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

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Abstract

Many goal-directed, as well as spontaneous everyday activities (e.g., planning, mind-wandering), rely on an internal focus of attention. This fMRI–eye-tracking coregistration study 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.

1. 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, Stevens, Chamberlain, Gilmore, & Schacter, 2010), imagination (Benedek, 2018; Zabelina, 2018) and problem-solving (Jung-Beeman et al., 2004; Kounios & Beeman, 2009; Salvi, Bricolo, Franconeri, Kounios, & Beeman, 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...
Neubauer, 2014, 2011; Ceh et al., 2020; Cooper, Croft, signatures as evidenced by research using fMRI (Benedek and thus are characterized by distinct neurophysiological mechanisms) coregistration to measure brain activation and eye behavior concurrently during an established paradigm that manipulates internal/external attention demands (Benedek et al., 2016, 2017, 2011; Ceh et al., 2020). This design enabled us to test 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. The most prominent contribution to the existing literature comes from examining the temporal covariation of brain activation and several oculometric parameters, investigating the neural correlates of attention-related eye behavior changes: how do neural and perceptual mechanisms interact to support an internal focus of attention?

1.1. 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, & Spreng, 2014; Thomas Yeo et al., 2011). Formerly being considered a task-negative network (M. D. 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, & Yarkoni, 2014; Andrews-Hanna, Smallwood, & Spreng, 2014; Axelrod, Rees, & Bar, 2017; Benedek et al., 2016; Buckner, Andrews-Hanna, & Schacter, 2008; Dixon et al., 2018; Konishi, McLaren, Engen, & Smallwood, 2015; Margulies et al., 2016; Murphy et al., 2019, Murphy et al., 2018; Poerio et al., 2017; Smallwood et al., 2013; Spreng, Sepulcre, Turner, Stevens, & Schacter, 2013, 2016, 2010; Stawarczyk & D’Argembeau, 2015).

Importantly, recent studies also 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 supports 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 (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).

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. 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 .5sec, 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 responds 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, Ganis, & Thompson, 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, & Spreng, 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, Givens, & Bruno, 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).

1.2. Eye tracking correlates of internal cognition

Differences between internal and external cognition are also found at the level of eye behavior (Annerer-Walcher et al., 2021, 2018; Benedek et al., 2017; Ceh et al., 2020; Walcher et al., 2017). 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, Bruce, Bonner, Longbotham, & Doyle, 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, Abbing, & van Schie, 2018; Salvi et al., 2015). Microsaccadic activity, which has been proposed as a mechanism to counteract perceptual fading (Martinez-Conde, Macknik, Troncoso, & Dyar, 2006, 2013), decreases during IDC (Gao, Yan, & Sun, 2015; Krueger et al., 2019). Similarly, vergence movements need to be considered: They refer to the rotation of the eyes in the 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, Li, Ngai, & Bulling, 2019). Both reduced microsaccadic activity and increasing disparity are assumed to represent a reduced adaptation of eye behavior to visual processing needs (Annerer-Walcher et al., 2018; McCamy et al., 2012). When engaging in internal cognition, our eyes do not only decouple from external stimulation but also 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, Mannix, & Laeng, 2018).

When comparing states of IDC versus EDC, some eye parameters appear to be general indicators of attentional focus, given that they show a very uniform pattern, even across different tasks (e.g., PD, blink behavior). Others show 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: IDC 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 a smaller angle of eye vergence (AoEV) and greater AoEV variance.

1.3. 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 IDC/EDC. 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 (Benedek, Bergner, Könen, Fink, & Neubauer, 2011; Benedek, Schickel, Jauk, Fink, & Neubauer, 2014; Benedek & Fink, 2019; Fink & Benedek, 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, Haarmeyer, & Jensen, 2011; Klimesch, 2012; Rihs, Michel, & Thut, 2007) and PD is linked to memory load (Beatty, 1982; Kahneman & Beatty, 1966), such inhibitory processes might reflect gating dynamics linked to working memory updating (cf. Chatham & Badre, 2015). Generally, PD 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.

Similarly, the investigation of blink activity has yielded promising results: While watching videos, spontaneous blinks led to momentarily decreases in DAN activity and increased activation in DMN regions (Nakano, Kato, Morito, Itoi, & Kitazawa, 2013). Interestingly, blackening the screen did not lead to such changes, suggesting that blinks are actively involved in attentional disengagement from external stimulation. Furthermore, in a MEG study, spontaneous blinks were also related to increased precuneus activity (Liu, Hajra, Cheung, Song, & D’Arcy, 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 the visual cortex (Bristow, Haynes, Sylvester, Frith, & Rees, 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, Otero-Millan, & MacKnik, 2013; Tse, Baumgartner, & Greenlee, 2010). In addition, 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.

1.4. 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 versus EDC. This approach enabled us to investigate the relationship between brain activation and eye behavior as indicators of internal attention with high spatial resolution, including subcortical brain regions implicated in internal attention (e.g., lingual gyrus; Benedek et al., 2016). As a first main line of analysis, we tested how sustained states of IDC versus EDC differ with respect to brain activation and eye behavior. Overall, we expected that IDC compared to EDC is associated with stronger brain activation in areas of the DMN as well as decreased brain activity in DAN-related areas. Specifically, we expected increased aIPL, lingual gyrus, and cuneus activation during IDC and increased activity in visual networks, including the occipital gyrus and SPL during EDC (Benedek et al., 2016). At the level of eye behavior, we expected that IDC is associated with increases in PD, saccade amplitude, fixation duration, and fixation disparity variance, as well as decreases in saccade and microsaccade count (Benedek et al., 2017; Ceh et al., 2020). As a second line of analysis, we investigated which brain areas activate as a function of eye behavior changes over time as an index of transient fluctuations in attention focus.

