

## Masterarbeit/Master's Thesis

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"Decomposing of sustained and transient activity in dorsal and ventral frontoparietal attention systems- a fMRI data analysis of a vigilance task"

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## Abstract

**Background:** The ability to sustain attention over long time periods like while driving a car on the highway or controlling air traffic is called vigilance. According to previous findings, two systems in the brain support attentional control: a bilateral dorsal and a right lateralized ventral frontoparietal attentional system. The dorsal system gets activated during top-down (voluntary) attention, hence, if a person focuses and searches the environment for relevant stimuli, based on internal goals or expectations. The ventral system is mediated by bottom-up sensory-guided pull of attention, according to behaviorally relevant stimuli that appear outside of the focus of attention. During visual search, the activation of the dorsal system goes in line with a suppression of the ventral system and visual areas. Shifts of attention, such as reorienting towards suddenly appearing behaviorally stimuli, are mediated by both attentional systems. It has been proposed that sustained and transient neural activity refer to different neuronal processing pathways of the brain. Task-related, sustained activity is associated with the general attentional state. Item-related, transient activity refers to moment-to-moment processing of single stimuli. Methods: To investigate the role of the dorsal and the ventral frontopariteal attention systems in vigilance, 23 subjects performed a vigilance task with two difficulty levels while their brain activity was scanned using fMRI. A mixed design was used to enable separate estimation of sustained and transient activity of brain regions involved in task performance and processing task difficulty at different points in time. Results: The results indicated of both attentional systems during the task in both hard and easy version. Only the Temporparietal Junction, a core region of the ventral system, showed no sustained activation. Furthermore both attentional systems governed control of transient activity. Due to limitations it was, however, not possible to reach any firm conclusions as to whether transient responses in the attentional systems were influenced by the difficulty of the task. A lateralization to the right hemisphere was found in regions of the ventral attention systems in all conditions showing sustained and transient responses. Overall, the results should be interpreted with due caution. Nevertheless, they indicate that both attentional systems work in concert to sustain the attention during task performance and react transiently to single stimuli in the vigilance task.

**Keywords:** fMRI, vigilance, dorsal frontoparietal attention system, ventral frontoparietal attention system, sustained activity, transient activity.

1.	Introduction	6
	1.1 Attention, vigilance and attention systems of the brain	6
	1.2 Dorsal frontoparietal attention system	8
	1.2.1 Components of the dorsal frontoparietal attention system	8
	1.2.2 Role of the dorsal frontoparietal system	9
	1.3 Components of Ventral frontoparietal attention system	10
	1.3.1 Components of the ventral frontoparietal attention system	10
	1.3.2 Role of the ventral frontoparietal attention system	11
	1.4 Collaborative roles of the dorsal and the ventral frontoparietal	12
	Attention systems	
	1.5 Research questions of the master thesis	13
2.	Methods	16
	2.1 Subjects/Study design	16
	2.2 fMRI data analysis	18
	2.2.1 Preprocessing	18
	2.2.2 The General Linear Model	20
	2.2.3 Analysis of sustained activity	22
	2.2.3.1 One-sample t-test	22
	2.2.3.2 Paired t-test	23
	2.2.4 Analysis of transient activity	23
	2.2.4.1 Repeated measurements ANOVA	23
	2.2.4.2 Post-hoc t-tests	24
	2.3 Visualization and further tools for the analysis of the results	25
3.	Results	27
	3.1 Sustained activity	27
	3.1.1 Sustained activity in the condition of hard discriminability vs. zero	27
	3.1.2 Sustained activity in the condition of easy discriminability vs. zero	29
	3.1.3 Activations differences between condition of hard discriminability	31
	and condition of easy discriminability	
	3.2 Transient activity	34
	3.2.1 How activation changes in response to task difficulty over time?	34
	3.2.2 Post-hoc t-tests of transient activity	37

4.	Discussion	41
	4.1 Sustained activity and the dorsal and ventral frontoparietal attention	41
	systems	
	4.1.2 Comparison of sustained activity in condition of hard discriminability	42
	and condition of easy discriminability	
	4.2 Transient activity and the dorsal and ventral frontoparietal attention	43
	systems	
	4.3 Collaborative roles of the dorsal and the ventral frontoparietal	45
	attention systems	
	4.4 Limitations and outlook	46
	4.5 Conclusions	51
Supp	Supplementary Material	
Refe	References	
Abbreviations		71
List of figures		72
List	List of tables	

## **1. Introduction**

#### 1.1 Attention, vigilance and attention systems of the brain

People are surrounded with auditory, visual, tactile, olfactory stimuli from the environment and affected by inner bodily sensory input. According to Tsuchiya & Koch (2016) each primate eye is connected to the brain via one million fiber tracts that transmit one megabyte of information per second. Therefore, the nervous system should solely select a small fraction of this information in order to prevent an intensive information overload. There are basically two attentional processing modes the brain has to constantly balance (Vossel, Geng & Fink, 2014). Firstly, humans have to focus the mind on particular stimuli and ignore possible distractors. Secondly, humans must react to salient stimuli that appear outside of the focus of attention. Animals or humans incapable of doing so, cannot focus on finding the right food source, interact in social situations (e.g. mating) or navigate through the environment, survive and reproduce (Corbetta, Patel and Shulman, 2008).

In the psychological literature, attention is divided in different types: Kubinger (2009) distinguishes between selective or focused, divided and sustained attention/vigilance. Selective attention describes the ability to ignore irrelevant stimuli and to focus on the relevant ones. Divided attention is the faculty of distributing the attention to different kind of stimuli at the same time (Nebel et al., 2005). Monitoring the environment for a longer time period "for infrequently occurring events, while ignoring irrelevant stimuli (Helton et al., 2010, p. 1683)" is called sustained attention or vigilance. Paus et al. (1997) defines vigilance as "focusing of attention on the detection of subtle changes in the environment that occur over a long period of time (p. 392). There are several imaginable situations in which it is necessary to focus the attention and concentrate over longer time periods. Successfully writing an article or a thesis requires vigilance and the ability to ignore distractors. It is crucial for safeness to sustain the attention while driving a car on a freeway, operating heavy machinery, air traffic controlling, piloting an aircraft, cyber operating and analyzing satellite imagery (Helton et al., 2010; Hilti et al., 2013; McIntire, McKinley, Goodyear& McIntire, 2014).

Several sources can cause the deterioration of the attention over time (Casner & Schooler, 2015). The depletion of cognitive resources and the unmatched replenishing of energy during a constant demand can lower the attentional state. External distractors can decrease the attention, such as, if a pilot has to monitor flight parameters and simultaneously react to calls from air traffic control or go through checklists. Another example is if a person is writing on a thesis in a library, noises and movements from other students, the ringing of a

cell phone or the sound of an incoming e-mail can negatively influence the performance of sustained attention. Internal distractors can also have an impact on vigilance. Mind wandering, task unrelated thoughts, daydreaming are just a few examples to mention (Casner and Schooler, 2015).

Attention is multimodal because tactile, auditory, visual, olfactory and gustatory sensory information is processed by the brain. Inner mind process like thoughts can also require attentional focusing. According to Corbetta and Shulman (2002) visual attention is dependent on bottom-up and as well on top-down factors, because "dynamic interaction of these factors controls, where, how and to what we pay attention in the visual environment (p. 201)", therefore, on the interplay between exogenous sensory information and on endogenous factors like current goals, knowledge and expectations.

As an illustration, one could imagine the following scenario: a hungry prehistoric man, who is wandering through the savannah, is searching for edible food sources like fruits and prey. Based on the internal goal to find food and information about edible sources (i.e. knowledge) the prehistoric man is searching the environment and focusing his attention. Out of the blue, the prehistoric man detects a predator in the periphery of his visual field and his focused attention gets immediately disrupted. In a groundbreaking review, Corbetta and Shulman (2002) firstly described two segregated neural systems that are controlling visual attention (i.e. The ventral and the dorsal frontoparietal attention systems, see Figure 1) and the interplay between top-down and bottom-up factors in a similar way to the example above.

The aim of this study was to analyze an fMRI-dataset of a vigilance task. During the vigilance task, visual stimuli characterized by slight modifications of brightness were displayed on a screen. The subjects had to focus their attention for a long period of time and react if the stimuli changed, which corresponds to an interplay between top-down and bottom-up cognitive factors. The fMRI-dataset was analyzed with a special focus on the dorsal and ventral frontoparietal attention systems and their role in attentional control. The neuroanatomical components, the distinct functional roles and the possible interaction between the dorsal and the ventral frontoparietal attention systems are therefore described in the next chapters.



**Figure 1**: Localization of the core regions of the dorsal (yellow) and the ventral (blue) frontoparietal systems. Source: Aboitiz, Ossandon, Zamorano, Palma & Carrasco, (2014), p.5. Fig. 3.

#### 1.2 Dorsal frontoparietal attention system of the brain

1.2.1 Components of the dorsal frontoparietal attention system

The dorsal frontoparietal attention system spreads bilaterally over both hemispheres (Corbetta & Shulman, 2002). According to Vossel et al. (2014) the core regions of the dorsal frontroparietal attention system are the frontal eye fields (FEF) and the intraparietal sulcus (IPS) (see figure 2). In dorsal posterior parietal cortex IPs extends into superior parietal lobule (SPL). In dorsal frontal cortex the FEF is located along the precentral sulcus (Corbetta et al., 2008).

The IPS is the most salient sulcus of the posterior parietal cortex (Binkofski, Klann & Caspers, 2015). The anterior subdivision contains mainly anatomical connections to prefrontal regions whereas the posterior part has predominant connections to "the posterior superior temporal gyrus and retinotopically defined visual areas of the occipital cortex (Binkofski et al., 2015, p.38)". More broadly, the IPS has connections to ventral premotor cortex and the middle frontal gyrus (MFG), extrastriate areas, insular cortex, striatum and the thalamus. According to Vandenberghe and Gilleberth (2009), the IPS represents the homologue of the area LIP (lateral intraparietal cortex) in non-human primates, which, as we can see below, sheds light on its functional role in humans.

In non-human primates the FEF is located in the frontal lobule in proximity to precentral sulcus and superior frontal sulcus (Vernet, Quentin, Chanes, Mitsumasu & Valero-Chabré, 2014). The FEF receives cortical input from other cortical eye fields and projects to areas within frontal, occipital and parietal cortex, such as areas like V2/V3/V4, area MT+ and IPS. However, even though these information are inherited from studies conducted on non-human primates like macaques, it has been suggested that anatomy and localization of the FEF in

non-human primates is similar in humans which allows for a direct comparison regarding localization and connectivity (Vernet et al., 2014).

Both areas, the FEF and the IPS, contain retinotopic maps of the contralateral space and are candidates for "covert spatial attention, saccade planning and visual working memory (Vossel et al., 2014, p. 151)". The FEF contains visual, motor und visuo-motor cells that are responsible gaze control (i.e. preparing, triggering and execution of eye movements) and saccades. Furthermore, the FEF participates in visuo-spatial attention and visual search (Vernet et al., 2014). The IPS is activated during a shift of visuo-spatial attention, eye movements and visual search (Binkofsky et al., 2015). Overall, visual search and the focusing on an object activate both areas, target detection solely produces increased activation within IPS (Corbetta et al., 2008). The latter is one characteristic function of area LIP in macaques. Both areas also influence activity in visual areas in a top-down fashion, as described below in more detail in section 1.3.2 (Vossel et al., 2014).



Figure 2: Localizations of the core regions of the dorsal frontoparietal attention system. Source: Purdy, (2005). Fig. 1.

#### 1.2.2 Role of the dorsal frontoparietal attention system

The dorsal system gets activated during top-down (voluntary) attention, hence, if a person focuses and searches the environment for relevant stimuli, based on internal goals or expectations (Corbetta & Shulman, 2002; Corbetta et al., 2008). The dorsal system selects sensory information about locations and features and sends signals to visual and motor areas in order to guide the attention to a certain location, sustain the focused search or to choose the adequate motor response as a reaction to the stimuli (Vossel et al., 2014). The dorsal system can bias the activity of visual areas via top-down connections "to modulate visual processing in preparation for expected input (Vossel et al., 2014, p.2)". In other words for a human observer it is easier to detect a stimuli if there is information provided in advance, such as information about location, motion or color. If someone searches for a friend wearing a red hat in a crowd, the predefined "perceptual set" (Corbetta & Shulman, 2002) about the color,

will ease the detection of the friend and bias the visual processing to that effect that red stimuli will cue the attention. All in all, the dorsal system is "involved in the generation of attentional sets- that is, goal-directed stimulus-response selection- and the application of those sets during stimulus processing (Corbetta & Shulman, 2002, p.212)".

