -8$ to 56).

Eye tracking results

Attention effects (IDC vs. EDC) and potential task effects (Conv vs. Div) on available eye parameters were analyzed with 2x2 ANOVAs for each eye parameter (see Table S3 for descriptive statistics regarding all eye parameters and Table S4 for ANOVA results). Looking at attention effects first, IDC involved lower microsaccade count ($F_{1,29} = 43.38, p < .001, \eta_p^2 = .60$), longer blinks ($F_{1,29} = 12.46, p = .001, \eta_p^2 = .30$), greater PD ($F_{1,29} = 32.95, p < .001, \eta_p^2 = .53$), greater PD variance ($F_{1,29} = 35.48, p < .001, \eta_p^2 = .55$) and greater fixation disparity variance ($F_{1,29} = 10.31, p = .003, \eta_p^2 = .26$). No differences between IDC and EDC were found for fixation count ($F_{1,29} = 6.65, p = .015$), fixation duration ($F_{1,29} = 9.58, p = .004$), saccade count ($F_{1,29} = 6.65, p = .015$), saccade amplitude ($F_{1,29} = 4.04, p = .054$), microsaccade amplitude ($F_{1,29} = 6.80, p = .014$), blink count ($F_{1,29} = 4.36, p = .046$) and fixation disparity ($F_{1,29} = 2.05, p = .163$). Effect sizes of all oculometric differences between IDC and EDC are displayed in Figure 4.

Significant task effects were found for fixation duration ($F_{1,29} = 12.50, p = .001, \eta_p^2 = .30$), microsaccade amplitude ($F_{1,29} = 13.15, p = .001, \eta_p^2 = .31$), blink duration ($F_{1,29} = 12.41, p = .001, \eta_p^2 = .30$) and PD ($F_{1,29} = 74.66, p < .001, \eta_p^2 = .72$). Fixation duration and blink duration were greater during convergent thinking, while microsaccade amplitude and PD were greater during divergent thinking. There were no significant TASK effects for fixation count ($F_{1,29} = 5.21, p = .003$), saccade count ($F_{1,29} = 0.05, p = .833$), saccade amplitude ($F_{1,29} = 1.44, p = .240$), microsaccade count ($F_{1,29} = 7.70, p = .009$), blink count ($F_{1,29} = 8.43, p = .007$), PD variance ($F_{1,29} = 0.59, p = .450$), fixation disparity ($F_{1,29} = 3.00, p = .094$) or fixation disparity variance ($F_{1,29} = 1.47, p = .236$).

Figure 4.

Effect sizes of oculometric differences between internally directed cognition (IDC) and externally directed cognition (EDC). PD = pupil diameter; *** $p < .001$, ** $p < .004167$ (Bonferroni-corrected).

Significant attention condition x task interaction effects for fixation count ($F_{1,29} = 10.70$, $p = .003$, $\eta_p^2 = .27$) and PD variance ($F_{1,29} = 11.55$, $p = .002$, $\eta_p^2 = .28$) reflected that attention effects were more pronounced in the convergent than in the divergent thinking task. No such interactions were observed for fixation duration ($F_{1,29} = 6.39$, $p = .017$), saccade count ($F_{1,29} = 6.65$, $p = .004$), saccade amplitude ($F_{1,29} = 0.16$, $p = .694$), microsaccade count ($F_{1,29} = 5.88$, $p = .022$), microsaccade amplitude ($F_{1,29} = 1.42$, $p = .244$), blink count ($F_{1,29} = 5.58$, $p = .025$), blink duration ($F_{1,29} = 5.33$, $p = .028$), PD ($F_{1,29} = 0.16$, $p = .697$), fixation disparity ($F_{1,29} = 3.75$, $p = .063$) or fixation disparity variance ($F_{1,29} = 0.12$, $p = .737$).

Temporal covariation between brain activation and eye behavior

Whole-brain analyses exploring the temporal covariation of eye parameters and brain activation revealed that greater PD is linked to increased bilateral activation in the BG (i.e., putamen, caudate nucleus), bilateral brainstem and right cuneus and calcarine cortex. Moreover, greater PD is associated with decreased bilateral activity in the pre- and postcentral gyrus and left-lateralized parietal and central operculum, bilateral parts of the insula, right putamen, as well as the left inferior occipital gyrus (see Table 3). Increased saccadic activity in terms of saccade count was associated with increased activity in the right-lateralized inferior occipital gyrus. No other eye parameter was associated with significant changes in brain activation.

Complimentary analyses further examined the PD- and saccade-related brain activation by applying FWE correction at cluster-level. This analysis showed that increased PD goes in hand with increased activity in bilateral parts of the lingual gyrus, cuneus, basal ganglia, as well as right insula, right SMG and bilateral supplementary motor cortex and MFG. Greater PD was further linked to decreased activity in bilateral parts of the anterior cingulate gyrus and pre- and postcentral gyrus (see Table S5 and Figure 5). More saccades associated with increased activity in bilateral inferior occipital gyrus, fusiform gyrus and middle cingulate, as well as supplementary motor cortex and pre- and postcentral gyrus (see Table S6).

Figure 5.