This study thus builds on previous work but also extends it in several ways. First, this fMRI study analyzed both sustained and transient changes in internal/external attention focus by analyzing attention condition effects (internal vs. external condition) and temporal covariation between MRI BOLD and eye parameters over time. Second, while most MRI-eye-tracking studies have focused on single eye parameters such as pupil diameter, this study considers six eye parameters: fixations, saccades, microsaccades, blinks, pupil diameter, and eye vergence. This enabled us to explore the unique effect of these six eye parameters on brain activation while controlling for the effect of the other eye parameters. Finally, the comprehensive eye tracking assessment enabled us also to control attention effects on brain activation for transient attention-related fluctuations in attention as indicated by eye behavior. Together, these findings are expected to shed further light on neurophysiological dynamics underlying internally directed cognition.

2. Methods

Materials, data, and analysis scripts are accessible via the Open Science Framework (OSF; https://doi.org/10.17605/OSF.IO/74VNO) and OpenNeuro (https://doi.org/10.18112/openneuro.ds003176.v1.0.1). No part of the study procedures or analyses was pre-registered. We report how we determined our sample size, all data exclusions, all inclusion/exclusion criteria, whether inclusion/exclusion criteria were established prior to data analysis, all manipulations, and all measures in the study.

2.1. Participants

Thirty-four adults participated in this study. Participants gave written informed consent before starting the MR session and completed a questionnaire to verify MRI safety. The sample size was determined based on previous similar neuroscientific work in this field (Benedek et al., 2016; Ceh et al., 2020), and data exclusion criteria were established after inspecting data quality. 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.

2.2. Experimental design, tasks & procedure

The experimental tasks and design were closely adapted from previous research (Benedek et al., 2016, 2017, 2011; 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). Analyzing the effects of attention manipulation across two tasks with differing task demands allows for testing the robustness of attention effects. 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 trial sequence outlined in Fig. 1 demonstrates that each trial started with a temporally variable fixation cross, ranging from three to 5 sec, 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 (.5sec), enforcing higher internal attention demands in the subsequent task performance, which lasted for 18.5 sec. In the other half of the 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 canceling 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 48 trials (18 Conv, 18 Div & 12 BL), half of which were masked. Trials were grouped into eight blocks of six trials and arranged 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 sec). 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 (~27.5 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).

2.3. Data collection, preprocessing and analysis

All measures and manipulations of this study are reported here.

2.3.1. 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 msec, TI = 1000 msec, TE = 1.88 msec, FA = 8°, 192 slabs, voxel size = .88 mm isotropic, FoV = 256 × 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 msec, TE = 38.4 msec, multiband acceleration factor = 4, flip angle = 60°, 48 slices, voxel size = 3 mm isotropic, FoV = 80 × 80 mm), amounting to an average of 1655 volumes per participant (range: 1645 to 1662, due to the temporally variable fixation periods). 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., 2019), 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 were 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). A composite transform was applied to correct for head-motion using six translation (i.e., x, y, z) and rotation (i.e., pitch, roll, yaw, respectively) parameters. A 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, DVARS, three global signals, and physiological regressors to allow for

Fig. 1 – Trial sequence. Each trial started with an initial fixation period lasting between three and 5 sec. Then, the stimulus word was shown for a) the full course of 20 sec (EDC condition) or b) .5 sec and then replaced by a mask (“XXXX”) for the remaining 19.5sec (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 1.5sec.
component-based noise correction (CompCor, Behzadi, Restom, Liau, & Liu, 2007). Temporal CompCor components were then calculated from the top 5% variable voxels within a mask covering the subcortical regions, cerebrospinal fluid, and white matter separately. The confound time series derived from head motion estimates and global signals were expanded with the inclusion of temporal derivatives and quadric terms for each (Satterthwaite et al., 2013). No subjects were excluded due to excessive movements (mean FD < .50 mm, Power, Barnes, Snyder, Schlaggar, & Petersen, 2012; range: .13–.34 mm). 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). Further details regarding MRI preprocessing and data quality are provided as supplemental resources at the OSF and OpenNeuro.

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 modeled with boxcar functions starting .5 sec 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 sec, convolved with the canonical hemodynamic response function (HRF). Additionally, six 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 sec; 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 (i.e., FD, white matter, CSF, and six rotation and translation parameters) 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-IDC + BL-EDC). Next, the effect of internal attention was analyzed with a contrast of internal versus 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 versus 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) ≥ 3. Attention effects were further explored using a slightly less conservative criterion by correcting for multiple comparison with FWE at the cluster level (cluster-forming threshold; p < .001, k ≥ 111). In addition, we conducted a follow-up ROI analysis to examine the predicted dissociation of attention effects with respect to the DMN and DAN. To this end, we defined a DMN ROI and a DAN ROI based on the 7-network parcellation by Thomas Yeo et al. (2011; https://surfer.nmr.mgh.harvard.edu/fswiki/CorticalParcellation_yeo2011; 7 network liberal mask) and reran analyses for attention conditions using these ROIs (p < .05, FWE-corrected for multiple comparisons, k ≥ 3).

2.3.2. 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 × 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 approximately 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 the 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, Sinn, Mergenthaler, & Trukenbrod, 2015), deviating from threshold settings as in previous studies (Benedek et al., 2017; Ceh et al., 2020; Walcher et al., 2017) to account for relatively smaller stimulus size because of increased distance to the screen, with microsaccades being defined as saccades with an amplitude below .633° visual angle, lasting for at least 6 msec and λ = 4. Saccades, and additional 20 msec periods before and after each saccade were removed from pupil and gaze position data. Blink periods, and additional 200 msec periods before and after each blink were removed 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 sec activation interval starting 1.5 sec after stimulus onset to account for possible influences related to stimulus presentation (Nikolaev, Meghanathan, & van Leeuwen, 2016). For continuous eye parameters (PD, fixation disparity), we computed an average and the 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 (IDC vs. EDC) and potential task effects (Conv vs. Div) were analyzed with 2 × 2 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 2 × 2 ANOVAs (i.e., critical alpha was set to .05/12 = .004167).

2.3.3. fMRI-eye-tracking covariation analyses
Eye tracking data of each parameter were sliced in 1 sec segments on the subject level to match the scanner’s repetition time (TR = 1.0 sec). 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 sec 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 Fig. 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 modeled the main tasks (Conv and Div) and the baseline task (BL) as two regressors of no interest (note that attention direction was not modeled 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 ≥ 3. Significant effects were further explored using a slightly less conservative criterion by correcting for multiple comparisons with FWE at the cluster level (cluster-forming threshold; p < .001, k ≥ 111).