#### 1.3 Ventral frontoparietal attention system of the brain

#### 1.3.1 Components of the ventral frontoparietal attention system

The ventral frontoparietal attention system is mainly lateralized to the right hemisphere (Corbetta et al., 2008). The core regions of the ventral system are the temporoparietal junction (TPJ) and the ventral frontal cortex (VFC) (Vossel et al., 2014) (see figure 3). In ventral posterior parietal cortex parts of the superior temporal sulcus (STS), superior temporal gyrus (STG) and to the ventral subdivision of the supramarginal gyrus (SMG)) are components of the ventral system. In ventral frontal cortex parts of the MFG, inferior frontal gyrus (IFG), frontal operculum and the anterior Insula can be associated with the ventral attention system (Corbetta et al., 2008).

By contrast to FEF and IPS (i.e. components of the dorsal attention system), the anatomical definitions of the TPJ and the VFC are not standardized. Reported coordinates in neuroimaging studies of TPJ are located in inferior parietal lobule (IPL) including the ventral subdivision of the supramarginal gyrus, the angular gyrus, and in posterior parts of the superior temporal gyrus/sulcus (Vossell & Geng, 2013). They therefore conclude that TPJ is not a singular processing unit of the brain, emphasizing that TPJ should be subdivided in multiple regions with distinct connectivity patterns. It is still under debate if TPJ has a non-human primate homologue "which precludes use of monkey models to constrain the human work (Geng & Vossel, 2013, p. 2616)." The same applies for the VFC and in respect to the retinotopic organization to contralateral space for both areas (Vossel et al., 2014).

The VFC plays a role in language processing and cognitive control (Neubert, Mars, Thomas, Sallet & Rushworth, 2014), attentional control and visuo-spatial attention (Corbetta & Shulman, 2008, Vossel et al., 2014) and social cognition (Wood, Heitmiller, Andreasen & Nopoulos, 2008). Other findings in the literature suggest that VFC is active in inhibition of motor control (Aron, 2007), cognitive task control (Dosenbach et al., 2006), cognitive flexibility (Brass, Derrfus & Forstman, 2005) and information updating (Duncan & Owen, 2000). The TPJ gets activated during attentional control, visuo-spatial attention, social cognition like theory of mind, altruism, empathy, perspective taking and imitation, processing

lies and evaluating emotional states of others and memory processes (Behrens, Hunt, Woolrich & Rushworth, 2008; Geng & Vossel, 2013; Morelli & Liebermann, 2013; Morishima, Shunk, Bruhin, Ruff & Fehr 2012; Santiesteban, Barissy, Catmur & Bird, 2012).



**Figure 3:** Localizations of the core regions of the ventral frontoparietal attention system. Source: Corbetta et al., (2008). p. 313. Fig. 6B.

#### 1.3.2 Role of the ventral frontoparietal attention system

The ventral system is activated by bottom-up stimulus-driven attentional control and reacts to immediate changes in the environment (Corbetta & Shulman, 2002). The saliency of a stimulus alone does not produce strong responses in the ventral system. Only behaviorally relevant stimuli or such stimuli that share target features evoke enhanced ventral activity. Activation of the ventral system is not exclusively triggered by external environmental sensory stimuli, but also by internal memory-based information (Cabeza, Ciramelli & Moscovitch 2012). In summary, if a person searches for a friend in a crowd wearing a red hat, the ventral system gets activated if for instance suddenly a siren rings out (i.e. behaviorally relevant stimuli, because it might be sign for a danger) or if other red objects appear in the periphery of the focused attention (e.g. a red scarf share target features).

According to Vossel et al. (2014) the ventral system is, apart from that, involved in contextual updating, attentional reorienting and distractor filtering. Geng and Vossel (2013) postulate that the role of TPJ is to "update internal models of the behavioral context for the purpose of generating appropriate responses (p.2609)", especially, if unexpected sensory stimuli appear in the periphery of the visual field. Previous studies report (Corbetta & Shulman, 2002, Corbetta et al., 2008, Weissman & Prado, 2012) that the ventral system sends a reorienting signal towards the dorsal system that leads to a shift in spatial attention, if a behaviorally relevant, unexpected stimulus appears outside of the focused attention. During visual search the activation of the ventral system is suppressed by activation of the dorsal system, in order to sustain the attention and to ignore possible distractors (Corbetta et al., 2008). The interaction of both systems will be described more thoroughly in the next section.

#### 1.4 Collaborative roles of dorsal and ventral frontoparietal attention systems

As stated above, both attentional systems have distinct functional roles. Previous work could, however, highlight their collaborative roles during top-down and bottom-up attentional control (Vossel et al., 2014). During visual search the dorsal system is activated, but at the same time the ventral system is deactivated through a top-down biasing signal from the dorsal system in order to sustain the attention and filter out possible distractors. For instance, when a person is writing on a thesis, a situation in which it is important to concentrate and focus, it is simultaneously necessary to ignore distracting environmental stimuli. The filter of the ventral system works to that effect, that only behaviorally important stimuli can (re-) activate its function and lift the suppression.

Studies such as conducted by Corbetta and Shulman (2002) have shown that especially the TPJ is deactivated during visual search. If suddenly behaviorally relevant stimuli appear, TPJ gets activated again, sending a reorienting or "circuit-breaking" signal to the dorsal system. The role of the TPJ as a "circuit breaker" is still under debate (Vossel et al., 2014), since electrophysiological studies showed that response latencies during visual search are shorter for FEF and IPS than for TPJ. Vossel et al. (2014) therefore suggest "that the TPJ plays a role in the later evaluation of sensory events with regard to top-down expectations rather than sending an early reorienting signal to dorsal regions (p. 155)". This is why it is more probable that both systems work in concert to reorient the attention. Support for this theoretical framework was provided by studies that applied TMS (transcranial magnet stimulation) on nodes of both systems (i.e. TPJ, IPS and FEF), which evoked a reorienting action. Furthermore, the dorsal system shows spatially selective response to contralateral stimuli and posses direct connections to motor areas to guide movements of eyes. Both characteristics provide the dorsal system with the "neural machinery for directing attention and the eyes to sensory stimuli appearing at unexpected locations (Corbetta et al., 2008, p. 312)." The ventral system does not contain spatial maps that are required to reorient the attention in space. Studies with neglect patients, which can be described as a disorder of spatial attention (Corbetta et al., 2008), reported that lesions in ventral areas like TPJ and in dorsal areas like IPS lead to a decrease of performance in reorienting the attention. All in all, further research is needed to clarify the distinctive and collaborative roles of both systems, but according to Vossel et al., (2014) it is likely that both systems "seem to work in concert to promote specific attentional processes and that top-down or bottom-up processing cannot

uniquely be attributed to one system in isolation 2014, p.156)". Weissman and Prado (2012) propose in this context that the dorsal system might start the reorienting of visual attention and that the later arriving signals from the ventral system are necessary to finish this process.

Even though the role as a "circuit breaker" of the TPJ cannot be perpetuated (Geng & Vossel, 2013), it is still a candidate for being a hub that mediates interaction between dorsal and ventral system. Another candidate is the MFG since recent functional connectivity studies have shown that activation of MFG correlates with the activity of both attentional systems (Fox, Corbetta, Snyder, Vincent & Raichle, 2006, He et al., 2007). Furthermore Corbetta et al. (2008) propose that during visual search a top-down filtering signal is send to ventral areas via MFG and that a signal is send during stimulus-driven reorienting via MFG from ventral to the dorsal system.

#### 1.5 Research questions

Corbetta and Shulman (2002) based their review, in which the two frontoparietal attention systems were firstly described in detail, mainly on neuroimaging studies using fMRI or PET (Positron Emission Tomography). In the following years further insight about the delineation and functional organization of the two attention system was derived from TMS studies, resting state, functional connectivity, effective connectivity and studies about spatial neglect reviewed thoroughly in Vossel et al. (2014).

To our knowledge only a few neuroimaging studies, investigating the neural basis of attentional control, focused on vigilance, applying paradigms in which subjects have to focus on a single location for a longer period of time. Therefore, in this master thesis an fMRI-dataset was analyzed in which subjects had to perform a vigilance task while recording their brain activity. In the vigilance task subjects had to detect subtle changes of brightness in a colored disk over a long time period. The experimental procedure comprised two conditions. In the *condition of easy discriminability* changes in brightness were easily to detect, in the *condition of hard discriminability* they were barely perceptible. Therefore, by contrast to previous studies in which subjects were cued to focus the attention towards a certain spot in the periphery of their visual field after which the stimuli appeared unexpected (see Corbetta et al., 2008 for a review), in this study subjects were requested to sustain their attention on the stimuli and react to changes that appeared at the same location.

We expected that regions of the dorsal system show increased activation during the *condition of hard discriminability*. Subjects had to focus strongly on the stimuli over a long

period of time, which requires voluntary top-down control, in order to detect the subtle changes in brightness. During spatial attention, the dorsal system sends top-down signals to the ventral system and visual areas of the brain (Corbetta & Shulman, 2002, Corbetta et al. 2008, Vossell et al., 2014), which leads to a temporary decrease/suppression of activation in the depicted areas. We, therefore, expected that activation in areas of the ventral system and visual areas is decreased/suppressed during sustained focusing. Performance of the *condition of easy discriminability* requires less engagement of top-down control. Altogether, we therefore expected that activity in the ventral system and visual show decreased responses during the performance of the easy version of the task.

It has been proposed that sustained and transient neural activity refer to different neuronal processing pathways of the brain. Task-related, sustained activity is associated with the general attentional state or level of arousal of the subject during the performance of a task (Visscher et al., 2003; Wenger, Visscher, Miezin, Petersen & Schlagger, 2004) to cognitive control, attentional top-down biasing /control (Marklund et al., 2007, Petersen & Dubis, 2012) and task-set maintenance (Dosenbach et al., 2006). Item- or trial-related, transient activity is associated with input, output, or intermediate of moment-to-moment processing of specific stimuli during each trial of a task (Visscher et al., 2003, Wenger et al., 2004, Petersen & Dubis, 2012) as well as with the selection of responses, motor execution, stimulus coding and retrieval control during memory search (Marklund et al., 2007).

According to Corbetta et al. (2008), if a person focuses the attention on an object then sustained activation in regions of the dorsal attention system, namely IPS, SPL and FEF can be identified. Transient responses are produced, however, in both attentional systems if the visual scenery changes. Furthermore, Mantini, Corbetta, Perruci, Romani and Del Gratta (2009) found trial-related transient responses in brain areas that are associated with the ventral attention network and sustained activation in brain areas that are associated with the dorsal attention system. Therefore, in line with previous work, we expect that the dorsal attention system shows increased activation during the performance of the task, whereas transient, trial-related processing of single stimuli will produce increased activation in regions of the ventral attention system. In summary, the discrimination of sustained and transient activity should lead to a more complete understanding of the functional role of brain regions and their associated time-courses. The approach used in this study presents a novelty in the research of vigilance and the dorsal and ventral frontoparietal attention systems.

In this data analysis, the sustained, task-related activation of brain regions that are produced throughout experimental manipulation and the transient, trial-related time-courses of activation were analyzed separately. Moreover, differences in activation due to changes in task difficulty were investigated. Sustained responses during performance of the task were first analyzed by computing separate estimations of brain activity for the *hard discriminability* and the *easy discriminability* condition. To assess the effect of the task difficulty more directly, the two conditions of *hard* and *easy discriminability* were then compared directly. Finally, moment-to-moment processing related to task input was analyzed to identify brain areas showing transient activity. Activation at different time points that evolved over time was also analyzed to reveal the influence of task difficulty on transient activity.

## 2. Methods

#### 2.1 Subjects/Study Design

A total of 30 subjects volunteered to participate in the vigilance task. Subjects were screened to ensure no history of neurological disorder, current psychoactive medication or other factors contra-indicating fMRI. 6 subjects were excluded from the data analysis after scanning due to technical difficulties or excessive movement during scans, hence, the data of 24 subjects were used for further data analysis (see table 1, supplementary material).

Subjects had to watch a colored circle disc displayed on a black screen and indicate via button press if they identified a change in brightness that presented as a short "blink" (blink duration= 100 milliseconds) in the target stimulus. The colored circle disc had a radius of 60px with a diameter of 120px (30mm) occupying 1.27 degrees of visual angle at distance of 135cm to the screen. Color of the circle changed according to the conditions. During resting condition the circle was blue (0, 75, 200 rgb), in *condition of easy discriminability* green (standard:0, 200, 0; target 0, 100, 0 rgb) and in *condition of hard discriminability* red (standard: 200, 0, 0, target: 197-x, 0, 0 rgb). Subjects were informed about the color of the stimuli of the corresponding condition to prepare them for the upcoming difficulty level.