Brain activation results for pupil diameter (Whole brain T-map, $p < .001$, FWE-corrected at cluster level; neurological display convention). Greater pupil diameter is associated with increased activation at brainstem ($z = -8$), bilateral lingual gyrus ($z = -8$ to 8), basal ganglia, cuneus and right insula ($z = 8$), right supramarginal gyrus ($z = 40$ to 56) and bilateral supplementary motor cortex, middle frontal gyrus and superior parietal lobe ($z = 56$) and with reduced activation at left inferior occipital gyrus ($z = -8$), bilateral anterior cingulate gyrus ($z = 8$) and bilateral pre- and postcentral gyrus ($z = 8$ to 40).

Discussion

This fMRI–eye-tracking coregistration study tested whether brain activity and eye behavior are reliable indicators of internal focus of attention and explored their temporal relationship. Using an established paradigm to realize within-task manipulations of internal versus external attention demands in the visual domain, we replicated the finding that an internal focus of attention is related to increased activity in areas related to visual imagery (Benedek et al., 2016; Corbetta et al., 2008; Kosslyn et al., 2001) and is related to reduced activation in areas of the visual and dorsal attention network (DAN). In accordance with previous studies, we also found a distinct eye behavior pattern distinguishing states of IDC versus EDC: Internally directed cognition was associated with reduced

microsaccade rate and increased PD (Ceh et al., 2020; Gao et al., 2015; Krueger et al., 2019; Smallwood et al., 2011; Walcher et al., 2017) and further involved increased PD variance and AoEV variance, as well as longer blinks (Benedek et al., 2017; Salvi et al., 2015). We further found that PD was correlated to BOLD activity in areas sensitive to internal and external attention demands (i.e., lingual gyrus, cuneus, basal ganglia and superior parietal lobe), pointing to the interplay of neural and perceptual mechanisms subserving sustained internal attention.

As in a previous study (Benedek et al., 2016), internally directed cognition was associated with increased activation of bilateral lingual gyrus (LG) and cuneus, thereby clearly replicating that LG activity is centrally involved in internally directed cognition. LG areas have been linked to visual imagination and letter/word processing (Benedek et al., 2016; Kosslyn et al., 2001; Mechelli et al., 2003), and may be involved in mental simulations and manipulations of the stimulus letters during task performance. LG activity has been further associated with the employment of visual imagery strategies in memory tasks (Leshikar et al., 2012). A recent study revealed that the generation of highly original associations for given adjectives (e.g., “round”) was related to the focused activation of bilateral LG, which was attributed to recruitment of visual strategies for retrieving particularly remote instances for these characteristics (Benedek et al., 2020). We assume that the absence of relevant external stimuli (i.e., internal attention condition) enforced stronger usage of visual imagination strategies to maintain and manipulate the stimulus letters mentally in the search of solutions to the convergent and divergent thinking problems.

Internally directed cognition further involved higher bilateral activation of the inferior parietal lobe (FWE corrected at cluster level). These regions have been hypothesized to play a role in sustaining internally directed cognition by top-down controlling visual processing (Shapiro & Hillstrom, 2002; Singh-Curry & Husain, 2009). Especially the right aIPL was found to show increased functional coupling with visual areas during internal attention suggesting that it exerts top-down control over occipital regions to suppress early visual information processing (Benedek et al., 2016). Neuroimaging studies further suggest strong IPL involvement during semantic memory processes, implicating a contribution to supporting imagination and mental simulation (Binder & Desai, 2011), thus constituting crucial aspects of IDC (Abraham & Bubic, 2015). It can be argued that the internal condition involved higher memory load, as it required participants to keep and manipulate the stimuli in their mind without external information. This is supported by behavioral findings demonstrating lower solution rates and greater perceived difficulty during IDC and also backed up by empirical evidence linking the IPL to working memory (Baldo & Cronkers, 2006; Berryhill et al., 2011). Engaging in internal cognition may place higher demands on working memory and therefore require stronger shielding of internal representations.

External attention, in contrast, was linked to the recruitment of the visual and dorsal attention networks, indicated by widespread activation of occipital regions as well as regions along the intraparietal sulcus (IPS), SPL and precentral gyrus (Corbetta & Shulman, 2002). Moreover, EDC was associated with ITG and SMG activity, regions implicated in visual perception (Conway, 2018) that are part of the ventral attention network and are said to interact with the DAN when salient stimuli occur (Corbetta et al., 2008). Taken together, our findings emphasize the notion that internal versus external attention states are dissociable by means of BOLD activity (Dixon et al., 2014). Specifically, the observed shift of neural activity from uni- to transmodal regions during IDC (i.e., decreased activity in visual and motor areas and increased activity in DMN-related areas) is in line with the assumption that internal cognition recruits brain networks distant from those involved in perception (Margulies et al., 2016; C. Murphy et al., 2018, 2019).