3. Results

3.1. Behavioral results
Participants were able to solve 76.67% (SE = 1.91) of all trials. A 2 × 2 repeated measures ANOVA (Table S1) regarding the within-subject factors attention (IDC vs EDC) and task (Conv vs Div) revealed 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 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. These effects were also reflected in subjective difficulty ratings (see also Table S1) and 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., 2017, 2011; Ceh et al., 2020).

Fig. 2 – Visualization of a dataset for one exemplary participant, including BOLD act for four selected regions and frequency/z-scores for the six eye parameters. The data are presented in 1 sec segments across the duration of the entire data acquisition (eight consecutive blocks). Note. EDC = externally directed cognition, IDC = internally directed cognition, SOG = superior occipital gyrus, LG = lingual gyrus, R = right, L = left.
3.2. fMRI results

We first computed task-general brain activation effects, reflecting the common brain activation across tasks and conditions (see Table S2 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), the 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 the 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 the bilateral precenral 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 S3 and Fig. 3). A follow-up ROI analysis further provided evidence of a double-dissociation with respect to internal/external attention with DMN and DAN activity, respectively: IDC was associated with increased activity in left-lateralized middle cingulate gyrus and cuneus areas, but not with any DAN activation; in contrast, EDC was associated with increased DAN activity including widespread areas of the middle and superior occipital gyrus, but not with any DMN activation (Table S4). Brain activation effects associated with the convergent versus divergent thinking largely replicate a previous study using the same tasks (Benedek et al., 2016) and are shown in Table S5.

3.3. Eye tracking results

Attention effects (IDC vs EDC) and potential task effects (Conv vs Div) on available eye parameters were analyzed with $2 \times 2$ ANOVAs for each eye parameter (see Table S6 for descriptive statistics regarding all eye parameters and Table S7 for ANOVA results). Looking at attention effects, IDC involved lower microsaccade count ($F_{1,29} = 43.38, p < .001, \eta^2_p = .60$), longer blinks ($F_{1,29} = 12.46, p = .001, \eta^2_p = .30$), greater PD ($F_{1,29} = 32.95, p < .001, \eta^2_p = .53$), greater PD variance ($F_{1,29} = 35.48, p < .001, \eta^2_p = .55$), and greater fixation disparity variance ($F_{1,29} = 10.31, p = .003, \eta^2_p = .26$). No differences between IDC and EDC were found for fixation count ($F_{1,29} = 6.65, p = .015$), fixation duration

| Region                        | Lat. | BA | Peak (MNI) x | y | z | k | T  | p  |
|-------------------------------|------|----|--------------|---|---|---|----|----|
| 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|
| FCg, 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 | -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    | 6  | -22          | -6 | 48 | 24  | 6.79 | .012|
| Precentral G                  | L    | 6  | -52          | 6  | 30 | 8   | 6.52 | .022|
| Cerebellum                    | R    | 28 | -28          | -70| -52| 8   | 6.45 | .025|
| Brainstem, Thalamus           | L    | 6  | -6           | -32| -2 | 7   | 8.08 | <.001|
| Cerebellum                    | L/R  | 0  | 0            | -48| -30| 6   | 7.14 | <.001|
| Thalamus                      | L    | 50 | -14          | -28| 12 | 6   | 7.05 | .007|
| Putamen                       | L    | 6  | -32          | -18| -4 | 4   | 6.66 | .016|
| Thalamus                      | L    | 6  | -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.
(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 = .16). Effect sizes of all oculometric differences between IDC and EDC are displayed in Fig. 4. Task effects (Conv vs. Div) and interaction effects (attention condition x task) were similar to those observed in previous studies and are reported in the supplementary material (Benedek et al., 2017; Ceh et al., 2020; see also Table S7).

### 3.4. 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 post-central 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 2). In addition, 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, right insula, right SMG, and

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Fig. 3 – Brain activation results for internally versus 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-)cuneous (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).

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Fig. 4 – Effect sizes of oculometric differences between internally directed cognition (IDC) and externally directed cognition (EDC). Note. PD = pupil diameter; ***p < .001, **p < .004167 (Bonferroni-corrected).
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 S8 and Fig. 5). More saccades were 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 S9).

4. 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

![Brain activation results for pupil diameter](Fig. 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).
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, including parts of the DMN (Benedek et al., 2016; Corbetta, Patel, & Shulman, 2008; Kosslyn et al., 2001), as well as 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). As a central novelty of this study, FMRI-eye tracking covariation analyses revealed 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 an internal focus of attention.

4.1. **Attention effects on brain activation**

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, Gorno-Tempini, & Price, 2003), and may be involved in mental simulations and manipulations of the stimulus letters during task performance. LG activity has been further associated with employing visual imagery strategies in memory tasks (Leshikar, Duarte, & Hertzog, 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 the recruitment of visual strategies for retrieving particularly remote instances for these characteristics (Benedek, Jurisch, Koschutnig, Fink, & Beatty, 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 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), representing 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 & Cronkners, 2006; Berryhill, Chein, & Olson, 2013). Thus, engaging in internal cognition may place higher demands on working memory and therefore require stronger shielding of internal representations.

Externally directed cognition, in contrast, was linked to the recruitment of the visual and dorsal attention networks, indicated by widespread activation of occipital regions and 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; Murphy et al., 2018, 2019). Yet, the DMN seems to be more sensitive to the kind of internal activity (e.g., imagination) rather than to internal attention in general (Andrews-Hanna & Grilli, 2021; Benedek et al., 2016). For example, studies have also reported DMN disengagement during internal focus periods such as hallucinations (Jardri, Thomas, Delmaire, Delton, & Pins, 2013; Lefevbre et al., 2016). In this context, it seems crucial to acknowledge the manifold facets of internally directed cognition including goal-directed processes (as in the present study) and more spontaneous thought experiences (Benedek & Jauk, 2018; Christoff, Irving, Fox, Spreng, & Andrews-Hanna, 2016).