The experiment started with a 15s resting period followed by task blocks that lasted 60s seperated by 30s resting periods (see fig. 4). During blocks targets were jittered with 1, 2 or 3 TR (TR represents repetition time and corresponds to the time between two excitation pulses; 1TR=2.5 seconds). Proportion of ITI (Inter-Trial-Interval) was set to 3:2:1 for 1TR, 2TR, 3TR in each block. Per single block in total 15 targets were presented. Brightness of the circle disc was calibrated for *condition of hard discriminability* for each subject separately before the start of the task. Starting from a value of 197, 0, 0 (rgb) subjects had to identify the targets and response via button press. If a subject missed more than one blink out of five, calibration was continued with subtracting again -3 from current target brightness value (197-3=194, 194-3=191 etc.) until the subject identified 4 of 5 blinks correctly. If a subject identified 4 out of 5 targets, the current value was used as the target value for the hard trials.



**Figure 4**: Timing of the BOLD runs. Each BOLD run started with 12.5 s of resting period (blue circle), followed by 60s of *condition of hard discriminability* (red circle), 30s of resting period and 60s of *condition of easy discriminability* (green circle), followed by another resting period. Between the standard trials, targets were jittered with 2.5s/5s/7.5s in proportion of 3/2/1. Target blinks were presented for 100 ms with individually calibrated value (197-x, 0, 0 rgb) in *condition of hard discriminability*.

Conducting an fMRI study must include also elaborative considerations about the particular study design that is well suited to answer the research questions one is interested in (Poldrack, Mumford & Nichols, 2011). In the classical block design, stimulations phases (experimental conditions) are alternated with blocks of no stimulation (i.e. resting periods). Unfortunately this design conveys some limitations (Petersen & Dubis, 2012). For instance with a block design it is not possible to dissociate sustained and transient effects of experimental manipulation because responses to single stimuli are averaged. As a consequence with a block design one cannot differentiate how brain regions process single trial types like correct and incorrect responses or the difficulty of single trials. Therefore the usage of a block design somehow constrains the understanding of the complexity of neural processing modes.

According to Petersen and Dubis (2012) the event-related design on the other hand is suited to analyze transient trial-by-trial response of brain activation, if trials are jittered and therefore vary in their occurrence over time across the experiment, in order to avoid overlapping of hemodynamic responses and allow for the separate extraction of individual time courses. By contrast to the block design an event-related design is not suited to detect sustained activation patterns that start and finish with on- and offset of a task. Therefore, to dissociate sustained from transient effects, in this study a mixed design was used. Blocks of the task were alternated with resting periods, while trials were jittered during the experimental blocks (see Figure 5).



**Figure 5**: Schematic overview of block design, event-related design and mixed design. A) Block design: Task blocks are alternated with resting blocks. B) Event-related design: Single trials are jittered and vary over time in between the task blocks. C) Displaying task-related sustained, transient trial-related activity applied in a mixed design. Source: Wenger et al., (2004), p. 976. Fig. 1.

## 2.2 fMRI data analysis

#### 2.2.1 fMRI-Preprocessing

Preprocessing is necessary to remove artifacts and prepare the raw functional MRI timeseries data from the scanner for later statistical analysis. Statistical models that are used for data analysis assume that voxels in brain volumes are acquired at the same time, with coherent signal source in specific voxels and that in case of group analysis the brains of the individual subjects are registered in a common space (Lindquist, 2008).

The data was organized and processed using the HCP (Human Connectome Project), minimal preprocessing pipelines. The advantages of HCP preprocessing are better image distortion correction and registration to a common atlas space in both volume as well as "grayordinate" (combined surface and volume) representations (Glasser et al., 2013)- it is important to notice that this represents a general benefit of this method, in this study, however, grayordinate representation was not used. Surface-constrained methods have the benefit, that the cortical sheet is analyzed as geodesic 2D (and not as Euclidean 3D) distances along the surface. Thus, surface-constraint comes closer to neurobiology and geometry of the human cerebral cortex. Subcortical gray matter like nuclei on the other hand are better described with 3D volume based methods. Therefore "because gray matter can be modeled as either cortical surface vertices or subcortical voxels, the more general term "grayordinates" is used to describe the spatial dimension in this combined coordinate system (Glasser et al., 2013,p. 106)". Combining cortical surface-constrained methods and subcortical volume-based

methods convey also benefits for spatial smoothing and result in better cross-subject registration.

The raw imaging data was slice time corrected, motion corrected, intensity normalized, linearly and nonlinearly coregistered to MNI (Montreal Neurological Institute) standard space and spatially smoothed (for details see Glasser et al., 2013). During the scanning procedure images of the brain are acquired in single 2D slices. Depending on the TR (e.g.) different slices of the brain are acquired at varying timepoints. Statistical models that are used for the analysis of the data assume that images are recorded at the same time, the data must therefore be slice time corrected (Poldrack et al., 2011). Motions artifacts during scanning can arise from head movements, respiration and pulsation of blood vessels (e.g.). Motions can have a huge impact on the accuracy of the collected data. For instance, it can change the location of images acquired at different points in time during a scanning session. Therefore motion correction should be applied as another preprocessing step to the data. In the HCP mini preprocessing pipeline each frame is registered and realigned to a 6 DOF FLIRT (6 degree of freedom rigid body transformation) single-band reference image in order to correct for subject motion (see Glasser et al., 2013). Intensity normalization is required to average the signals from each volume of the brain across time because they can vary in functional images due to scanner drift or physiologic fluctuations (e.g.) (Macey, Macey, Kumar & Harper, 2004). Functional images are rather blurred and have lower spatial resolution than anatomically more detailed structural images. Therefore with coregistration functional and structural images are aligned together to map functional information into anatomical space (Lindquist, 2008). Because brains of individuals differ in shape and size, for cross-subject comparisons, individual subjects images are normalized together into to a standardized stereotactic space. However, in this study raw imaging data was nonlinearly coregistered to MNI standard space as described in Glasser et al., 2013. To enhance the signal-to-noise-ratio of the original data are spatially smoothed. Spatial smoothing is also used to reduce effects of residual anatomical variations across subjects that can remain after normalization. However, the intensity value of a voxel gets replaced with a weighted average of the intensity of its neighboring voxels, determined by a Gaussian kernel placed at the center of the particular voxel. In this study, functional images were convolved with a Gaussian kernel with FWHM (Full Width at Half Maximum) of 6mm.

#### 2.2.2 The General Linear Model

After being pre-processed the fMRI data can be used for further statistical analysis. The fMRIblood blood volume signal is based on changes in flow. and oxygenation/deoxygenation of hemoglobin and its relation to changes in neural activity (hemodynamic response) (Monti, 2011). The hemodynamic response refers to an increase in local blood flow in response to neuronal activation. Unlike the direct neuronal activity that is measured in milliseconds, the increase of local blood flow is a rather slow procedure. After a short period with undersupply (2-3 seconds) of oxygenated hemoglobin, oxygenated blood reaches the activated local brain regions with a peak of supply after 5 seconds, followed by an undershoot that needs 15-20 seconds to return to baseline (see figure 6). The fMRI signal describes, therefore, an indirect measurement of brain activity. The amount of blood that reaches the neurons is more than needed to replenish the consumed oxygen by the cells. Hence, neuronal activity leads to a surplus of oxygen in local blood supply of the brain. The signal that is measured by the scanner is finally based on the change of oxygenated and deoxygenated blood and their differing magnetic properties and is referred to as blood oxygenation level dependent (BOLD)-signal (Poldrack et al., 2011). The hemodynamic response function (HRF) describes the relationship between neuronal activity and the BOLDsignal.



**Figure 6**: The diagram illustrates the hemodynamic response function. TP= time from stimulus to peak of oxygenated blood flow; H=Height of the response; W= the width of the HRF at half of the height; PSU= poststimulus undershoot; ID=Initial dip. Source: Poldrack et al., (2011), p.72. Fig. 5.2.

The fMRI-dataset is a set of voxels that have associated time-series. Voxels are roughly cube-shaped. Depending on the scanner resolution, a whole brain scan acquires a total number of 40.000 to 500.000 voxels. In a Bold-run a new image gets recorded every 2 or 3, resulting in the time-series of the corresponding voxels (Vul, Harris, Winkielsman & Pashler, 2009). The goal of statistical analysis is to relate activation within a voxel to experimental manipulation. The General Linear Model (GLM) is a standard tool that is used for over 20 years for the purpose of statistical analysis of fMRI data (Poline & Brett, 2012). In case of fMRI analysis, the GLM models the weighted sum of predictor variables (regressors) plus an error term and associates it with the time-course of each voxel (Monti, 2011). As a consequence "the aim of the analysis is to estimate if, and to what extend, each predictor variable contributes to the variability observed in the voxels time-course (Monti, 2011, p. 2)". Because statistical analysis of fMRI-data is a *massive univariate approach*, for each voxel in the brain and for each participant a multiple regression equation is fitted separately.

The dependent variable (Y) in this model corresponds to the time series of activation for that voxel and the independent variable (regressor) (X) is associated with experimental manipulations (blocks and events e.g.). Every regressor is associated with a beta coefficient ( $\beta$ ) that should quantify the contribution of the regressor for changes in the time-course of the voxels. Due to possible noise in the data the equation is completed with an error term ( $\epsilon$ ).

#### $Y = X\beta + \varepsilon$

The goal of the GLM is to minimize the error term and to estimate the beta coefficients associated with different regressors. Finally, the fitting of the GLM tells us how much a change in a particular independent variable influences the dependent variable or in case of fMRI analysis, the activation within a voxel (Poldrack et al., 2012).

Using a mixed design implies two different approaches to choose the predictor variables for the GLM (Wenger et al., 2004). First, the assumed approach uses the canonical HRF (Boynton, Engel, Glover & Heeger, 1996) and convolutes it with the experimental manipulation as a continuous predictor, which is used to model blocks. Second, the unassumed approach does not use the HRF as a single regressor. Instead it includes with each time point multiple regressors. As a consequence, no single beta coefficients for particular events (target stimulus of the attention task e.g.) are computed, but several coefficients (7 frames e.g.), one for every timepoint following the specific event. In this data analysis the assumed approach was used to model transient activity following the onset of a correct response in *condition of easy discriminability* and *condition of hard discriminability*. To

model sustained, task-related effects, two different analyses were carried out: the first with an assumed response shape and the second with an assumed response shape and the other time with an unassumed response shape.

According to Poldrack at al., (2011) the GLM, because it is a general model, can also be used to carry out subsequent statistical analyses like t-tests, analysis of variance (ANOVA) and analysis of covariance (ANCOVA). In order to answer the research questions (see section 1.6) a one-sample t-test, a paired t-test and a repeated measurements ANOVA were performed, as described in the following sections more thoroughly. All statistical analysis of the data was performed with FIDL, a Linux based IDL application.

#### 2.2.3 Analysis of sustained activity

#### 2.2.3.1 One sample t-test

To analyze the sustained activation patterns of the condition of easy discriminability and condition hard discriminability two one-sample t-tests with random effects were performed. One-sample t-test explores if the mean of a sample differs significantly from an empirical value set in the null hypothesis. Random effect analysis is used in fMRI to find areas with same activation patterns across all subjects. It includes both within subject as well as between subject variances (Poldrack et al., 2011). For instance, the response to a stimulus may vary over time within a subject but also between the subjects during the scanning session. Both possibilities are taken into account by the random effects analysis. The usage of a random effect analysis makes it possible to generalize the results taken from (randomly) selected subjects for a larger population. In contrast to the fixed effect analysis in which activation patterns are averaged across subjects, between subject variances are neglected and research is interested in particular subjects (Poldrack et al., 2011). The null hypothesis of the analysis was treated by the GLM as that the effect magnitude is zero. Therefore the statistical contrasts were carried out as condition of easy discriminability vs. effect magnitude of zero and condition of hard discriminability vs. effect magnitude of zero. The voxel-by-voxel analysis across all 24 subjects resulted in *uncorrected z-maps*. Voxel-wise statistical analysis of fMRI data is a mass univariate approach that requires correction for multiple comparisons in order to not inflate the Type 1 error (Woo, Krishnan & Wager, 2014). Inflating the Type 1 error leads to an increase of false positive results, therefore, to display activation in voxels where in reality is no activation. Correction for multiple comparisons was not applied online in fidl. An in-house algorithm was used, in which, based on previous Monte Carlo simulations, only contiguous clusters of at least 70 voxels that exceeded the voxel threshold of z=3 (p=0.0027) were considered as significant.