We were also able to largely replicate findings from previous eye tracking studies suggesting that an internal focus of attention is associated with a distinct pattern of eye behavior (Annerer-Walcher et al., 2018, 2020; Benedek et al., 2017; Ceh et al., 2020; Walcher et al., 2017). Specifically, IDC involved increased PD and PD variance, longer blinks, greater fixation disparity variance and a reduction in microsaccade rate. Longer blinks and reduced microsaccade rate are consistent with the notion that IDC implies reduced visual engagement. Increased blink duration reduces visual inflow (Salvi et al., 2015; Walcher et al., 2017), just as increased blink rate (e.g., Chen & Epps, 2014; Grandchamp et al., 2014; Smilek et al., 2010). Decreased microsaccadic activity has been previously observed during IDC (Gao et al., 2015; Krueger et al., 2019), reflecting visual fading of external information (Martinez-Conde et al., 2006, 2013; McCamy et al., 2012). Other studies reported that moments of spontaneous “in-sight” were also associated with increased blink rate as well as lower microsaccade rate (cf. Kounios & Beeman, 2009; Salvi et al., 2015, 2020). Increased variance in PD and fixation disparity are again consistent with the view that IDC implies perceptual decoupling and potential coupling to internal processes, as eye behavior is no longer determined by the static visual input and becomes affected by visual imagination (Smallwood & Schooler, 2015).

PD increases are a particularly robust finding for increased internal attention demands as they were consistently observed across different studies and experimental designs and typically showed the strongest effect sizes when comparing IDC vs EDC, as in this study (e.g., Annerer-Walcher et al., 2020; Franklin et al., 2013; Konishi et al., 2017). Considering that PD increases have also been observed when orienting attention to external events (Sara & Bouret, 2012), PD may not represent an index of internal attention per se, but of corresponding higher mental load (Unsworth & Robison, 2018). In fact, higher PD has been consistently associated with higher memory load and related increases of task difficulty (Kahneman & Beatty, 1966; Piquado et al., 2010; Porter et al., 2007). PD increases have also been linked to insight problem-solving, a process characterized by internal

attention allocation (Salvi et al., 2020). Still, PD is considered a promising metric to index momentary changes of attention (Kang et al., 2014; Kang & Wheatley, 2015), especially, when weighing in factors such as task characteristics, task focus, and time-on-task effects (Van Den Brink et al., 2016), as it reflects increases of mental load that are characteristic for internally directed cognition.

We conclude that robust and replicable differences in eye behavior can be observed between IDC and EDC, even in technically complex setups, such as coregistration with neurophysiological measures. Specifically, we find strong recurring evidence that IDC is associated with reduced visual engagement as indicated by increased blink rate or duration and reduced microsaccade rate, perceptual decoupling as evidenced greater variability of eye behavior (i.e., PD variance, saccadic amplitudes and vergence measures) and greater PD reflecting higher mental load. In summary, these robust associations imply that the assessment of eye behavior makes for a promising tool to depict fluctuations of attentional focus.

As a central novelty of this study, the concurrent recording of BOLD signal as index of brain activity and several continuous indicators of eye behavior enabled us to investigate their relationship over time. This analysis showed that larger PD was related to increased brain activation in bilateral basal ganglia (i.e., putamen, caudate nucleus), brain stem, and calcarine cortex/cuneus extending to dorsal parts of lingual gyrus (when FWE corrected at cluster level). Larger PD was further associated with decreased activation of pre- and postcentral gyrus, insula, and the left IOG. Interestingly, we observed no significant associations with brain activation for the other eye parameters, except for saccade count, which was related to activity in bilateral IOG, fusiform gyrus, middle cingulate, SMC and pre-, as well as postcentral gyrus (when applying FWE correction at cluster level), thus exhibiting an association with areas typically involved in perception and saccadic movements (e.g., Kimmig et al., 2001; Tse et al., 2010). Hence, as a first interesting general observation, PD stood out from the other eye parameters in showing the strongest attention effects as well as the most substantial associations with brain activation over time, which included brain regions that showed attention effects. This finding is strikingly similar to a previous EEG study, where PD also showed the strongest attention effect for IDC vs EDC, and was the only eye parameter showing significant temporal covariation with concurrently recorded alpha activity, which also showed attention effects (i.e., relatively higher posterior alpha power during IDC; Ceh et al., 2020). PD thus appears to be a particularly sensitive and reliable index of attentional focus, and its temporal correlation with neural markers of internal attention suggests that it plays a role or is at least indicative of an underlying neurophysiological mechanism supporting sustained internal attention.

More insights come from a closer look at the specific findings from the temporal covariation analysis. For instance, greater PD was associated with increased activation of cuneus and bilateral

lingual gyrus, regions that also showed increased brain activation during higher internal demands. As previously noted, these areas are involved in visual imagery, and thus, PD may reflect higher mental load during the generation and manipulation of complex mental representations. Specifically, we propose that during IDC conditions, the lack of externally available stimuli placed higher demands on visual working memory to imagine and manipulate the previously encoded stimulus, thus imposing higher workload as compared to EDC conditions, where the stimulus was continuously available. Other studies also reported PD increases when greater demands were placed on visuo-spatial working memory (Klingner et al., 2011)) and showed that PD is sensitive to individual differences in visuo-spatial working memory capacity (Unsworth & Robison, 2015). In summary, internal attention requires recall and manipulation of the previously encoded stimuli, activating imagination-related brain areas and placing higher demands on visual working memory, which is reflected by increased PD and corresponding brain regions.