4.2. **Attention effects on eye behavior**

We were also able to essentially replicate findings from previous eye tracking studies suggesting that internally directed cognition is associated with a distinct pattern of eye behavior (Annerer-Walcher, Körner, Beatty, & Benedek, 2020, 2018; 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, Braboszcz, & Delorme, 2014; Smilek, Carriere, & Cheyne, 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., 2013, 2006; McCamy et al., 2012). Other studies reported that spontaneous “in-sight” moments were also associated with
increased blink rate and lower microsaccade rate (cf. Kounios & Beeman, 2009; Salvi et al., 2015, 2020). Increased variance in PD and fixation disparity is 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 versus EDC, as in this study (e.g., Annerer-Walcher et al., 2021; Franklin, Broadway, Mrazek, Smallwood, & Schooler, 2013; Konishi, Brown, Battaglini, & Smallwood, 2017). Yet, PD increases have also been observed when orienting attention to external events (Sara & Bouret, 2012). For, a recent study found greater PD to indicate visual distraction during an IDC task (Annerer-Walcher et al., 2020), while executive functioning and attention capacity only marginally predicted distractibility. In fact, higher PD has been consistently associated with higher memory load and related increases of task difficulty (Kahneman & Beatty, 1966; Piquado, Isaacowitz, & Wingfield, 2010; Porter, Trosclair, & Gilchrist, 2007). Taken together, PD may not represent an index of internal attention per se but of corresponding higher mental load (Unsworth & Robison, 2018). PD increases have also been linked to insight problem-solving, a process characterized by internal attention allocation (Salvi, Simoncini, Grafman, & Beeman, 2020). PD can be considered a promising metric to index transient changes of attention (Kang, Huffer, & Wheatley, 2014; Kang & Wheatley, 2015), especially when weighing in factors such as task characteristics, task focus, and time-on-task effects (Van Den Brink, Murphy, & Nieuwenhuis, 2016), since mental load arguably is a common characteristic of 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, there is 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.

4.3 Temporal covariation between fMRI and eye tracking indicators of IDC

As a central novelty of this study, the concurrent recording of BOLD signal as an index of brain activity and several continuous indicators of eye behavior enabled us to investigate their relationship during task performance 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 the 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 and the most substantial associations with brain activation over time, which included brain regions that showed attention effects (e.g., cuneus). This finding is strikingly similar to a previous EEG study, where PD also showed the strongest attention effect for IDC versus EDC and was the only eye parameter showing significant temporal covariation during rest 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 susceptible 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 internal attention. In this context, it is interesting to note that the temporal covariation of PD with BOLD activity involved brain areas that were partly overlapping and partly unique to those observed from the experimental manipulation of sustained internal attention. For example, transient increases of PD as well as experimentally induced sustained IDC both implicated increased activation of the cuneus, but the latter was associated with increased activity in the posterior cingulate cortex, and PD was associated with increased caudate activity, but not vice versa. These findings may point to common and distinct neural processes associated with sustained and transient internal attention states.

Further 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 the 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 a 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 a higher workload than EDC conditions, where the stimulus was continuously available. Other studies also reported PD increases when greater demands were placed on visuospatial working memory (Annerer-Walcher et al., 2020; Klingner, Tversky, & Hanrahan, 2011) and showed that PD is sensitive to individual differences in visuospatial 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, reflected by increased PD and activity in 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 precisely 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.

4.4. Task effects

In general, we found that the attention effects investigated in the present study were robust across the two tasks with varying levels of self-generated thought (i.e., convergent versus divergent thinking). We further observed independent task effects that replicated findings of previous eye tracking studies (Benedek et al., 2017; Ceh et al., 2020), as well as of a previous fMRI study: Divergent thinking activated the left IFG and SFG, consistent with much previous research (Benedek et al., 2016; Madore, Thakral, Beaty, Addis, & Schacter, 2019; Zabelina & Ganis, 2018; for a meta-analysis, see; Gonen-Yaacovi et al., 2013). These regions have been associated with cognitive control (Brass, Derrfuss, Forstmann, & von Cramon, 2005) and semantic/conceptual processing (Andrews-Hanna, Smallwood, & Spreng, 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 and Jauk, 2019). Interestingly, we did not replicate that divergent thinking is associated with higher DMN activity than convergent thinking (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, Benedek, Silvia, & Schacter, 2016; Zabelina & Andrews-Hanna, 2016).

4.5. 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 PD 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). Thus, we conclude that internally and externally directed cognition are characterized by distinct neurophysiological signatures reflecting perceptual and neural mechanisms subserving sustained attention to internal versus external worlds.

Credit authorship contribution statement

Conceptualization: SMC, SAW, MB, CK; Data acquisition: SMC, KK; Formal analysis: SMC, MB, KK; Funding acquisition: SAW, MB, AF, CK; Writing – original draft: SMC, SAW, KK, CK, AF, MB; Writing – review & editing: SMC, CK, MB.

Ethics approval statement

This study was approved by the local ethics committee.

Declaration of competing interest

The authors declare no conflict of interest.

Data availability

Materials, data, and analysis scripts are accessible via the Open Science Framework (OSF; https://doi.org/10.17605/OSF.IO/74VNQ) and OpenNeuro (https://doi.org/10.18112/openneuro.ds003176.v1.0.1).

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Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.3389/fpsyg.2015.00325.

R E F E R E N C E S

Abeles, D., & Yuval-Greenberg, S. (2017). Just look away: Gaze aversions as an overt attentional disengagement mechanism. Cognition, 168, 99–109. https://doi.org/10.1016/j.cognition.2017.06.021

Abraham, A., & Bubic, A. (2015). Semantic memory as the root of imagination. Frontiers in Psychology, 6, 1–5. https://doi.org/10.3389/fpsyg.2015.00325
Abraham, A., Pieritz, K., Thbyusch, K., Rutter, B., Kroger, S., Schweckendiek, J., et al. (2012). Creativity and the brain: Uncovering the neural signature of conceptual expansion. Neuropsychologia, 50(8), 1906–1917. https://doi.org/10.1016/j.neuropsychologia.2012.04.015

Alnaes, D., Sneve, M. H., Espeseth, T., Endestad, T., van de Pavert, S. H. F., & Laeng, B. (2014). Pupil size signals mental effort deployed during multiple object tracking. Journal of Vision, 14(4), 1–20. https://doi.org/10.1167/14.4.1