#### 2.2.3.2 Paired t-test

The direct comparison between the sustained activation patterns of the two experimental conditions was performed with a paired t-test. The activation differences between *condition of hard discriminability* and *condition of easy discriminability* shed light on the "pure" sustained activation during the performance of the task. Typically in a paired t-test, a single subject group is tested several times (e.g. repeated measurements before and after a treatment, repeated measurements with two different methods). The comparison is, therefore, made between group values at the differing timepoints. In the voxel-by-voxel analysis Fidl carried out with GLM, the different blocks of the experimental conditions were treated as the repeated measurements in between the group values. As in the one-sample t-test, the voxel-by-voxel analysis finally resulted in *uncorrected z-maps*. For the correction for multiple comparison an in-house algorithm was used, in which, based on previous Monte Carlo simulations, only contiguous clusters of at least 70 voxels that exceeded the voxel threshold of z=3 (p=0.0027) were considered as significant.

## 2.2.4 Analysis of transient activity 2.2.4.1 Repeated Measurements ANOVA

A two-way repeated measurements ANOVA was performed to investigate transient activity that occurred in response to moment-to-moment processing of single trials. The ANOVA included two factors: "Difficulty" and "Time". The levels of the factor "Difficulty" represented transient responses corresponding to correct target identification in *condition of easy discriminability* and condition *hard discriminability*. In regard to the factor "Time", the levels were the 7 frames as across which the transient responses were modelled.

In a repeated measurement design values taken at different points in time might be dependent, because they are taken from the same person (e.g.). It is, therefore, necessary that the test statistics does not violate the assumption of sphericity. Sphericity means that the differences of the variances between the factor levels have to be equal and as a consequence that the level of dependence between the measurements at different points in time is roughly

equal (Chen, Saad, Britton, Pine & Cox, 2013). Statistical images were, therefore, corrected for sphericity.

Voxel-by-voxel analysis was carried out using the default threshold of p=0.01 to mask out voxels without activation. In this step of the analysis, the cluster level interference thresholding approach was used to correct for multiple comparisons. According to Woo et al. "This approach detects statistically significant clusters on the basis of the number of contiguous voxels whose voxel-wise statistic values lie above a pre-determined primary threshold (p.2, 2014)".

An in-house algorithm was used, in which, based on previous Monte Carlo simulations, only contiguous clusters of at least 70 voxels that exceeded the voxel threshold of z=3 (p=0.0027) were considered as significant. Monte Carlo simulation parameters were specified at a smoothing of FWHM=3mm in order that it matches the estimated intrinsic smoothness of the images, thus, of the real data, in order to derive the empirical cluster size distribution (see Poldrack et al., 2011). Finally, the statistical analysis resulted in *Monte Carlo sphericity corrected adjusted z-maps*.

#### 2.2.4.2 Post-hoc t-test

Three post-hoc t-tests were performed in order to identify activation and deactivation patterns of transient brain responses. The ANOVA is not suited for detecting deactivation of brain regions and it cannot reveal in which particular condition the response was stronger or weaker. Three t-tests were performed on activity estimates obtained by using an assumed response shape in the first level GLM analysis. A second run of the same t-tests was performed with unassumed modeling of activity. In general, the HRF shows its peak after 6 seconds, which is, considering the images were acquired with a TR of 2.5s, at time points three and four. Therefore, transient responses at time points three and four after the correct identification of a target blink were analyzed for condition of *hard* and *condition of easy discriminability* separately. Each t-test was used to compare the activation and deactivation. In addition, a third t-test was performed contrasting time-courses of activation and deactivation after correct responses in both experimental conditions directly.

#### 2.3 Visualization and further tools for the analysis of the results

The statistical images showing the results of the specific measurements were analyzed using NeuroLens (Hodge & Lissot, 2004) and mRIcron (Rorden & Brett, 2000). NeuroLens is a plugin-based environment to allow the visualization and analysis of functional neuroimages. The program mRIcron was used for surface renderings and displaying of activation slices.

Peaks within clusters of brain activation were extracted using an in-house watershed algorithm. Minimal peak size was set at 200 (in voxels) and images were smoothed with 1.5voxel Gaussian smoothing. Subsequently, to assign reported stereotactic coordinates to brain regions the SPM Anatomy toolbox and Neurosynth was applied. The SPM Anatomy toolbox employs 3D probabilistic zytoarchitectonic maps of the human brain in order to localize and label regions based on MNI coordinates (Eickhoff et al., 2005). Neurosynth is a web-based platform, containing the data of several thousand neuroimaging studies, to perform meta-analyses on fMRI datasets (e.g.) but also to localize brain regions based on stereotactic coordinates (Yarkoni, Poldrack, Nichols, Van Essen & Wager 2011).

Because the main focus within this fMRI data analysis was on the dorsal and ventral frontoparietal attention systems, the Monte Carlo corrected activation z-maps were compared with 7Networks defined by Yeo et al. (2011). Based on intrinsic functional connectivity MRI data of 1000 subjects, the authors defined 7 cortical networks including the dorsal and the ventral attention networks (Figure 7). For the interpretation of the results, overlaps between the Monte Carlo corrected activation z-maps and the 7Networks were computed using an inhouse Matlab script. The script computed the percent overlap as number of voxels in a specific network that overlap with activation difference divided by the total number of voxels in that network multiplied by 100. In addition the script computed all voxels that were more active during a specific condition that fall into a specific network.



**Figure 7**: Cortical Renderings of the 7Networks parcellation based on resting-state functional connectivity. 1=Visual Network, Purple; 2=Somatomotor Network, Blue; 3=Dorsal Attention Network, Green; 4=Ventral Attention Network, Violet; 5= Limbic Network, Cream; 6=Frontoparietal Network, Orange; 7=Default Network, Red. Source: Yeo et al., (2011), p.1137. Fig. 1

## 3. Results

#### 3.1 Results of the sustained activity

#### 3.1.1 Sustained activity in condition of hard discriminability vs. zero

Sustained, task-related activation was found in large parts of the cortical surface of the brain, which is also reflected in the large number of activation clusters resulting from the peak extraction from Monte Carlo corrected z-maps (see table 2 in supplementary material.). Activation was found in ventral and dorsal regions of frontal cortex and in posterior parietal cortex (see Figure 8). Parts of these locations of the activation patterns in frontal and parietal cortices can be associated with portions of the ventral and dorsal frontoparietal attention systems of the brain. All in all the activation patterns visualized in the z-map indicate that both systems were activated during the *condition of hard discriminability* to a similar degree.

Sustained activation that unfolded throughout the task performance was also found in other regions of frontal and parietal cortex, in temporal cortex and in somato-motor regions of the brain. Visual areas also showed sustained activation, but the size of activation patterns were smaller compared with other cortical regions of the brain. Deactivation of brain regions was barely existent in the data by contrast to patterns of activation (compare figure 8 and 9). Only small portions in ventral frontal cortex, in dorsal parietal cortex and in occipital cortex showed decreased activation compared to baseline of zero



**Figure 8:** The surface renderings show the sustained activation of brain areas in *condition of hard discriminability* compared to a baseline activation of zero. Axial slices demonstrate that both attention systems were activated by perforemance of the task to a similar degree. Peak extraction revealed that the range of activation strength went from z-values 3 to 7, which is also illustrated in the color range displaying the strength of activation.



**Figure 9**: Axial slices of sustained deactivation illustrate the extremely small portions in ventral frontal cortex, in dorsal parietal cortex and in occipital cortex that showed decreased activation in *condition of hard discriminability* compared to baseline activation of zero.

#### 3.1.2 Sustained activity in condition of easy discriminability vs. zero

During *condition of easy discriminability* the extent of sustained, task-related activation clusters is in general smaller than during *condition of hard discriminability*, which is also apparent in the smaller number of peaks that were extracted from the data (see table 3). The analysis of data of *condition of easy discriminability* showed larger activation clusters in ventral and dorsal frontal cortex, in dorsal and ventral parietal cortex and in visual areas of the brain (see figure 10). Activation in frontal and parietal areas could be related to dorsal and ventral frontoparietal attention systems. Patterns of sustained activation in ventral areas exceeded activation patterns in the dorsal system in size. Sustained activation strength in both attentional systems showed no difference. In addition, a small tendency towards a lateralization of activation to the right hemisphere is visible in the data, especially in ventrally located regions of the brain.

Significant sustained activation could be additionally identified in somato-motor and frontoparietal areas of the brain that are not associated with the dorsal and ventral systems. Increased activation was also found in visual areas, with a peak of activation in posterior portion of the occipital cortex. As in *condition of hard discriminability*, deactivation patterns were barely existent in comparison to activation patterns of brain regions. Only small portion of dorsal parietal cortex and medial occipital lobule showed sustained deactivation during the *condition of easy discriminability* compared to baseline activation of zero (see Figure 11).



**Figure 10:** The surface renderings display the sustained activation in *condition of easy discriminability* compared to a baseline of zero. In the axial slices it is shown that both attentional systems are activated by the performance of the task. It can be also inferred that there is a slight tendency toward the right hemisphere in regard to ventral areas of parietal and frontal cortex. The color range illustrates the strength of activation in brain areas that showed sustained activation.



Figure 11: Axial slices showing areas with decreased activation compared to a baseline of zero.

# 3.1.3 Activation differences between condition of hard discriminability and condition of easy discriminability

For a more detailed investigation of brain regions that demonstrated activation differences between the dorsal or the ventral attention systems, overlaps between activation differences and the 7Networks defined by Yeo et al. (2011) were computed (see Figure 12). Computing of the overlaps revealed that 50% of the dorsal attention network, 40% of the ventral attention network and 30% of the frontoparietal and the visual network showed increased sustained activation during the performance of the task. Activation differences between both conditions also overlapped with the somato-motor (12%) and the default mode network (4%). The largest amount of activation differences was found within the dorsal attention network (17%), followed by the visual network (14%), the frontoparietal (13%) and the ventral attention network (12%). These results indicate that the dorsal attention system participates in the maintenance of the task-set and therefore in sustaining the attention over a longer time period. But in addition, the analysis points into the direction that also about one third of the ventral system controls the sustaining of the attention/vigilance.



B

**Figure 12**: A= Activation differences between *condition of hard discriminability* and *condition of easy discriminability* are shown in purple; the dorsal attention network of the 7Networks is displayed in green; Overlaps between activation differences and the dorsal attention network are displayed in yellow/orange. **B**= Activation differences between *condition of hard discriminability* and *condition of easy discriminability* are shown in purple; the ventral attention network of the 7Networks is displayed in green; Overlaps between activation differences and the ventral attention network of the 7Networks is displayed in green; Overlaps between activation differences and the ventral attention network are displayed in green; Overlaps between activation differences and the ventral attention network are displayed in green; Overlaps between activation differences and the ventral attention network are displayed in green; Overlaps between activation differences and the ventral attention network are displayed in green; Overlaps between activation differences and the ventral attention network are displayed in green; Overlaps between activation differences and the ventral attention network are displayed in yellow/orange.

Peak extraction above a threshold of minimum peak size of 200 voxels that were presmoothed with 1.5 gaussian kernel resulted in a total number of 95 clusters. Significant values of all activation clusters are listed in the supplementary material (see table 3). Sustained activation could be identified in frontal, parietal and occipital cortices of the brain, including regions of dorsal and to a lesser degree of ventral frontoparietal networks as displayed in figure 13. Sustained activation could be identified in dorsal frontal cortex, including FEF that extended into the precentral sulcus. Therefore, sustaining of attention activated brain regions that are associated with dorsal frontoparietal attention system defined by Corbetta and Shulman (2002) and Corbetta et al. (2008). Furthermore, activation were identified in right FEF (x=29, y=-5, z= 57) and left FEF (x=-27, y=-5, z=55), in right IPS (x=25, y=-63, z=55) and left IPS (x=-25, y=-61, z=53). In line with previous work of He et al. (2006) in which the authors included the area MT+ as region of the dorsal attention system, activation differences were also found in right area MT+ (x=51, y=-55, z=-15) and left area MT+(x=-41, y=-69, z=-9).