Larger PD was also associated with increased activity in basal ganglia regions (i.e., putamen and caudate nucleus). The BG are implicated in working memory in a multi-faceted role, possibly acting as a sensory input-output gate and/or being involved in working memory reallocation (Chatham & Badre, 2015). Interestingly, IDC was linked to decreased BG activity, albeit not exactly at the very same location. These findings may point to distinct modes of BG involvement in working memory, with different subregions being sensitive to sensory versus non-sensory (i.e., external versus internal) input to update working memory. Unlike other studies, we did not find correlations between PD and locus coeruleus activity (e.g., Joshi et al., 2016; P. R. Murphy et al., 2014). While we did find a correlation between PD and brainstem activity, the location differs from those previously reported as LC (Keren et al., 2009). Importantly, the use of different methods to identify LC and its assumed involvement in a variety of functions motivates further research of brainstem structures (Chandler et al., 2019; K. Y. Liu et al., 2017).

Looking at task effects, divergent thinking activated the left IFG and SFG, consistent with much previous research (Benedek et al., 2016; ; Madore et al., 2019; Zabelina & Ganis, 2018; for a meta analysis, see Gonen-Yaacovi et al., 2013). These regions have been associated with cognitive control (Brass et al., 2005) and semantic/conceptual processing (Andrews-Hanna, Smallwood, et al., 2014) and may be especially relevant for the guiding cued recall and assessing grammatical and syntactical correctness of self-generated sentences. This finding is also in line with behavioral findings showing that divergent thinking implies high executive control (e.g., Benedek et al., 2014; Benedek & Jauk, 2019). Interestingly, we did not replicate that divergent thinking is associated with higher DMN activity compared to convergent thinking, as found in a previous study (Benedek et al., 2016). Since participants found the convergent thinking task to be very easy, a possible explanation might be that this task led to more episodes of mind-wandering, which in turn recruited the DMN

(e.g., Poerio et al., 2017). Hence, while the DMN is known to be relevant to creative cognition and self-generated thought, this may become more apparent when matching tasks for difficulty (Abraham et al., 2012) and applying a brain connectivity perspective (Beaty et al., 2016; Zabelina & Andrews-Hanna, 2016).

Summary and conclusion

This fMRI–eye-tracking coregistration study corroborated the notion that eye behavior and brain activation are sensitive to an internal versus external focus of attention. Performing mental tasks with an internal focus of attention yields an eye behavior pattern reflecting visual disengagement (longer blinks, and reduced microsaccade activity), perceptual decoupling (increased FD and PD variance), and increased mental load (increased pupil diameter). Internally directed cognition further recruited areas related to visual imagination and semantic processing (bilateral lingual gyrus and inferior parietal lobe), even when controlled for attention-related differences in eye behaviors. Importantly, pupil diameter, which showed the highest sensitivity to internal attention demands, was related to increased activation in brain regions associated with working memory gating (basal ganglia) and visual imagination (lingual gyrus). We conclude that internally and externally directed cognition are characterized by distinct neurophysiological signatures reflecting perceptual and neural mechanisms subserving a sustained attention focus to internal versus external worlds.

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Tables

Table 1.

Brain activation for internally vs. externally directed cognition (FWE-corrected at voxel-level, $p < .05$, $k \geq 3$).

Region	Lat.	BA	Peak (MNI)			k	T	p
			x	y	z			
IDC > EDC								
Lingual G	L	19	-16	-64	-10	27	7.82	.001
Lingual G	R	18	18	-72	-8	8	6.50	.023
Precuneus, Cuneus	R	7	10	-72	40	5	7.06	.007
PCG, Precuneus	L	31	-10	-40	40	4	6.64	.017
EDC > IDC								
ITG, IOG	L	37	-40	-62	-8	1413	13.12	< .001
SPL	R	7	26	-66	48	1377	11.20	< .001
IOG, FuG, ITG	R	19	44	-66	-14	913	10.94	< .001
SPL	L	7	-26	-72	30	886	10.44	< .001
Cerebellum	R	-	10	-74	-38	373	12.69	< .001
Precentral G	L	6	-40	0	28	76	7.18	.005
Putamen	L	49	-20	8	4	51	7.72	.001
Precentral G	R	6	44	4	30	45	8.40	< .001
MOG	R	19	38	-84	16	34	8.00	.001
MFG, Precentral G	L	6	-46	4	44	31	7.49	.002
Precentral G	R	6	26	-8	52	26	6.97	.008
SFG	L	-	-22	-6	48	24	6.79	.012
Precentral G	L	6	-52	6	30	8	6.52	.022
Cerebellum	R	-	28	-70	-52	8	6.45	.025
Brainstem, Thalamus	L	-	-6	-32	-2	7	8.08	< .001
Cerebellum	L/R	-	0	-48	-30	6	7.14	.006
Thalamus	L	50	-14	-28	12	6	7.05	.007
Putamen	L	-	-32	-18	-4	4	6.66	.016
Thalamus	L	-	-20	-34	8	3	6.65	.016

Note. IDC = internally directed cognition, EDC = externally directed cognition, Lat. = Laterality, BA = Brodmann area, k = cluster size, L/R = left/right, G = Gyrus, PCG = Posterior Cingulate Gyrus, ITG = Inferior Temporal Gyrus, IOG = Inferior Occipital Gyrus, SPL = Superior Parietal Lobe, FuG = Fusiform Gyrus, MOG = Middle Occipital Gyrus, MFG = Middle Frontal Gyrus, SFG = Superior Frontal Gyrus.