Andrews-Hanna, J. R., & Grilli, M. D. (2021). Mapping the imaginative mind: Charting new paths forward. Current Directions in Psychological Science, 30(1), 82–89. https://doi.org/10.1177/0963721420980753

Andrews-Hanna, J. R., Saxe, R., & Yarkoni, T. (2014). Contributions of episodic retrieval and mentalizing to autobiographical thought: Evidence from functional neuroimaging, resting-state connectivity, and fMRI meta-analyses. Neuroimage, 91, 324–335. https://doi.org/10.1016/j.neuroimage.2014.01.032

Annerer-Walcher, S., Körner, C., Beatty, R. E., & Benedek, M. (2020). Eye behavior predicts susceptibility to visual distraction during internally directed cognition. Attention, Perception, and Psychophysics, 1. https://doi.org/10.3758/s13414-020-02068-1

Annerer-Walcher, S., Körner, C., Beatty, R. E., & Benedek, M. (2018). Eye behavior does not adapt to expected visual distraction during internally directed cognition. Plos One, 13(9), 1–19. https://doi.org/10.1371/journal.pone.0204963

Axelrod, V., Rees, G., & Bar, M. (2017). The default network and the combination of cognitive processes that mediate self-generated thought. Nature Human Behaviour, 1(12), 896–910. https://doi.org/10.1038/s41562-017-0244-9

Baldo, J. V., & Cronkers, N. F. (2006). The role of inferior parietal and inferior frontal cortex in working memory. Neuropsychology, 20(5), 529–538. https://doi.org/10.1077/1089-4105.20.5.529

Beatty, J. (1982). Task-evoked pupillary responses, processing load, and the structure of processing resources. Psychological Bulletin, 91(2), 276–292. https://doi.org/10.1037/0033-2909.91.2.276

Beatty, R. E., Benedek, M., Silvia, P. J., & Schacter, D. L. (2016). Creative cognition and brain network dynamics. Trends in Cognitive Sciences, 20(2), 87–95. https://doi.org/10.1016/j.tics.2015.10.004

Behzadi, Y., Restom, K., Liu, J., & Liu, T. T. (2012). A component based noise correction method (CompCor) for BOLD and perfusion based fMRI. Neuroimage, 37(1), 90–101. https://doi.org/10.1016/j.neuroimage.2007.04.042

Benedek, M. (2018). Internally directed attention in creative cognition. In R. E. Jung, & O. Vartanian (Eds.), The Cambridge handbook of the neuroscience of creativity (pp. 180–194). Cambridge University Press. https://doi.org/10.1017/9781108253231.011

Benedek, M., Bergner, S., Konen, T., Fink, A., & Neubauer, A. C. (2011). EEG alpha synchronization is related to top-down processing in convergent and divergent thinking. Neuropsychologia, 49(12), 3505–3511. https://doi.org/10.1016/j.neuropsychologia.2011.09.004

Benedek, M., & Fink, A. (2019). Toward a neurocognitive framework of creative cognition: The role of memory, attention, and cognitive control. Current Opinion in Behavioral Sciences, 27, 116–122. https://doi.org/10.1016/j.cobeha.2018.11.002

Benedek, M., & Jauk, E. (2018). Spontaneous and controlled processes in creative cognition. In K. C. R. Fox, & K. Christoff (Eds.), The Oxford handbook of spontaneous thought: Mind-wandering, creativity, dreaming, and clinical conditions (pp. 285–298). Oxford University Press.

Benedek, M., & Jauk, E. (2019). Creativity and cognitive control. In J. Kaufman, & R. Sternberg (Eds.), The Cambridge handbook of creativity (pp. 200–223). Cambridge University Press. https://doi.org/10.1017/9781316979839.012

Benedek, M., Jauk, E., Beatty, R. E., Fink, A., Koschutnig, K., & Neubauer, A. C. (2016). Brain mechanisms associated with internally directed attention and self-generated thought. Scientific Reports, 6, 1–8. https://doi.org/10.1038/srep22959

Benedek, M., Jurisch, J., Koschutnig, K., Fink, A., & Beatty, R. E. (2020). Elements of creative thought: Investigating the cognitive and neural correlates of association and bi-association processes. Neuroimage, 210, 116586. https://doi.org/10.1016/j.neuroimage.2020.116586

Benedek, M., Schickel, R. J., Jauk, E., Fink, A., & Neubauer, A. C. (2014). Alpha power increases in right parietal cortex reflects focused internal attention. Neuropsychologia, 58(1), 393–400. https://doi.org/10.1016/j.neuropsychologia.2014.02.010

Benedek, M., Stoiser, R., Walcher, S., & Körner, C. (2017). Eye behavior associated with internally versus externally directed cognition. Frontiers in Psychology, 8, 1–9. https://doi.org/10.3389/fpsyg.2017.01092

Berryhill, M. E., Chein, J., & Olson, I. R. (2011). At the intersection of attention and memory: The mechanical role of the posterior parietal lobe in working memory. Neuropsychologia, 49(5), 1306–1315. https://doi.org/10.1016/j.neuropsychologia.2011.02.033

Binder, J. R., & Desai, R. H. (2011). The neurobiology of semantic memory. Trends in Cognitive Sciences, 15(11), 527–536. https://doi.org/10.1016/j.tics.2011.10.001

Brass, M., Derrfuss, J., Forstmann, B., & von Cramon, D. Y. (2005). The role of the inferior parietal junction area in cognitive control. Trends in Cognitive Sciences, 9(7), 312–314. https://doi.org/10.1016/j.tics.2005.05.013

Bristow, D., Haynes, J. D., Sylvester, R., Frith, C. D., & Rees, G. (2005). Blinking suppresses the neural response to unchanging retinal stimulation. Current Biology, 15(4), 1296–1300. https://doi.org/10.1016/j.cub.2005.06.025

Buckner, R. L., Andrews-Hanna, J. R., & Schacter, D. L. (2008). The brain’s default network: Anatomy, function, and relevance to disease. Annals of the New York Academy of Sciences, 1124, 1–38. https://doi.org/10.1196/annals.1440.011