As described above, activation differences overlapped also with the ventral attention network of the 7Networks. Sustained activation was found in ventral area of the frontal cortex in MFG, IFG (pars opercularis and pars orbitalis) and in anterior Insula. In parietal cortex, significant clusters were located in SMG and Inferior Parietal Lobule (IPL). According to Corbetta and Shulman (2002) and Corbetta et al. (2008) the activation of the ventral frontoparietal system is lateralized to the right hemisphere. A first look at the activation peaks of this analysis could not confirm this hypothesis (see table 3). Since sustained effects were shown in bilateral MFG, IPL, anterior Insula and SMG. On the other hand, identifying regions of those activation clusters that actually overlapped with the ventral attention network from Yeo et al. (2011) reveals that sustained activation within ventral frontoparietal attention system showed a small tendency towards a right-lateralized activation. Activation differences were found in right MFG (x=37, y= 48, z=31), right anterior Insula (x=39, y=5, z=-11), right IFG (x=53, y=11, z=11) and right SMG (x=59, y=-33, z=37). Sustained, task-releated activation in the left hemisphere was localized in left MFG (x=-33, y=47, z=23) and left anterior Insula (x=-40, y=17, z=-3).

Overall, deactivation scarcely occurred in the data, as shown in figure 14. In particular, deactivation patterns were found in posterior parietal cortex, namely SPL, and in frontal cortex orbital gyrus, rectal gyrus and superior frontal gyrus.



**Figure 13:** Surface renderings of brain regions that showed significant, task-releated sustained activation differences. On the cortical surface, a tendency toward right lateralization of activity is visible. The axial slices that expose deeper layers of the brain, show that activation in ventral regions of frontal and parietal cortices shows a tendency towards a right lateralization. However, sustained processing of vigilance in the brain activated both attentional systems.



Figure 14: Axial slices showing the extreme small deactivation patterns in *condition of hard discriminability*.

#### 3.2 Results of the transient activity

#### 3.2.1 How activation patterns change in response to task difficulty over time?

Item-related, transient activation was identified in all of the 7Networks as displayed in figure 16. 70% of the visual network, around 50% of the limbic, the default and the frontoparietal networks, 40% of the somato-motor and the dorsal network and 34% of the ventral network were activated during moment-to-moment processing task difficulty. The largest percentage of voxels that showed significant activation was located in the visual network (14%). The percentage of activation in the dorsal and the ventral networks demonstrated only slight differences, with a small tendency towards the dorsal network (5.76% vs. 4.22%).



#### B

Figure 15: A= Transient activation illustrated in the axial slices is shown in purple; the dorsal attention network of the 7Networks is displayed in green; Overlaps between transient activation and the dorsal attention network are displayed in yellow/orange. B= Transient activation is shown in purple; the ventral attention network of the 7Networks is displayed in green; Overlaps between transient activation and the ventral attention network are displayed in yellow/orange.

Peak extraction above a threshold of minimum peak size of 200 voxels that were presmoothed with 1.5 gaussian kernel resulted in a total number of 55 clusters. Significant values of all activation clusters are listed in the supplementary material (see table 3). Figure 17 below show the transient activation of brain regions in moment-to-moment processing of target identification.

Regions of the ventral system in ventral frontal cortex that showed transient activity were located in left anterior Insula (x=-41, y=15, z=3), right frontal Operculum/IFG (x=63, y=7, z=3) and left IFG (x=-57, y=4, z=-3). Transient activation in posterior parietal cortex was identified in right SMG (x=63, y=-29, z=25), right STG (x=59, y=-27, z=13), left STG (x=-61, y=-31, z=15), right TPJ (x=57, y=-50, z=5) and left TPJ (x=57, y=-49, z=4). Overall, a slight tendency toward a lateralization to the right hemisphere could be found in parietal portions of the ventral system.

Transient activation was also found in brain areas that are associated with the dorsal frontoparietal attention system. In fact, activation was found in right FEF (x=45, y=-13, z=43) and left FEF (x=-29, y=-8, z=43). Regions in dorsal parietal cortex that are compounds of the dorsal attention system, showing transient activity were the right SPL (x=1, y=-71, z=55), the left SPL (x=1, y=-53, z=51), the right IPS (x=25, y=-65, z=48) and the left IPS (x=-25, y=60, z=44).



**Figure 16**: The Surface renderings illustrate transient activation in response to a correct identification of a target in both experimental conditions. A tendency towards a right lateralization in posterior parietal cortex is evident. The largest amount of transient activation was found in visual areas of the brain. The surface renderings display the participation of dorsal and ventral attentional systems in the processing of single trials. The color range that presents the activation strength in terms of z-values, shows that the peak of activation is located in visual areas of the brain which is also illustrated in the axial slices.


#### 3.2.2 Post-Hoc t-tests of transient activity

Brain regions showed predominantly deactivations at timepoints three and four after the subject identified a change in brightness in hard and easy version of the task. Peak extraction of the Monte Carlo corrected z-maps resulted in 46 clusters for correct target identification in *condition of hard discriminability* and 38 clusters in *condition of easy discriminability*. The MNI coordinates, the corresponding brain regions, z-values and the size of the clusters are displayed in the supplementary material down below (see table 6 and table 7). The direct contrast between target identification in both experimental conditions generated almost no results as displayed in Figure 18 down below. As a consequence, peak extraction that was performed on the Monte Carlo corrected z-maps resulted in zero activation clusters.



Figure 17: Axial slices illustrating small clusters of deactivation derived from the contrast between correct identification of a target in hard and easy version of the task.

As illustrated in figure 19, deactivations patterns for transient activation as a response to a correct identification of the target stimulus in *condition of hard discriminability* were located in large portions of occipital cortex, in right and left dorsal and ventral parietal cortex, in left and right superior and middle temporal gyrus and in right superior frontal cortex. Deactivation patterns in occipital cortex were identified in inferior and middle occipital gyrus. These patterns spread in temporal cortex into regions like cuneus and fusiform gyrus. Deactivations in parietal cortex, were identified in SMG and in Precuneus. In frontal cortex, a cluster in right FEF (x=41, y=-17, z=51) could be identified. Deactivation patterns in frontal and parietal areas of the brain were larger in size in the right hemisphere of the brain.

Transient activation was found in only small parts of the brain, in fact, in right and left Cerebellum, in lateral areas of the parietal cortex, like in primary motor cortex, and in dorsal parietal cortex. The analysis of transient brain responses in *condition of easy discriminability vs. zero* demonstrated mainly deactivations. The largest deactivation patterns occurred in visual areas of the brain. The deactivation spread in temporal areas like lingual gyrus and fusiform gyrus. Regarding the dorsal frontoparietal attention system, in temporal cortex, a peak deactivation cluster was found in left and right area MT+ (x=-37,y=-79,z=-9;x=45, y=-63, z=17). Furthermore, deactivation could be identified in dorsal parietal cortex and in right paracentral Lobule. In frontal cortex, deactivation occurred in right FEF (x=45, y=-11, z=49) as part of the dorsal system. Deactivation in parietal and frontal areas were larger in the right hemisphere. Transient activation was found in right Cerebellum, in right and left lateral occipital cortex, in left supplementary motor area, and in right SPL.



**Figure 18**: Cortical renderings and axial slices showing transient responses related to correct identification of the target stimuli in condition of hard discriminability vs. baseline. Because of possible movement artifacts or spatial smoothing the first results located activation outside of the brain. Therefore the z-maps were masked with a tighter brain mask using FSL. The results show mainly deactivations, especially, in visual areas and areas of the dorsal and ventral attention system that formerly showed activation in the ANOVA.





**Figure 19:** Cortical renderings and axial slices displaying the results for transient responses to a correct identification of the target stimuli in condition of easy discriminability vs. baseline. The original z-maps were masked with a tighter MNI mask, using FSL. Visual areas show deactivation as a response to a correct target identification. Deactivation in FEF, SMG, STG could be also identified. Deactivations were present in areas that were formerly activated in the ANOVA.



### 4. Discussion

The aim of this master thesis was to analyze an existing fMRI-dataset, containing the timecourses of brain activation from 24 subjects that performed a hard and an easy version of a vigilance task. A specialty of this analysis was to discriminate sustained and transient activity (i.e. activation during task performance, activation during target identification) in regions of the the dorsal and ventral frontoparietal attention system. Additional analyses were carried out to investigate the influence of task difficulty on the activation of the dorsal and ventral attentional systems.

#### 4.1 Sustained responses and the dorsal and ventral frontoparietal attention system

Contrary to a priori expectations, the results did not clearly indicate that the dorsal system is activated by the performance of the task, accompanied by a decrease of activation in areas of the ventral system and in visual areas of the brain. Indeed the comparison with the 7Networks revealed that the largest percentage of activation differences between condition of hard discriminability and condition of easy discriminability is located in the dorsal attention network. Nevertheless, large patterns of activation differences were also found in the ventral attentional system. The investigation of activation strength in core regions of the dorsal system (i.e. IPS, FEF) and regions of the ventral system (i.e. IFG, SMG and MFG) could not reveal significant differences. To our knowledge solely, sustained activation in regions of the ventral system was in a single previous study. Marklund et al. (2007) reported sustained activation in MFG, IFG, anterior Insula, lingual gyrus and Inferior occipital gyrus. The BOLD-responses were inferred from a vigilance task, applying a similar task design to this study (i.e. subjects had to detect subtle changes in luminance in a sequence of letters). However, most research has consistently shown that the ventral system does not engage in sustained focused attention. Further work needs to be done to establish whether the ventral system plays a specific role in vigilance or the specialty of the task design might have caused the results.

The top-down signals of the dorsal system biases activation in the ventral system in form of a filter that prevents the ventral system from disrupting the focused attention (Corbetta et al., 2008). Several studies reported that especially activation of TPJ is suppressed during focused attention and high cognitive load (Anticevic, Repovš, Shulman & Bach, 2010; Fox et al., 2006; Geng & Vossell, 2013, Vossell et al. 2014). Corbetta et al. (2008) postulated that TPJ shows sustained deactivation during focused attention. Nevertheless, in this analysis no sustained deactivation in TPJ could be identified. The absence of sustained TPJ activation, however, indicates that this region of the ventral system does not participate in vigilance.

In previous work TMS was applied to regions in dorsal frontal cortex and dorsal parietal cortex resulting in a decrease of the BOLD-signal in visual areas during visual search (Duecker & Sack, 2015; Ruff, Blankenburg, Bjoertomt & Bestmann, 2009). In this analysis, a decrease of activation in visual areas was not evident. Sustained activation in visual areas could be explained by modulation through the dorsal system. According to previous findings, the dorsal attention system sends top-down biases to visual areas during focused attention in order to prepare visual areas for upcoming sensory stimulation (Bressler, Tang, Sylvester, Shulman & Corbetta, 2008; Vossel, Weidner, Driver, Friston & Fink, 2012).

Activation in regions of the dorsal attention system is bilateral. Evidence from literature suggests that overall activity in the ventral system might be right lateralized (Corbetta & Shulman, 2002, Corbetta et al., 2008). Recent neuroimaging suggests that this view can't be entirely perpetuated, since activity in TPJ serves different functions in attentional control depending on the lateralization of activation (Geng & Vossel, 2013; Vossell et al., 2014). The results of this analysis showed a tendency towards a right-lateralization of the ventral system throughout task-related activity. In particular, sustained activation in IFG and SMG was only present in the right hemisphere. Activation in anterior Insula and MFG could be identified in both hemispheres. It has been proposed that MFG serves as a link to forward top-down bias signals and reorienting signals between dorsal and ventral attention systems (Corbetta et al., 2008; He et al., 2007). This could explain, both the possibility for interhemispheric signaling and the bilateral activation of MFG during the vigilance task.

All in all, the results indicate that both systems governed sustained attention during task performance. The absence of activity in TPJ and the smaller amount of voxels that overlapped with the 7Network in the ventral system might suggest, however, a stronger engagement of the dorsal system in sustaining the attention throughout task performance.

# 4.1.2 Comparison of sustained activation in condition of hard discriminability and condition of easy discriminability

One objective of this study was to establish whether the dorsal frontoparietal attention system showed increased responses in *condition of hard discriminability*, while sending top-down

signals led to a suppression of activation in the ventral system. Another objective was to examine whether in *condition of easy discriminability*, higher activity in the ventral attention system and visual areas occurred, because the top-down biasing through the dorsal system was decreased.

Overall, no evidence of differences between the activation in dorsal and ventral system in *condition of hard discriminability* and *condition of easy discriminability* were found. The percentage of activated voxels in the hard discriminability version of the task compared to a baseline of zero activation, was larger in the ventral system than in the dorsal system. The contrast between *condition of easy discriminability* and zero revealed a stronger activation of the ventral attention system.

Interpreting the z-scores of the peak activation in the specific conditions (see tables 2, 3, 4) did not reveal significant differences between the activation strength of regions of the dorsal, ventral attention network and visual areas of the brain. It can be only inferred from the data, that TPJ is not activated in condition of hard discriminability and that throughout all conditions activation of the ventral attention system has a tendency towards a right-lateralization.