Table 2.

Brain activation for divergent vs. convergent thinking (FWE-corrected at voxel-level, $p < .05$, $k \geq 3$).

Region	Lat.	BA	Peak (MNI)			k	T	p
			x	y	z			
Div > Conv								
Cerebellum	R	-	16	-68	-26	417	10.70	< .001
IFG	L	44	-54	18	20	312	9.75	< .001
MTG, STG	L	-	-46	-42	4	92	7.70	.001
SFG	L	6	-8	8	66	91	9.17	< .001
Cerebellum, FuG	R	-	32	-62	-22	87	7.67	.001
FO, Insula	L	45	-32	28	10	54	7.60	.002
Caudate	L	48	-16	0	22	49	7.49	.002
Cerebellum	R	-	30	-64	-50	20	6.73	.013
Caudate	R	-	18	18	16	14	6.87	.010
Precentral G	L	6	-42	-4	52	9	6.80	.011
Brainstem	L	-	-8	-20	-12	6	7.09	.006
SFG	L	9	-12	52	34	6	6.71	.014
Caudate	L	-	-14	18	14	4	6.25	.038
Caudate	R	-	18	28	2	3	6.41	.026
Conv > Div								
AG, SMG	R	40	48	-48	44	41	6.82	.011
SPL	R	7	36	-44	42	17	6.46	.023
MTG, STG	R	21	64	-26	-6	14	8.25	< .001

Note. Div = divergent, Conv = convergent, Lat. = Laterality, BA = Brodmann area, k = cluster size, L/R = left/right, IFG = Inferior Frontal Gyrus, MTG = Middle Temporal Gyrus, STG = Superior Temporal Gyrus, SFG = Superior Frontal Gyrus, FuG = Fusiform Gyrus, G = Gyrus, AG = Angular Gyrus, SMG = Supramarginal Gyrus, AnG = Angular Gyrus, MTG = Middle Temporal Gyrus.

Table 3.

Brain activation for eye parameters (FWE-corrected at voxel-level, $p < .05$, $k \geq 3$).

Region	Lat.	BA	Peak (MNI)			k	T	p
			x	y	z			
PD (+)								
Caudate, Putamen	L	-	-14	12	0	71	8.78	< .001
Calcarine Cortex, Cuneus	R	-	20	-70	14	10	7.08	.006
Putamen, Caudate	R	49	18	14	-4	9	7.18	.005
Brainstem	L/R	7	-4	-22	-8	3	6.49	.023
PD (-)								
Pre-, Postcentral G	L	4	-56	-6	18	445	9.11	< .001
Pre-, Postcentral G	R	4	46	-12	32	333	8.78	< .001
Pre-, Postcentral G	L	4	-18	-28	62	32	7.81	.001
Putamen	R	-	30	-6	-10	18	7.05	.007
Pre-, Postcentral G	R	4	20	-28	60	17	6.93	.009
CO, Insula	L	4	-38	-12	18	16	7.62	.002
Putamen, Insula	R	49	32	-8	4	13	7.04	.007
PT, PO	L	41	-44	-34	12	7	6.85	.011
SMG	L	39	-60	-42	28	5	6.49	.024
IOG	L	19	-36	-82	-10	4	6.69	.015
Saccade Count (+)								
IOG	R	18	36	-90	2	6	7.64	.001
Saccade Count (-)								
-	-	-	-	-	-	-	-	-
Fixation Disparity (+ / -)								
-	-	-	-	-	-	-	-	-
Blink Count (+ / -)								
-	-	-	-	-	-	-	-	-
Fixation Count (+ / -)								
-	-	-	-	-	-	-	-	-
Microsaccade Count (+ / -)								
-	-	-	-	-	-	-	-	-

Note. + = positive contrast, - = negative contrast, Lat. = Laterality, BA = Brodmann area, k = cluster size, L/R = left/right, G = Gyrus, CO = Central Operculum, PT = Planum Temporale, PO = Parietal Operculum SMG = Supramarginal Gyrus, IOG = Inferior Occipital Gyrus.

Supplementary Material

Table S1.

Task-general brain activation across all tasks and conditions (FWE-corrected at voxel level, $p < .05$, $k \geq 3$).