Ceh, S. M., Annerer-Walcher, S., Körner, C., Rominger, C., Kober, S. E., Fink, A., et al. (2020). Neurophysiological indicators of internal attention: An EEG-eye-tracking coregistration study. Brain and Behavior, Article e01790. https://doi.org/10.1002/brb3.1790

Chatham, C. H., & Badre, D. (2015). Multiple gates on working memory. Current Opinion in Behavioral Sciences, 1, 23–31. https://doi.org/10.1016/j.cobeha.2014.08.001

Chen, S., & Epps, J. (2014). Using task-induced pupil diameter and blink rate to infer cognitive load. Human-Computer Interaction, 29(4), 390–413. https://doi.org/10.1080/07370024.2014.892428

Christoff, K., Irving, Z. C., Fox, K. C. R., Spreng, R. N., & Andrews-Hanna, J. R. (2016). Mind-wandering as spontaneous thought: A dynamic framework. Nature Reviews Neuroscience, 17(11), 718–731. https://doi.org/10.1038/nrn.2016.113

Chun, M. M., Golomb, J. D., & Turk-Browne, N. B. (2011). A Taxonomy of external and internal attention. Annual Review of Psychology, 62, 73–101. https://doi.org/10.1146/annurev.psych.093008.100427
Killingsworth, M. A., & Gilbert, D. T. (2010). A wandering mind is an unhappy mind. Science, 330(6006), 932. https://doi.org/10.1126/science.1192439

Kimmig, H., Greenlee, M. W., Gondan, M., Schira, M., Kassubek, J., & Mergner, T. (2001). Relationship between saccadic eye movements and cortical activity as measured by fMRI: Quantitative and qualitative aspects. Experimental Brain Research, 141(2), 184–194. https://doi.org/10.1007/s002210100964

Klimesch, W. (2012). Alpha-band oscillations, attention, and controlled access to stored information. Trends in Cognitive Sciences, 16(12), 606–617. https://doi.org/10.1016/j.tics.2012.10.007

Klingner, J., Tversky, B., & Hanrahan, P. (2011). Effects of visual and verbal presentation on cognitive load in vigilance, memory, and arithmetic tasks. Psychophysiology, 48(3), 323–332. https://doi.org/10.1111/j.1469-8986.2010.01069.x

Konishi, M., Brown, K., Battaglini, L., & Smallwood, J. (2017). When attention wanders: Pupillometric signatures of fluctuations in external attention. Cognition, 168, 16–26. https://doi.org/10.1016/j.cognition.2017.06.006

Konishi, M., McLaren, D. G., Engen, H., & Smallwood, J. (2015). Shaped by the past: The default mode network supports cognition that is independent of immediate perceptual input. Plos One, 10(6), 1–18. https://doi.org/10.1371/journal.pone.0132209

Kosslyn, S. M., Ganis, G., & Thompson, W. L. (2001). Neural foundations of imagery. Nature Reviews Neuroscience, 2(9), 635–645. https://doi.org/10.1038/35090055

Kounios, J., & Beeman, M. (2009). The Aha! Moment: The cognitive neuroscience of insight. Current Directions in Psychological Science, 18(4), 210–216. https://doi.org/10.1111/j.1467-8721.2009.01638.x

Krueger, E., Schneider, A., Sawyer, B. D., Chavaillaz, A., Sonderegger, A., Groner, R., et al. (2019). Microsaccades distinguish looking from seeing. Journal of Eye Movement Research, 12(6), 1–15. https://doi.org/10.1631/jemr.12.6.2

Kucyi, A., Hove, M. J., Esterman, M., Hutchison, R. M., & Valera, E. M. (2017). Dynamic brain network correlates of spontaneous fluctuations in attention. Cerebral Cortex (New York, N.Y.), 27(3), 1831–1840. https://doi.org/10.1093/cercor/bhw029. 1991.

Laeng, B., & Sulutvedt, U. (2014). The eye pupil adjusts to imaginary light. Psychological Science, 25(1), 188–197. https://doi.org/10.1177/0956797613503556

Lefebvre, S., Demeulemeester, M., Leroy, A., Delmaire, C., Lopes, R., Pins, D., et al. (2016). Network dynamics during the different stages of hallucinations in schizophrenia. Human Brain Mapping, 37(7), 2571–2586. https://doi.org/10.1002/hbm.23197

Leschikar, E. D., Duarte, A., & Hertzog, C. (2012). Task-selective memory effects for successfully implemented encoding strategies. Plos One, 7(5). https://doi.org/10.1371/journal.pone.0038160

Liu, C. C., Hajra, S. G., Cheung, T. P. L., Song, X., & D’Arcy, R. C. N. (2017). Spontaneous blinks activate the precuneus: Characterizing blink-related oscillations using magnetoencephalography. Frontiers in Human Neuroscience, 11, 1–12. https://doi.org/10.3389/fnhum.2017.00489

Madore, K. P., Thakral, P. P., Beaty, R. E., Addis, D. R., & Schacter, D. L. (2019). Neural mechanisms of episodic retrieval support divergent creative thinking. Cerebral Cortex, 29(1), 150–166. https://doi.org/10.1093/cercor/bhx312

Margules, D. S., Ghosh, S. S., Goulas, A., Falkiewicz, M., Huntenburg, J. M., Langs, C., et al. (2016). Situating the default-mode network along a principal gradient of macroscale cortical organization. Proceedings of the National Academy of Sciences of the United States of America, 113(44), 12574–12579. https://doi.org/10.1073/pnas.1608282113

Martinez-Conde, S., Macknik, S. L., Troncoso, X. G., & Dyar, T. A. (2006). Microsaccades counteract visual fading during fixation. Neuron, 49(2), 297–305. https://doi.org/10.1016/j.neuron.2005.11.033

Martinez-Conde, S., Otero-Millan, J., & Macknik, S. L. (2013). The impact of microsaccades on vision: Towards a unified theory of saccadic function. Nature Reviews Neuroscience, 14(2), 83–96. https://doi.org/10.1038/nrn3405