#### 4.2 Transient activity in the dorsal and ventral frontoparietal attention systems

In line with previous findings (Chica, Bourgeois & Bartolomeo, 2014; Fox et al., 2006, Mantini et al., 2009), we hypothesized that transient activation would predominantly occur in areas of the ventral attention system. The ventral attention system reacts to bottom-up sensory stimulation (i.e. to changes in the environment) (Downar, Crawley, Mikulis & Davis, 2000), if a stimuli is salient and behaviorally relevant at the same time, if it is a target stimulus or shares target features (Corbetta et al., 2008).

Transient responses were identified in the ventral and dorsal attention system of the brain. Activation peaks were found in bilateral FEF, SPL and IPS, IFG, STS, TPJ and unilateral in anterior Insula and supramarginal gyrus. A similar percentage of activated voxels in dorsal and in ventral attention systems overlapped with both attention networks of the 7Networks. Despite our expectations, the ventral attention system was not predominantly responsive towards the processing of the difficulty of single trials. As discussed in detail below, the results could indicate that both systems work in concert to process single stimuli. The results showed a tendency towards a right-lateralization in ventral frontal cortex (anterior Insula) and ventral parietal cortex (SMG), which confirms previous findings (Corbetta et al.,

2008). According to the proposed model of Corbetta and Shulman (2002), bilateral activity in TPJ is unexpected. Otherwise, recent studies indicated that activation in TPJ in attentional control might not be restricted to the right hemisphere (DiQuattro & Geng, 2011, Geng & Vossel, 2013).

The largest percentage of significant voxels overlapped with the visual network of the 7Networks (70%). The peak of activation, indicated by the highest z-scores (see figure 17) across all activated regions, was located in inferior occipital gyrus, superior occipital gyrus, lingual gyrus, cuneus and calcarine gyrus. Strong activation in visual areas might have occurred because the top-down biasing by dorsal areas is not present during the processing of visual stimuli. Corbetta and Shulman (2002) reported that areas in occipital cortex react transiently to stimuli, which "might reflect the sensory analysis (p. 202)" of these stimuli. Dosenbach et al. (2006) also reported transient activation in visual areas, concluding that this specific activation could be associated with the processing of the visual characteristics of a stimulus.

The ANOVA analyses differences in responses across time and possible interactions of high and low difficulty of the task. The ANOVA does not report deactivations and whether the transient response was larger in high or lower difficulty of the task. To further analyze the results, three post-hoc t-tests were calculated. The direct comparison between time-courses of brain activation following identification of a target with either subtle or enhanced changes in brightness did not produce valid results. Testing activations differences between time-courses of target identification and a statistical baseline of zero mainly produced deactivations for both versions of the task. It seems more than counterintuitive that deactivation occurred as a response to the task, especially in regions that formerly showed activation in the ANOVA (see figure 21). In addition, almost no activation in motor areas was found, even though subjects had to response via button press. The results are therefore thoroughly discussed below (4.4 Limitations).



**Figure 20:** Axial slices displaying activations derived from the ANOVA analysis and deactivations derived from the post-hoc t-tests. The first row of slices shows the overlap of the ANOVA and the post-hoc t-test in *condition of hard discriminability*. The second row displays the overlaps between both analyses in *condition of easy discriminability*.

4.3 Collaborative roles of the dorsal and the ventral frontoparietal attention systems

With minor exceptions, throughout all conditions regions associated with the dorsal and the ventral attention system showed sustained and transient activity. Several reasons may have caused sustained and transient activation to occur in both attentional systems. To our knowledge, sustained signal changes in the ventral system were only found in a study conducted by Marklund et al. (2007). In the present study subjects did not have to choose between several targets, hence, the absence of concurrent stimuli, functioning as distractors, could explain the strong activity in the ventral system, especially in the hard version of the task, since like that, no suppression of the ventral attention system was required. The absence of sustained activation in TPJ that particularly reacts to behaviorally relevant stimuli, confirms evidence that the TPJ does not participate in maintaining the attentional set (Corbetta et al., 2008). Nevertheless, additional research would be needed to characterize the general role of the ventral system (i.e. supporting the dorsal system to maintain the attenional state), because previous models proposed that the ventral systems is coactivated with dorsal system in reorienting of attention and not in visual search. Of course, it might be different in vigilance, since the usage of a vigilance task presented a novelty in approaching the domain

of attentional control. Further research would be needed, however, to replicate the findings of this study.

Conversely, heightened transient activation in the dorsal system could be explained by the fact that both attentional systems work in concert to process single trials. Studies that examined attentional control, applied different experimental paradigms and reported transient activation in the ventral system at task onset and offset (Fox et al, 2006) or after the processing of a start-cue (Dosenbach et al., 2006). Carter et al. (2010) found transient responses in the ventral attention system after the onset of single targets. In the present study, the moment-to-moment processing of single trials was analyzed, after the subjects correctly identified a target. Even though the dorsal attention system is mainly associated with sending sustained top-down signals in visual attention (Corbetta & Shulman, 2002), several studies found transient responses in regions of the dorsal attention system. Dosenbach et al., (2006) reported that bilateral IPS, the right TPJ and right ventral frontal cortex showed transient start-cue activity. In a subsequent study Dosenbach et al. (2007) suggested that a frontoparietal system that comprises regions of the dorsal attention system originally defined by Corbetta & Shulman (2002), forms a control network that initiates attentional control and participates in the processing of "performance feedback on a trial-by-trial basis (p.102)". Focusing the attention is supposed to produce sustained responses in the dorsal attention system and sustained deactivations in the ventral attention system. Reorienting the attention towards an unexpected, behaviorally relevant stimulus produces transient responses in the formerly deactivated ventral system and in the dorsal system (Corbetta et al., 2008). Therefore activation in both systems might reflect that the targets evoked a reorienting of attention that was mediated by both systems. It is important to notice that reorienting of attention must not be spatial in nature. It could, however, also reflect the processing of the stimuli and the initialization of adequate responses. Even though both attentional systems have distinct roles (top-down vs. bottom-up attention e.g.), the results of this analysis strongly indicated that both systems work in concert to dynamically maintain the general attentional state and to process single stimuli. Nevertheless, the collaborative roles of both systems in sustained recruitment and moment-to-moment processing should be addressed in further research.

#### 4.4 Limitations and Outlook

Overall, the analysis did not reveal clear distinctions in activation of the dorsal and the ventral attention system in both experimental conditions and in sustained and transient activation.

Beside a possible interplay of both systems, the results could reflect limitations in task design, study design an analysis methods. It is as well possible that the results ensue from the novelty of the experimental paradigm (the vigilance task) in research of both frontoparietal attention systems. In most previous neuroimaging studies (i.e. studies that investigated the role of dorsal and ventral systems in attentional control), subjects were presented with different cues, placed at the center or the periphery of the visual field, followed by valid or invalid targets (e.g. Posner's location-cuing paradigm, Posner, 1980). Typically in these studies preparatory control signals and advanced information were presented as a cue (e.g. a small arrow) to provide the subjects with instructions about "relevant aspects of the forthcoming visual scene (such as location or direction of motion of a target stimulus)(Corbetta & Shulman, 2002, p. 202)". In valid trials targets appear at the cued position and in invalid trials targets appear unexpected. Another category of studies applied infrequent stimuli presentation as in "oddball" paradigms (for an overview see Corbetta et al., 2008, Vossell et al., 2014).

The original model of Corbetta and Shulman (2002) described the roles of the dorsal and the ventral system as the following: 1. The dorsal system is active when a person orients its attention in space, as in visual search based on goals, knowledge and expectations. 2. The ventral system responds to behaviorally relevant stimuli that appear outside the focus of attention/in the periphery of the attentional focus. In this study a single stimulus was presented at the center of the attentional focus and targets in between standards were jittered. Hence, in the applied paradigm subjects did not need to search the environment. Therefore, no shift of spatial attention was required (i.e. a non spatial shift might have occurred however), because the location for standards and targets was the same. Furthermore, subjects underwent the task procedure for a long period of time and previous studies, did not investigate attentional control in vigilance. Targets were, however, infrequently presented between standards that were continuously shown.

Therefore, the experimental paradigm in this study might have requested different demands for the attentional systems than previous studies. The absence of a required shift in spatial attention and absence of concurrent stimuli might have led to distinct activation in dorsal and ventral frontoparietal areas compared to previous work. Concurrent stimuli might have elicited stronger suppression of the ventral system to filter possible distractors. A spatial shift of attention could have produced stronger activation in the ventral system to mediate the reorienting of the attention. Furthermore, the presentation of the target in the stream of standards with infrequent occurrence could have combined several processes of brain activity. Corbetta et al. (2008) discussed issues in interpreting brain responses due to the distinction of

oddballs and standards as the following. The range of processes in these tasks can be characterized as response selection (i.e. categorization of an object, selecting an adequate response), response execution and performance monitoring. The vigilance task in this study, however, was not designed as a classical oddball paradigm, but shared similar features. Unfortunately, the analysis failed to decompose different processes in the sense that both attentional systems showed transient (i.e. response selection, response execution) and sustained activity (i.e. maintaining of the attentional state) to a similar degree.

Therefore, future research could apply a different task design, include concurrent stimuli and/or require target selection as in previous research (e.g. such as in choice reaction tasks) to further explore the BOLD-responses of both attentional systems in sustained attention. In this analysis, the sustained activity should have represented the attentional state (vigilance), and transient activity should have reflected moment-to-moment processing of the single trials. Nevertheless, we could not find significant differences in the BOLD-signals of both attentional systems in sustained and transient processes. The results of the post-hoc tests were counterintuitive and did not enter the interpretation of the results. However, the post-hoc t-tests should have supported further exploration of the specific influence of task difficulty in transient activation.

Therefore, a number of important limitations need to be considered. First, the direct comparison of brain transient signals between correct responses in condition of hard and easy discriminability did not show any results. Second, the deactivation patterns of the post-hoc t-tests (i.e. 1. correct responses in hard version of the task vs. baseline, 2. correct responses in easy version of the task vs. baseline) overlapped with the activation patterns in the ANOVA. The factor time in ANOVA represented the transient brain responses at 7 time points after a correct response in either hard version or easy version of the task. The post-hoc t-tests examined the transient responses at time points three and four. It is highly counterintuitive that the brain responses decreased exactly at time point three and four, which is supposed to represent the peak of activation. Third, deactivation was found in visual areas and in motor cortex. Subjects had to press a button if they identified a target, and subjects had to focus on visual stimuli. Both factors should have lead to observable activations in motor and visual areas.

In this study an assumed response shape was applied to model transient events by using a single regressor (for details see section 2.2.2). Petersen and Dubis (2012) recommended that assumed response shapes should not be used for the modeling of transient events. If the transient activity deviates from the canonical waveform of the HRF, it could be

"aliased as (misapplied) sustained activity (Petersen & Dubis, p. 1179, 2012)". In the original paper, Visscher et al. (2003) simulated sustained and transient activity applying either an assumed or an unassumed response shape to model sustained and transient effects respectively. The simulation revealed that the misapplication of sustained regressors, that influenced the transient results, could be decreased with the usage of 7 regressors or more (i.e. the more regressors the better the results). A rerun of our analysis using an unassumed approach with 7 regressors to model transient effects, however, showed similar results such as the modeling of transient effects with an assumed response shape produced. Nevertheless, it is likely that an artifact in the modeling, regarding the estimated beta coefficients, affected both sustained and transient results. Further investigating of the issues goes beyond the scope of this thesis and should be addressed in a possible consecutive project.

Beside possible artifacts in the modeling, the task design and the study design might have influenced the transient effects in this analysis. Targets were displayed for 100ms (see figure 4) and jittered throughout the experimental blocks with 1, 3, 5 TR. According to previous findings activation in the ventral system due external stimuli is transient, with a time course between 100 and 300ms. Nevertheless, it might be the case that the temporal resolution of fMRI is not sensitive enough to detect these short transient responses (Chica, Bourgeois & Bartolomeo, 2014). A reasonable approach to tackle these issues could be to conduct another study, with short inter-stimulus-intervals (ISI) between the single trails, such as in a rapid event-related design (Amaro & Baker, 2006). Shorter ISI can enhance the temporal resolution, the efficiency of an event-related design if ISI are randomized (Dale, 1999) and increase the statistical power of an fMRI-study (Amaro & Baker, 2006). However, issues with this kind of design are that using shorter ISI would require to prolong the experimental procedure (Dale, 1999), which could lead to subject fatigue and habituation (Poldrack et al., 2010). The latter could be controlled with behavioral measurements, such as, in assessing the decrease of response time from subjects and correlate it with decrease in maintaining the attentional state (Hilti et al., 2013).