Region	Lat.	BA	Peak (MNI)			k	T	p
			x	y	z			
Task-positive activation								
IFG	L	44	-48	12	26	1706	12.66	< .001
Cerebellum	R	-	28	-62	-24	1518	15.67	< .001
SMG	L	40	-48	-40	50	903	9.59	< .001
SMC	L	6	-4	2	62	446	11.19	< .001
Insula	L	13	-30	22	2	258	11.77	< .001
Cerebellum	R	-	32	-70	-52	244	10.42	< .001
MFG, SFG	R	6	28	6	54	233	9.53	< .001
SMG	R	40	46	-34	42	193	11.13	< .001
Caudate	L	8	-6	16	44	141	10.30	< .001
Insula	L	13	-30	22	2	133	9.63	< .001
SPL	R	7	32	-64	34	130	8.26	< .001
Insula	R	13	32	24	2	129	10.99	< .001
Caudate	R	-	18	-16	26	66	8.94	< .001
Brainstem	L	-	-6	-26	-8	63	9.47	< .001
HC	R	-	26	-36	12	62	11.41	< .001
HC	L	-	-24	-38	12	32	8.04	.001
SMC	R	8	10	22	42	22	7.86	.001
Caudate	R	-	18	20	14	22	7.51	.003
Brainstem	R	-	8	-22	-10	14	7.78	.001
Caudate	L	-	-22	18	10	9	7.29	.005
Thalamus	L	-	-16	-22	22	9	6.99	.009
Cerebellum	L	-	-30	-62	-28	9	6.48	.027
Caudate	R	-	20	28	4	7	7.66	.002
Cerebellum	L	-	-20	-36	-42	6	7.18	.006
SPL	R	7	16	-66	58	5	6.95	.010
MFG	R	9	44	36	26	5	6.37	.034
Caudate	R	-	18	8	20	3	6.45	.029
Task-negative activation								
MCG	L/R	24	4	-20	40	5229	14.81	< .001
MTG, AG	R	37	56	-54	12	3548	12.21	< .001
SFG	L/R	-	2	54	6	2350	12.00	< .001
Insula	L	34	-30	0	-16	960	10.71	< .001
AG	L	39	-50	-56	28	767	12.89	< .001
Precentral G	L	1	-34	-22	42	419	10.11	< .001
Cerebellum	L	-	-22	-78	-34	232	11.52	< .001
MTG, STG	L	21	-60	-24	-8	221	10.12	< .001
Precentral G	R	-	22	-22	60	119	9.63	< .001
SFG	L	9	-20	44	32	96	7.91	.001

Precentral G	R	-	38	-12	42	90	8.53	< .001
HC	L	-	-30	-36	-12	82	8.00	.001
Insula	R	-	30	-20	18	51	8.05	.001
PO	L	40	-50	-26	18	46	7.17	.006
Thalamus	L	50	-10	-30	4	39	8.72	< .001
Thalamus	R	50	12	-28	4	32	7.90	.001
FuG, IOG	L	18	-24	90	-12	28	7.14	.006
FuG	R	36	30	-38	-12	27	7.62	.002
SFG	R	8	20	30	46	25	7.28	.005
MFG, SFG	L	8	-24	26	42	25	7.22	.005
Postcentral G	R	1	20	-38	68	24	7.77	.001
SFG	R	8	14	36	48	23	7.44	.003
SFG	L	8	-10	32	52	18	7.34	.003
Insula	R	13	34	6	6	17	7.38	.004
Thalamus	L	-	-18	-38	0	17	7.22	.005
Insula	L	13	-34	4	12	14	7.00	.009
ACG	L/R	-	0	28	20	13	6.90	.011
MCG	L	24	-4	10	30	11	6.97	.009
Cerebellum	L	-	-6	-52	-42	10	6.85	.012
SFG	R	6	12	28	58	10	6.61	.020
HC	R	54	28	-20	-14	9	7.53	.002
OP	L	18	-20	-94	2	3	6.48	.027
Cerebellum	R	-	32	-78	-34	3	6.44	.029

Note. Lat. = Laterality, BA = Brodmann area, k = cluster size, L/R = Left/right, IFG = Inferior frontal gyrus, SMG = Supramarginal gyrus, SMC = Supplementary motor cortex, MFG = Middle frontal gyrus, SFG = Superior frontal gyrus, SPL = Superior parietal lobe, HC = Hippocampus, MCG = Middle cingulate gyrus, MTG = Middle temporal gyrus, AG = Angular gyrus, G = Gyrus, STG = Superior temporal gyrus, PO = Parietal operculum, FuG = Fusiform gyrus, IOG = Inferior occipital gyrus, ACG = Anterior cingulate gyrus, OP = Occipital pole.

Table S2.

Brain activation for internally vs. externally directed cognition (cluster-forming threshold; $p < .001$, $k \geq 111$).

Region	Lat.	BA	Peak (MNI)			k	T	p
			x	y	z			
IDC > EDC								
Lingual G	L	19	-16	-64	-10	3946	7.82	< .001
AG	R	39	56	-54	28	350	5.07	< .001
SMG, AG	L	39	-52	-50	28	333	5.45	< .001
Lingual G	L	19	-34	-48	0	124	5.35	.023
Precuneus	R	31	14	-48	38	118	4.30	.028
EDC > IDC								
ITG, IOG	L	37	-40	-62	-8	6092	13.12	< .001
SPL	R	7	26	-66	48	6052	11.20	< .001
MFG, Precentral G	L	6	-46	4	44	2997	7.49	< .001
Brainstem, Thalamus	L	-	-6	-32	-2	2250	8.08	< .001
Cerebellum	R	-	10	-74	-38	1556	12.69	< .001
Precentral G	R	6	26	-8	52	711	6.97	< .001
Caudate	R	48	18	20	4	574	6.04	< .001
Precentral G	R	6	44	4	30	566	8.40	< .001
Cerebellum	L/R	-	0	-48	-30	177	7.14	.004
Cerebellum	L	-	-14	-50	-44	164	5.53	.006

Note. IDC = internally directed cognition, EDC = externally directed cognition, Lat. = Laterality/Lateral, BA = Brodmann area, k = cluster size, L/R = left/right, G = Gyrus, AG = Angular Gyrus, SMG = Supramarginal Gyrus, ITG = Inferior Temporal Gyrus, IOG = Inferior Occipital Gyrus, SPL = Superior Parietal Lobe, MFG = Middle Frontal Gyrus.