McCamy, M. B., Otero-Millan, J., Macknik, S. L., Yang, Y., Troncoso, X. G., Baer, S. M., et al. (2012). Microsaccadic efficacy and contribution to foveal and peripheral vision. Journal of Neuroscience, 32(27), 9194–9204. https://doi.org/10.1523/JNEUROSCI.0515-12.2012

Mechelli, A., Gorno-Tempini, M. L., & Price, C. J. (2003). Neuroimaging studies of word and pseudoword reading: Consistencies, inconsistencies, and limitations. Journal of Cognitive Neuroscience, 15(2), 260–271. https://doi.org/10.1162/08989290321208196

Murphy, C., Jefferies, E., Rueschemeyer, S. A., Sormaz, M., Wang, H. T., Margulies, D. S., et al. (2018). Distant from input: Evidence of regions within the default mode network supporting perceptually-decoupled and conceptually-guided cognition. Neuroimage, 171, 393–401. https://doi.org/10.1016/j.neuroimage.2018.01.017

Murphy, C., Wang, H. T., Konu, D., Lowndes, R., Margulies, D. S., Jefferies, E., et al. (2019). Modes of operation: A topographic neural gradient supporting stimulus dependent and independent cognition. Neuroimage, 186, 487–496. https://doi.org/10.1016/j.neuroimage.2018.11.009

Nakano, T., Kato, M., Morito, Y., Ito, S., & Kitazawa, S. (2013). Blink-related momentary activation of the default mode network while viewing videos. Proceedings of the National Academy of Sciences of the United States of America, 110(2), 702–706. https://doi.org/10.1073/pnas.1214804110

Nikolaev, A. B., Meghanathan, R. N., & van Leeuwen, C. (2016). Combining EEG and eye movement recording in free viewing: Pitfalls and possibilities. Brain and Cognition, 107, 55–83. https://doi.org/10.1016/j.bandc.2016.06.004

Piquado, T., Isaacowitz, D., & Wingfield, A. (2010). Pupillometry as a measure of cognitive effort in younger and older adults. Psychophysiology, 47(3), 560–569. https://doi.org/10.1111/j.1469-8986.2009.00947.x

Poerio, G. L., Sormaz, M., Wang, H. T., Margulies, D., Jefferies, E., & Smallwood, J. (2017). The role of the default mode network in component processes underlying the wandering mind. Social Cognitive and Affective Neuroscience, 12(7), 1047–1062. https://doi.org/10.1093/scan/nss041

Porter, G., Troscianko, T., & Gilchrist, I. D. (2007). Effort during visual search and counting: Insights from pupillometry. The Quarterly Journal of Experimental Psychology: QJEP, 60(2), 211–229. https://doi.org/10.1080/17470210600673818

Power, J. D., Barnes, K. A., Snyder, A. Z., Schlaggar, B. L., & Petersen, S. E. (2012). Spurious but systematic correlations in functional connectivity MRI networks arise from subject motion. Neuron, 59, 2142–2154. https://doi.org/10.1016/j.neuron.2011.10.018

R Core Team. (2020). R: A language and environment for statistical computing.

Raichle, M. E., MacLeod, A. M., Snyder, A. Z., Powers, W. J., Gusnard, D. A., & Shulman, G. L. (2001). A default mode of brain function. Proceedings of the National Academy of Sciences of the United States of America, 98(2), 676–682. https://doi.org/10.1073/pnas.98.2.676