In this study a variety of regions were activated (see tables in supplementary material) in frontal, parietal, temporal and occipital cortex but also in subcortical regions of the brain that do not belong to dorsal and ventral attention systems. The high number of reported regions might have influenced the interpretation of the results in two possible ways. First, the lack experience of the author in associating MNI coordinates with anatomical labels might have resulted in a non-detection of actual activations in dorsal and ventral attentional systems. The anatomy toolbox is a precise tool for that purpose, nevertheless, it provides, beside its

accuracy, a rather broad labeling of anatomical region. For instance, TPJ, IPS and FEF activation are not specifically reported. Especially in the case of TPJ, delineation of activation has its limitations, since anatomical definition for TPJ is not standardized (Vossell et al., 2013) and reported locations in IPL, SMG, angular gyrus, STG, STS could refer to TPJ activation. A region of interest analysis could have helped to further delineate and characterize activation patterns (see Poldrack et al., 2011), constrained to regions of the dorsal and ventral frontoparietal attention systems. Second, the narrowing of the focus on the dorsal and ventral attention systems might have constrained the overall interpretation of the results of this study. Overlaps with the 7Networks indicated that regions of the visual network, the somatomotor network, the frontoparietal control network and the default network were activated during the vigilance task. Hilti et al. (2013) found a control network consisting of dorsal anterior Insula, dorsal anterior cingulate cortex, supplementary motor area and regions of the frontal and parietal cortex that were activated by a vigilance task and might participate in sustaining of attention. Dosenbach et al. (2006) hypothesized that the anterior Insula, the anterior cingulate cortex and the frontal operculum are part of a cognitive control network that plays a role in attention. Cole, Repovš and Anticevic (2014) described a cognitive control system that comprises different subsystems (i.e. a dorsal attention system, a cingulo-opercular, a frontoparietal system) while each subsystem serves related but distinct processes in the brain. More broadly, future research is therefore needed to clarify the interaction of the dorsal and the ventral frontoparietal attention systems with other brain regions and networks.

A possible way to further explore the collaborative role of dorsal and ventral attention system, how both systems are engaged with other systems to flexibly control sustained attention, could be achieved with brain connectivity studies. Connectivity can be analyzed using graph theory, demonstrating properties of the modeled system (Power et al., 2011). Graph theory is a mathematical method to analyze complex systems, like the brain, and to display the interaction and organization of their single components in a network structure (Sporns, 2011). To describe the functional role of such a network a future study could apply functional connectivity and graph theory to delineate both systems, find regions that are important hubs and examine (correlational) relationships between them (Rubinov and Sporns, 2010). Corbetta et al., (2008) and Vossell et al., (2014) proposed that MFG serves as a link between the dorsal and the ventral system, because in previous functional connectivity studies activation was correlated with both attentional systems (Fox et al., 2006, He et al., 2007). In this analysis, the MFG was activated in all conditions showing sustained and transient activation along with regions of the dorsal and the ventral attention system. A future study

could therefore specifically address the role of MFG in vigilance, examining whether it is a central hub displaying dense interconnectivity with regions of both systems. The graph theoretical approach would additionally allow for investigating whether the dorsal and ventral system frontoparietal attention systems are actual networks of the brain or functional systems that are coactivated in a variety of tasks (Power et al., 2011).

#### 4.5 Conclusions

In this data analysis, regions of the dorsal and ventral frontoparietal attention systems showed similar sustained activity in a hard version and in an easy version of a vigilance task. This indicates that both systems govern attentional state during the performance of the vigilance task, in stark contrast to previous results. Absence of sustained TPJ activation goes in line with previous reports, indicating that TPJ does not play a role in focused attention. In addition, as in previous studies about the dorsal and ventral attention systems, a tendency towards a right lateralization of the ventral system was evident. In contrast to previous work and to our a priori expectations about the activation patterns of both systems, we found similar activation patters within both attentional systems in sustained and transient responses. Due to limitations we could not examine whether transient responses are stronger in *condition of hard discriminability* or *condition of easy discriminability*. Finally, the overall comparison between sustained and transient activation is constrained by the limitations of this study.

A possible follow-up study should address these limitations, taking into consideration applying a task design that allows the subjects to search the environment. In order to demand a strong spatial reorienting response in target/standard discrimination to evoke stronger differences in activation between both atentional systems. Because the low temporal resolution of fMRI might have contributed to the limitations of this study, a follow-up study could use a rapid-event related design to increase the temporal resolution and further examine the transient responses in dorsal and ventral attention system. Even though the overall results should be interpreted with due caution, a follow up study could use functional connectivity to further research whether both systems work in concert to sustain the attention over a long period of time.

## **Supplementary Material**

ID	Age	Gender	Years of education after primary school
1	23	F	17
2	19	F	14
3	19	F	14
4	19	F	14
4	25	F	17
5	19	F	14
6	21	F	15
7	19	F	14
8	20	F	14
9	20	М	14
10	19	F	14
11	19	F	14
12	20	М	15
13	19	F	14
14	19	F	14
15	19	F	14
16	19	F	15
17	22	F	17
18	25	F	15
19	19	F	14
20	22	F	14
21	70	F	16
22	25	F	17
23	27	F	18
24	21	M	14

**Table 1**: The 24 subjects whose data was used in the analysis. 21 female; mean age = 23.7; mean years of education after primary school= 15.5.

**Table 2**: Regions that showed significant activation in *condition of hard discriminability*. In onesample t-test null hypothesis was treated as effect magnitude of zero. Peaks of activation clusters were extracted with a watershed algorithm. Anatomical Labels were defined with SPM Anatomy Toolbox and Neurosynth. Value corresponds to z-value, positive values stand for activation and negative values for deactivation. Number of voxels corresponds to cluster size. Coordinates are reported in MNI.

label	value	voxels	peak_x	peak_y	peak_z	anatomical label
2	4.3	341	65.0	-27.0	-13.0	(Right Middle Temporal Gyrus)
3	5.2	360	65.0	-35.0	-3.0	(Right Middle Temporal Gyrus)
4	5.9	474	65.0	-41.0	29.0	(Right Supramarginal Gyrus)
5	5.3	886	63.0	-19.0	27.0	(Right Supramarginal Gyrus)
6	5.5	360	63.0	-35.0	9.0	(Right Superior Temporal Gyrus)
7	5.7	841	61.0	-37.0	17.0	(Right Superior Temporal Gyrus)
8	4.9	454	59.0	-17.0	17.0	(Right Rolandic Operculum)
9	5.5	797	59.0	-21.0	-1.0	(Right Superior Temporal Gyrus)
10	5.9	283	57.0	15.0	23.0	(Right Inferior Frontal Gyrus (p. Opercularis))
11	5.2	260	57.0	5.0	25.0	(Right Precentral Gyrus)
12	6.3	750	55.0	9.0	9.0	(Right Inferior Frontal Gyrus (p. Opercularis))
13	6.0	807	55.0	-53.0	1.0	(Right Middle Temporal Gyrus)
14	6.5	1361	53.0	-35.0	47.0	(Right Inferior Parietal Lobule)
15	6.0	328	51.0	21.0	19.0	(Right Inferior Frontal Gyrus (p. Triangularis))
						(Right Inferior Frontal Gyrus (p.
16	6.2	727	51.0	15.0	-1.0	Triangularis))
17	5.1	358	51.0	-21.0	45.0	(Right Postcentral Gyrus)
18	5.3	309	51.0	-29.0	3.0	(Right Superior Temporal Gyrus)
19	5.3	215	51.0	-47.0	49.0	(Right Inferior Parietal Lobule)
20	4.9	343	49.0	41.0	-9.0	(Right Inferior Frontal Gyrus (p. Orbitalis))
21	6.0	206	49.0	-57.0	-3.0	(Right Middle Temporal Gyrus)
22	5.5	369	47.0	47.0	1.0	(Right Inferior Frontal Gyrus (p. Triangularis))
23	5.9	628	47.0	17.0	33.0	(Right Inferior Frontal Gyrus (p. Opercularis))
24	6.3	940	47.0	1.0	43.0	(Right Precentral Gyrus)
25	5.9	677	47.0	-11.0	43.0	(Right Precentral Gyrus)
26	5.6	445	47.0	-23.0	-5.0	(Right Insula)
27	5.3	340	47.0	-59.0	-31.0	(Right Cerebellum)
28	6.3	734	47.0	-65.0	3.0	(Right Middle Temporal Gyrus)
29	6.4	772	45.0	33.0	19.0	(Right Middle Frontal Gyrus)
30	6.9	806	45.0	7.0	29.0	(Right Intraparietal Sulcus)
31	6.3	1334	45.0	-49.0	-15.0	(Right Inferior Temporal Gyrus)
32	6.7	610	45.0	-67.0	-9.0	(Right Inferior Temporal Gyrus)
33	5.5	377	43.0	41.0	5.0	(Right Middle Frontal Gyrus)
34	6.2	318	43.0	-3.0	57.0	(Right Premotor Cortex)
35	6.1	1220	41.0	49.0	15.0	(Right Middle Frontal Gyrus)
36	6.1	516	41.0	17.0	-7.0	(Right Insula)

37	5.3	261	41.0	5.0	3.0	(Right Insula)
38	5.3	673	41.0	-23.0	39.0	(Right Postcentral Gyrus)
39	6.2	1484	41.0	-41.0	43.0	(Right Inferior Parietal Lobule)
40	6.3	201	41.0	-69.0	-1.0	(Right Middle Temporal Gyrus)
41	5.5	648	39.0	3.0	-9.0	(Right Insula)
42	5.1	247	39.0	-71.0	-27.0	(Right Cerebellum)
43	6.3	437	39.0	-85.0	1.0	(Right Middle Occipital Gyrus)
						(Right Inferior Frontal Gyrus (p.
44	4.7	326	37.0	27.0	-21.0	Orbitalis))
45	5.2	382	37.0	-29.0	17.0	(Right Insula)
46	5.8	333	35.0	41.0	21.0	(Right Middle Frontal Gyrus)
47	5.3	326	35.0	-7.0	-5.0	(Right Putamen)
48	6.1	990	35.0	-51.0	49.0	(Right Inferior Parietal Lobule)
49	5.4	293	35.0	-57.0	-29.0	(Right Cerebellum)
50	6.6	955	35.0	-61.0	-13.0	(Right Fusiform Gyrus)
51	5.1	248	35.0	-73.0	-25.0	(Right Cerebellum)
52	6.0	547	35.0	-77.0	-11.0	(Right Inferior Occipital Gyrus)
53	6.3	575	35.0	-81.0	5.0	(Right Middle Occipital Gyrus)
54	6.6	1383	33.0	27.0	1.0	(Right Insula)
55	6.1	1156	33.0	1.0	55.0	(Right Middle Frontal Gyrus)
56	5.5	577	33.0	-17.0	3.0	(Right Putamen)
57	4.4	385	33.0	-31.0	63.0	(Right Postcentral Gyrus)
58	5.9	786	33.0	-71.0	25.0	(Right Middle Occipital Gyrus)
59	5.6	463	31.0	45.0	27.0	(Right Middle Frontal Gyrus)
60	5.6	396	31.0	41.0	29.0	(Right Middle Frontal Gyrus)
61	5.5	562	31.0	-65.0	-53.0	(Right Cerebellum)
62	5.2	423	31.0	-67.0	35.0	(Right Middle Occipital Gyrus)
63	4.3	450	29.0	59.0	-5.0	(Right Superior Orbital Gyrus)
64	6.1	1228	29.0	-89.0	-1.0	(Right Middle Occipital Gyrus)
65	4.9	394	27.0	47.0	-15.0	(Right Middle Orbital Gyrus)
66	3.9	227	27.0	13.0	-1.0	(Right Putamen)
67	5.5	476	25.0	-45.0	-23.0	(Right Cerebellum)
68	5.6	248	25.0	-53.0	-23.0	(Right Cerebellum)
69	4.9	502	25.0	-61.0	45.0	(Right Angular Gyrus)
70	5.5	213	23.0	-35.0	-31.0	(Right Cerebellum)
71	5.7	822	23.0	-69.0	-47.0	(Right Cerebellum)
72	5.1	215	21.0	7.0	63.0	(Right Superior Frontal Gyrus)
73	5.4	374	19.0	-37.0	-25.0	(Right Cerebellum)
74	5.1	499	15.0	-53.0	-39.0	(Right Cerebellum)
75	5.4	462	15.0	-77.0	-21.0	(Right Cerebellum)
76	6.2	400	13.0	-9.0	-5.0	(Right Basal Ganglia)
77	6.1	829	13.0	-9.0	3.0	(Right Thalamus)
78	5.8	592	13.0	-13.0	15.0	(Right Thalamus)
80	5.1	644	13.0	-31.0	67.0	(Right Paracentral Lobule)
81	5.4	269	13.0	-45.0	-15.0	(Right Cerebellum)
82	5.8	700	13.0	-73.0	-43.0	(Right Cerebellum)