Table S3.

Mean (and SE) for each eye parameter during externally directed cognition (EDC) and internally directed cognition (IDC) for each task (Conv, Div) and the baseline condition (BL).

Eye parameter	EDC				IDC				Total			
	Conv	Div	BL	Total	Conv	Div	BL	Total	Conv	Div	BL	Total
Fixation count [1/s]	1.43 (0.06)	1.37 (0.06)	0.92 (0.08)	1.24 (0.05)	1.14 (0.10)	1.31 (0.10)	0.82 (0.09)	1.09 (0.06)	1.29 (0.06)	1.34 (0.06)	0.87 (0.06)	1.17 (0.04)
Fixation duration [ms]	273.82 (18.29)	272.42 (21.95)	924.85 (325.85)	490.37 (112.61)	373.22 (38.35)	306.95 (30.04)	912.54 (158.48)	530.90 (61.74)	323.52 (22.03)	289.69 (18.58)	918.70 (179.63)	510.63 (64.05)
Saccade count [1/s]	1.11 (0.08)	0.99 (0.08)	0.67 (0.08)	0.29 (0.05)	0.80 (0.11)	0.92 (0.11)	0.58 (0.08)	0.77 (0.06)	0.95 (0.07)	0.96 (0.07)	0.63 (0.06)	0.84 (0.04)
Saccade amplitude [degree]	0.94 (0.02)	1.00 (0.03)	0.96 (0.05)	0.97 (0.02)	1.55 (0.29)	1.65 (0.36)	0.97 (0.05)	1.39 (0.16)	1.24 (0.15)	1.33 (0.18)	0.96 (0.04)	1.18 (0.08)
Microsaccade count [1/s]	1.11 (0.11)	0.95 (0.09)	1.01 (0.09)	1.02 (0.06)	0.72 (0.10)	0.69 (0.10)	1.00 (0.10)	0.81 (0.06)	0.92 (0.08)	0.82 (0.07)	1.01 (0.07)	0.92 (0.04)
Microsaccade amplitude [degree]	0.31 (0.01)	0.34 (0.01)	0.32 (0.01)	0.32 (0.01)	0.27 (0.01)	0.31 (0.01)	0.30 (0.01)	0.29 (0.01)	0.29 (0.01)	0.32 (0.01)	0.31 (0.01)	0.31 (0.01)
Blink count [1/s]	0.37 (0.05)	0.49 (0.07)	0.30 (0.05)	0.39 (0.03)	0.44 (0.06)	0.50 (0.07)	0.27 (0.04)	0.40 (0.03)	0.40 (0.04)	0.50 (0.05)	0.29 (0.03)	0.40 (0.02)
Blink duration [ms]	61.8 (3.30)	58.07 (2.91)	79.93 (6.90)	66.60 (2.88)	71.04 (5.25)	60.54 (2.89)	84.47 (8.81)	72.01 (3.66)	66.42 (3.13)	59.30 (2.04)	82.20 (5.56)	69.31 (2.33)
PD [z-score]	-0.30 (0.04)	0.36 (0.07)	-0.88 (0.04)	-0.27 (0.06)	0.23 (0.08)	0.85 (0.07)	-0.78 (0.05)	0.10 (0.08)	-0.04 (0.06)	0.61 (0.06)	-0.83 (0.03)	-0.09 (0.05)

PD variance [z-score ²]	0.17 (0.02)	0.24 (0.02)	0.20 (0.03)	0.21 (0.01)	0.43 (0.03)	0.40 (0.03)	0.22 (0.03)	0.35 (0.02)	0.30 (0.03)	0.32 (0.02)	0.21 (0.02)	0.28 (0.01)
Fixation disparity [mm]	-12.22 (2.69)	-9.29 (2.69)	-16.58 (2.65)	-12.70 (1.56)	-8.88 (2.77)	-8.37 (3.00)	-15.81 (2.52)	-11.02 (1.62)	-10.55 (1.92)	-8.83 (2.00)	-16.20 (1.81)	-11.86 (1.12)
Fixation disparity variance [mm ²]	22.25 (2.40)	32.72 (3.68)	33.24 (11.89)	29.40 (4.21)	84.08 (20.13)	90.52 (19.13)	41.14 (12.60)	71.91 (10.31)	53.16 (10.83)	61.62 (10.36)	37.19 (8.60)	50.66 (5.78)

Note. Conv = Convergent thinking, Div = Divergent thinking, BL = Baseline condition, PD = Pupil Diameter.

Table S4.

Results of 2x2 within-subject ANOVAs for each eye parameter.