Ray, W. J., & Cole, H. W. (1985). EEG alpha activity reflects attentional demands, and beta activity reflects emotional and
cognitive processes. Science, 228(4700), 750–752. https://doi.org/10.1126/science.3992243
Rihs, T. A., Michel, C. M., & Thut, G. (2007). Mechanisms of selective inhibition in visual spatial attention are indexed by α-band EEG synchronization. European Journal of Neuroscience, 25(2), 603–610. https://doi.org/10.1111/j.1460-9568.2007.05278.x
Ritter, S. M., Abbé, J., & van Schie, H. T. (2018). Eye-closure enhances creativity performance on divergent and convergent creativity tasks. Frontiers in Psychology, 9, 1–9. https://doi.org/10.3389/fpsyg.2018.01315
Salvi, C., Bricolo, E., Franconeri, S. L., Kounios, J., & Beeman, M. (2015). Sudden insight is associated with shutting out visual inputs. Psychonomic Bulletin & Review, 22(6), 1814–1819. https://doi.org/10.3758/s13423-015-0845-0
Salvi, C., Simoncini, C., Graffman, J., & Beeman, M. (2020). Oculometric signature of switch into awareness? Pupil size predicts sudden insight whereas microsaccades predict problem-solving via analysis. NeuroImage, 217, 116933. https://doi.org/10.1016/j.neuroimage.2020.116933
Sara, S. J., & Bouret, S. (2012). Orienting and reorienting: The locus coeruleus modulates cognition through arousal. Neuron, 76(1), 130–141. https://doi.org/10.1016/j.neuron.2012.05.011
Sarter, M., Givens, B., & Bruno, J. P. (2001). The cognitive neuroscience of sustained attention: Where top-down meets bottom-up. Brain Research Reviews, 35(2), 146–160. https://doi.org/10.1016/S0165-0173(01)00044-3
Satterthwaite, T. D., Elliott, M. A., Gerraty, R. T., Raper, K., Lougheed, J., Calkins, M. E., … Wolf, D. H. (2013). An improved framework for confound regression and filtering for control of motion artifact in the preprocessing of resting-state functional connectivity data. NeuroImage, 64, 240–256. https://doi.org/10.1016/j.neuroimage.2012.08.052
Shapiro, K., & Hillstrom, A. P. (2002). Control of visuotemporal attention by inferior parietal and superior temporal cortex. Current Biology, 12(15), 1320–1325. https://doi.org/10.1016/S0960-9822(02)00400-0
Singh-Curry, V., & Husain, M. (2009). The functional role of the inferior parietal lobe in the dorsal and ventral stream dichotomy. Neuropsychologia, 47(6), 1434–1448. https://doi.org/10.1016/j.neuropsychologia.2008.11.033
Smallwood, J., Brown, K. S., Tipper, C., Giesbrecht, B., Franklin, M. S., Mrazek, M. D., et al. (2011). Pupilometric evidence for the decoupling of attention from perceptual input during offline thought. Plos One, 6(3). https://doi.org/10.1371/journal.pone.0018298
Smallwood, J., & Schooler, J. W. (2006). The restless mind. Psychological Bulletin, 132(6), 946–958. https://doi.org/10.1037/0033-2909.132.6.946
Smallwood, J., & Schooler, J. W. (2015). The Science of Mind Wandering: Empirically Navigating the Stream of Consciousness. Annual Reviews of Psychology, 66, 487–518. https://doi.org/10.1146/annurev-psych-010814-015331
Smallwood, J., Tipper, C., Brown, K., Baird, B., Engen, H., Michaels, J. R., et al. (2013). Escaping the here and now: Evidence for a role of the default mode network in perceptually decoupled thought. NeuroImage, 69, 120–125. https://doi.org/10.1016/j.neuroimage.2012.12.012
Smilek, D., Carriere, J. S. A., & Cheyne, J. A. (2010). Out of mind, out of sight: Eye blinking as indicator and embodiment of mind wandering. Psychological Science, 21(6), 786–789. https://doi.org/10.1177/0956797610368063
Solé Puig, M., Pérez Zapata, L., Aznar-Casanova, J. A., & Super, H. (2013a). A role of eye vergence in covert attention. Plos One, 8(1), Article e52955. https://doi.org/10.1371/journal.pone.0052955
Solé Puig, M., Puigcerver, L., Aznar-Casanova, J. A., & Super, H. (2013b). Difference in visual processing assessed by eye vergence movements. Plos One, 8(9), 1–8. https://doi.org/10.1371/journal.pone.0072041
Song, X., & Wang, X. (2012). Mind wandering in Chinese daily lives - an experience sampling study. Plos One, 7(9). https://doi.org/10.1371/journal.pone.0044523
Spreng, R. N., Sepulcre, J., Turner, G. R., Stevens, W. D., & Schacter, D. L. (2013). Intrinsic architecture underlying the relations among the default, dorsal attention, and frontoparietal control networks of the human brain. Journal of Cognitive Neuroscience, 25(1). https://doi.org/10.1162/jocn_a_00440
Spreng, R. N., Stevens, W. D., Chamberlain, J. P., Gilmore, A. W., & Schacter, D. L. (2010). Default network activity, coupled with the frontoparietal control network, supports goal-directed cognition. Neuron, 53(1), 303–317. https://doi.org/10.1038/nn.24194.2017
Spreng, R. N., Stevens, W. D., Viviano, J. D., & Schacter, D. L. (2016). Attenuated anticorrelation between the default and dorsal attention networks with aging: Evidence from task and rest. Neurobiology of Aging, 45, 149–160. https://doi.org/10.1016/j.neurobiaging.2016.05.020
Stawarczyk, D., & D’Argembeau, A. (2015). Neural correlates of personal goal processing during episodic future thinking and mind-wandering: An ALE meta-analysis. Human Brain Mapping, 36(8), 2928–2947. https://doi.org/10.1002/hbm.22818
Sulutvedt, U., Mannix, T. K., & Laeng, B. (2018). Gaze and the eye pupil adjust to imagined size and distance. Cognitive Science, 42(8), 3159–3176. https://doi.org/10.1111/cogs.12684
Thomas Yeo, B. T., Krienen, F. M., Sepulcre, J., Sabuncu, M. R., Lashkari, D., Hollinshead, M., et al. (2011). The organization of the human cerebral cortex estimated by intrinsic functional connectivity. Journal of Neurophysiology, 106(3), 1125–1165. https://doi.org/10.1152/jn.00388.2011
Tse, P. U., Baumgartner, F. J., & Greenlee, M. W. (2010). Event-related functional MRI of cortical activity evoked by microsaccades, small visually-guided saccades, and eyeblinks in human visual cortex. Bone, 49(1), 805–816.
Unsworth, N., & Robison, M. K. (2015). Individual differences in the allocation of attention to items in working memory: Evidence from pupillometry. Psychonomic Bulletin & Review, 22(3), 757–765. https://doi.org/10.3758/s13423-014-0747-6
Unsworth, N., & Robison, M. K. (2018). Tracking arousal state and mind wandering with pupillometry. Cognitive, Affective & Behavioral Neuroscience, 18(4), 638–664. https://doi.org/10.3758/s13415-018-0594-4
Van Den Brink, R. L., Murphy, P. R., & Nieuwenhuis, S. (2016). Pupil diameter tracks lapses of attention. Plos One, 11(10), 1–16. https://doi.org/10.1371/journal.pone.0155274
Verschooren, S., Schindler, S., De Raedt, R., & Pourtois, G. (2019). Switching attention from internal to external information processing: A review of the literature and empirical support of the resource sharing account. Psychonomic Bulletin & Review, 26(2), 468–490. https://doi.org/10.3758/s13423-019-01568-y
Vortmann, L. M., Kroll, F., & Putze, F. (2019). EEG-based classification of internally- and externally-directed attention in an augmented reality paradigm. Frontiers in Human Neuroscience, 13, 1–14. https://doi.org/10.3389/fnhum.2019.00348
Walcher, S., Körner, C., & Benedek, M. (2017). Looking for ideas: Eye behavior during goal-directed internally focused
Zabelina, D. L. (2018). Attention and creativity. In R. E. Jung, & O. Vartanian (Eds.), The Cambridge handbook of the neuroscience of creativity (pp. 161–179). Cambridge University Press. https://doi.org/10.1017/9781316556238.010.

Zabelina, D. L., & Andrews-Hanna, J. R. (2016). Dynamic network interactions supporting internally-oriented cognition. Current Opinion in Neurobiology, 40, 86–93. https://doi.org/10.1016/j.conb.2016.06.014

Zabelina, D. L., & Ganis, G. (2018). Creativity and cognitive control: Behavioral and ERP evidence that divergent thinking, but not real-life creative achievement, relates to better cognitive control. Neuropsychologia, 118, 20–28. https://doi.org/10.1016/j.neuropsychologia.2018.02.014