Tests of within-subject effects			
ATTENTION effects (IDC vs. EDC)			
Eye parameter	<i>F</i> (1,29)	<i>p</i>	η^2 (part)
Fixation count	6.65	.015	.19
Fixation duration	9.58	.004	.25
Saccade count	6.65	.015	.019
Saccade amplitude	4.04	.054	.12
Microsaccade count	43.38	< .001	.60
Microsaccade amplitude	6.80	.014	.19
Blink count	4.36	.046	.13
Blink duration	12.46	.001	.30
PD	32.95	< .001	.53
PD variance	35.48	< .001	.55
Fixation disparity	2.05	.163	.07
Fixation disparity variance	10.31	.003	.26
TASK effects (Conv vs. Div)			
Eye parameter	<i>F</i> (1,29)	<i>p</i>	η^2 (part)
Fixation count	5.21	.030	.15
Fixation duration	12.50	.001	.30
Saccade count	0.05	.833	.00
Saccade amplitude	1.44	.240	.05
Microsaccade count	7.70	.010	.21
Microsaccade amplitude	13.15	.001	.31
Blink count	8.43	.007	.23
Blink duration	12.41	.001	.30
PD	74.66	< .001	.72
PD variance	0.59	.450	.02
Fixation disparity	3.00	.094	.09
Fixation disparity variance	1.47	.236	.05
TASK (Conv vs. Div) x ATTENTION (IDC vs. EDC) effects			
Eye parameter	<i>F</i> (1,29)	<i>p</i>	η^2 (part)
Fixation count	10.70	.003	.27
Fixation duration	6.39	.017	.18
Saccade count	9.60	.004	.25
Saccade amplitude	0.16	.694	.01
Microsaccade count	5.88	.022	.17
Microsaccade amplitude	1.42	.244	.05
Blink count	5.58	.025	.16
Blink duration	5.33	.028	.16
PD	0.16	.697	.01
PD variance	11.55	.002	.28
Fixation disparity	3.75	.063	.11
Fixation disparity variance	0.12	.737	.00

Note. Bold *p*-Values denote significant effects at the Bonferroni-corrected level ($.05/12 = .004167$). PD = Pupil diameter, $F(df1, df2)$, η^2 (part) = partial eta squared.

Table S5.

Brain activation for pupil diameter (cluster-forming threshold; $p < .001$, $k \geq 100$).

Region	Lat.	BA	Peak (MNI)			k	T	p
			x	y	z			
PD (+)								
Calcarine Cortex, Cuneus, Lingual G	R	-	20	-70	14	3328	7.08	< .001
Caudate, Putamen	L	-	-14	12	0	1477	8.78	< .001
SMC	L	6	-8	8	52	616	6.15	< .001
Cerebellum	R	-	32	-58	-30	459	6.15	< .001
SFG	R	-	20	4	56	430	5.60	< .001
Brainstem	L/R	-	-4	-22	-8	356	6.49	< .001
Cerebellum	R	-	36	-64	-50	301	6.46	< .001
Cerebellum	L	-	-36	-50	-32	174	6.05	.004
SMG	R	-	38	-28	34	168	4.78	.005
Cerebellum	L/R	-	2	-58	-56	161	5.28	.006
MFG	R	-	34	40	36	160	5.47	.006
Insula, FO	R	45	32	24	8	129	5.32	.018
SPL	R	7	20	-64	50	113	4.64	.032
Cerebellum	L	-	-8	-68	-28	111	5.67	.035
PD (-)								
Pre-, Postcentral G	L	4	-56	-6	18	4007	9.11	< .001
Pre-, Postcentral G	R	4	46	-12	32	3580	8.78	< .001
IOG	L	19	-36	-82	-10	450	6.69	< .001
ACG	L/R	24	0	34	8	279	6.02	< .001
Pre-, Postcentral G	L	4	-18	-28	62	263	7.81	< .001
SFG	L/R	10	2	56	22	193	5.61	.002
Pre-, Postcentral G	R	4	20	-28	60	179	6.93	.003

Note. + = positive contrast, - = negative contrast, Lat. = Laterality/Lateral, BA = Brodmann area, k = cluster size, L/R = left/right, SMC = Supplementary Motor Cortex, SFG = Superior Frontal Gyrus, SMG = Supramarginal Gyrus, MFG = Middle Frontal Gyrus, FO = Frontal Operculum, SPL = Superior Parietal Lobe, G = Gyrus, IOG = Inferior Occipital Gyrus, ACG = Anterior Cingulate Gyrus.

Table S6.

Brain activation for saccade count (cluster-forming threshold; $p < .001$, $k \geq 100$).

Region	Lat.	BA	Peak (MNI)			k	T	p
			x	y	z			
Saccade count (+)								
IOG	L	18	-32	-84	4	478	6.23	< .001
Precentral G	R	4	46	-10	36	316	6.34	< .001
Postcentral G	L	1	-44	-20	40	281	5.39	< .001
MCG, SMC	L/R	8	2	16	38	204	5.04	< .001
IOG	R	18	36	-90	2	160	7.64	< .001
Cerebellum, FuG	L	-	-28	-64	-20	124	5.02	.001
FuG	R	19	32	-82	-14	113	5.51	.002
Saccade count (-)								
-	-	-	-	-	-	-	-	-

Note. + = positive contrast, - = negative contrast, Lat. = Laterality/Lateral, BA = Brodmann area, k = cluster size, L/R = left/right, IOG = Inferior Occipital Gyrus, G = Gyrus, MCG = Middle Cingulate Gyrus, SMC = Supplementary Motor Cortex, FuG = Fusiform Gyrus.