83	5.0	781	11.0	41.0	19.0	(Right Anterior Cingulate Cortex)
84	5.9	245	11.0	15.0	35.0	(Right Middle Cingulate Cortex)
85	5.4	268	11.0	5.0	9.0	(Right Nucleus Caudatus)
86	6.0	538	11.0	-15.0	-5.0	(Right Basal Ganglia)
87	6.0	208	9.0	25.0	37.0	(Right Middle Cingulate Cortex)
88	5.9	364	9.0	19.0	33.0	(Right Middle Cingulate Cortex)
89	5.0	207	9.0	13.0	5.0	(Right Nucleus Caudatus)
90	6.0	390	9.0	7.0	63.0	(Right SMA)
91	5.8	706	9.0	-1.0	63.0	(Right SMA)
92	4.7	641	9.0	-19.0	41.0	(Right Middle Cingulate Cortex)
93	5.0	569	9.0	-31.0	49.0	(Right Middle Cingulate Cortex)
94	5.0	417	7.0	37.0	39.0	(Right Superior Medial Gyrus)
95	5.6	672	7.0	33.0	47.0	(Right Superior Medial Gyrus)
96	6.4	765	7.0	11.0	49.0	(Right SMA)
97	5.0	332	7.0	-5.0	33.0	(Right Middle Cingulate Cortex)
98	5.9	202	7.0	-13.0	-1.0	(Right Thalamus)
99	6.3	1577	7.0	-65.0	-19.0	(Cerebellar Vermis)
100	5.8	230	7.0	-75.0	-35.0	(Right Cerebellum)
101	6.0	764	5.0	21.0	43.0	(Right Superior Medial Gyrus)
102	5.5	976	5.0	-17.0	-25.0	(Brain Stem)
103	5.4	594	5.0	-25.0	23.0	(Right Posterior Cingulate Gyrus)
104	4.5	495	5.0	-37.0	-47.0	(Brain Stem)
105	5.0	243	3.0	19.0	23.0	(Right Anterior Cingulate Cortex)
106	5.9	714	3.0	-41.0	-15.0	(Cerebellar Vermis)
107	5.8	1413	1.0	-53.0	-37.0	(Cerebellar Vermis)
108	5.9	285	1.0	-75.0	-35.0	(Cerebellar Vermis)
109	4.8	273	-1.0	35.0	29.0	(Left Anterior Cingulate Cortex)
110	4.9	534	-3.0	-11.0	29.0	(Left Anterior Cingulate Cortex)
111	5.1	299	-5.0	23.0	25.0	(Left Anterior Cingulate Cortex)
112	5.4	408	-5.0	9.0	29.0	(Left Anterior Cingulate Cortex)
113	6.3	1106	-5.0	-5.0	63.0	(Left SMA)
114	5.8	514	-5.0	-7.0	57.0	(Left SMA)
115	5.5	883	-5.0	-25.0	49.0	(Left Middle Cingulate Cortex)
116	4.9	575	-7.0	35.0	19.0	(Left Anterior Cingulate Cortex)
117	6.2	801	-7.0	11.0	47.0	(Left SMA)
118	6.1	623	-7.0	-73.0	-39.0	(Left Cerebellum)
119	5.2	554	-9.0	17.0	7.0	(Left Nucleus Caudatus)
120	5.3	237	-9.0	7.0	11.0	(Left Nucleus Caudatus)
121	5.2	1088	-9.0	-41.0	-21.0	(Left Cerebellum)
122	6.2	798	-9.0	-75.0	-23.0	(Left Cerebellum)
123	6.7	1898	-11.0	-11.0	-1.0	(Left Thalamus)
124	4.6	203	-11.0	-27.0	67.0	(Left Paracentral Lobule)
125	4.4	227	-11.0	-35.0	67.0	(Left Paracentral Lobule)
126	4.9	311	-13.0	-5.0	19.0	(Left Nucleus Caudatus)
127	5.7	332	-13.0	-15.0	9.0	(Left Thalamus)

128	5.2	371	-15.0	-79.0	-33.0	(Left Cerebellum)
129	5.0	339	-17.0	-53.0	-23.0	(Left Cerebellum)
130	4.2	205	-19.0	-41.0	-45.0	(Left Cerebellum)
131	6.0	434	-19.0	-93.0	-13.0	(Left Lingual Gyrus)
132	4.7	483	-21.0	-63.0	41.0	(Left Superior Parietal Lobule)
133	5.9	491	-21.0	-99.0	-3.0	(Left Middle Occipital Gyrus)
134	5.2	347	-23.0	3.0	13.0	(Left Putamen)
135	5.9	687	-23.0	-69.0	-45.0	(Left Cerebellum)
136	5.1	592	-25.0	3.0	-1.0	(Left Putamen)
137	6.1	548	-25.0	-69.0	-51.0	(Left Cerebellum)
138	5.2	532	-25.0	-73.0	23.0	(Left Superior Occipital Gyrus)
139	4.9	691	-27.0	-27.0	63.0	(Left Precentral Gyrus)
140	4.7	202	-27.0	-47.0	-19.0	(Left Fusiform Gyrus)
141	5.0	343	-27.0	-59.0	53.0	(Left Superior Parietal Lobule)
142	4.5	230	-29.0	51.0	19.0	(Left Middle Frontal Gyrus)
143	6.3	660	-29.0	27.0	3.0	(Left Insula)
144	5.3	326	-29.0	-35.0	61.0	(Left Postcentral Gyrus)
145	6.2	1643	-29.0	-65.0	-27.0	(Left Cerebellum)
146	4.6	257	-31.0	57.0	11.0	(Left Middle Frontal Gyrus)
147	5.3	446	-31.0	-17.0	1.0	(Basal Ganglia)
148	5.4	388	-31.0	-25.0	7.0	(Left Superior Temporal Gyrus)
149	5.2	415	-31.0	-85.0	11.0	(Left Middle Occipital Gyrus)
150	5.4	591	-33.0	-3.0	51.0	(Left Frontal Eye Fields)
151	5.6	1155	-33.0	-49.0	47.0	(Left Inferior Parietal Lobule)
152	4.7	336	-33.0	-55.0	-49.0	(Left Cerebellum)
153	5.4	266	-33.0	-75.0	-15.0	(Left Fusiform Gyrus)
154	6.4	625	-33.0	-89.0	-11.0	(Left Inferior Occipital Gyrus)
155	5.4	406	-35.0	-21.0	53.0	(Left Precentral Gyrus)
156	5.9	904	-35.0	-61.0	-15.0	(Left Fusiform Gyrus)
157	5.7	363	-35.0	-87.0	-1.0	(Left Middle Occipital Gyrus)
158	4.8	695	-37.0	45.0	17.0	(Left Middle Frontal Gyrus)
159	5.9	625	-39.0	1.0	45.0	(Left Precentral Gyrus)
160	6.0	1021	-39.0	-29.0	17.0	(Left Rolandic Operculum)
161	6.5	1461	-41.0	17.0	-1.0	(Left Insula)
162	4.3	587	-41.0	-1.0	-19.0	(Left Hippocampus)
163	6.5	1772	-41.0	-9.0	53.0	(Left Precentral Gyrus)
164	4.7	466	-41.0	-13.0	-9.0	(Left Superior Temporal Gyrus)
165	4.8	292	-41.0	-27.0	5.0	(Left Superior Temporal Gyrus)
166	5.6	606	-41.0	-49.0	-17.0	(Left Inferior Temporal Gyrus)
167	5.5	442	-41.0	-61.0	-33.0	(Left Cerebellum)
168	6.7	1423	-41.0	-69.0	-3.0	(Left Inferior Occipital Gyrus)
100	C 1	0.40	42.0	FO	20.0	(Left Inferior Frontal Gyrus (p.
169	0.1	843	-43.0	5.0	29.0	(Left Inferior Frontal Gyrus (n
170	4.2	542	-45.0	27.0	25.0	triangularis))
171	5.3	491	-45.0	1.0	3.0	(Left Insula)

172	4.9	231	-45.0	-53.0	7.0	(Left Middle Temporal Gyrus)
						(Left Inferior Frontal Gyrus (p.
173	4.3	264	-47.0	43.0	-5.0	Orbitalis))
174	6.1	605	-49.0	1.0	37.0	(Left Precentral Gyrus)
175	5.0	216	-49.0	-37.0	47.0	(Left Inferior Parietal Lobule)
						(Left Inferior Frontal Gyrus (p.
176	5.6	365	-51.0	15.0	-1.0	triangularis))
177	4.7	294	-51.0	-25.0	9.0	(Left Superior Temporal Gyrus)
						(Left Inferior Frontal Gyrus (p.
178	6.1	913	-53.0	7.0	19.0	Opercularis))
179	5.1	424	-53.0	5.0	3.0	(Left Rolandic Operculum)
180	5.6	752	-53.0	-31.0	39.0	(Left Inferior Parietal Lobule)
181	5.4	253	-53.0	-39.0	13.0	(Left Superior Temporal Gyrus)
182	5.3	930	-53.0	-47.0	41.0	(Left Inferior Parietal Lobule)
183	5.3	922	-55.0	-49.0	13.0	(Left Middle Temporal Gyrus)
184	5.1	718	-61.0	-19.0	21.0	(Left Postcentral Gyrus)
185	4.8	525	-63.0	-27.0	-1.0	(Left Middle Temporal Gyrus)

**Table 3**: Regions that showed significant activation differences in *condition of easy discriminability*. In onesample t-test null hypothesis was treated as effect magnitude of zero. Peaks of activation clusters were extracted with a watershed algorithm. Anatomical Labels were defined with SPM Anatomy Toolboox and Neurosynth. Value corresponds to z-value, positive values stand for activation and negative values for deactivation. Number of voxels corresponds to cluster size. Coordinates are reported in MNI. MNI coordinates were labeled with SPL Anatomy toolbox and Neurosynth.

label	value	voxels	peak_x	peak_y	peak_z	anatomical label
2	4.4	557	67.0	-35.0	17.0	(Right Superior Frontal Gyrus)
3	4.5	277	59.0	17.0	19.0	(Right Inferior Frontal Gyrus (p. opercularis))
4	4.5	569	57.0	-33.0	7.0	(Right Superior Temporal Gyrus)
5	4.7	398	55.0	19.0	9.0	(Right Inferior Frontal Gyrus (p. opercularis))
6	4.0	376	53.0	5.0	9.0	(Right Rolandic Operculum)
7	4.0	311	53.0	-19.0	-1.0	(Right Superior Temporal Gyrus)
8	4.0	284	53.0	-47.0	43.0	(Right Inferior Parietal Lobule)
9	4.7	542	51.0	35.0	-9.0	(Right Inferior Frontal Gyrus (p. orbitalis))
10	4.6	222	51.0	11.0	-1.0	(Right Inferior Frontal Gyrus (p. opercularis))
11	4.0	627	51.0	-45.0	37.0	(Right Supramarginal Gyrus)
12	4.7	245	47.0	7.0	1.0	(Right Insula)
13	5.2	400	47.0	3.0	31.0	(Right Precentral Gyrus)
14	5.1	715	47.0	1.0	39.0	(Right Frontal Eye Fields)
15	4.4	353	47.0	-27.0	-1.0	(Right Superior Temporal Gyrus)
16	5.2	924	47.0	-63.0	7.0	(Right Middle Temporal Gyrus)
17	4.3	399	45.0	17.0	37.0	(Right Inferior Frontal Gyrus (p. opercularis))
18	4.9	577	43.0	25.0	-3.0	(Right Insula)
19	4.4	243	43.0	9.0	-37.0	(Right Medial Temporal Pole)
20	4.5	311	43.0	-9.0	47.0	(Right Precentral Gyrus)

21	4.5	696	41.0	33.0	19.0	(Right Middle Frontal Gyrus)
22	4.7	400	41.0	23.0	21.0	(Right Prefrontal Cortex)
23	5.7	757	41.0	-75.0	-9.0	(Right Inferior Occipital Gyrus)
24	4.7	346	39.0	49.0	17.0	(Right Middle Frontal Gyrus)
25	3.9	379	39.0	-25.0	11.0	(Right Heschis Gyrus)
26	5.7	378	37.0	-81.0	-9.0	(Right Inferior Occipital Gyrus)
27	4.4	260	35.0	1.0	49.0	(Right Precentral Gyrus)
28	5.2	789	33.0	27.0	5.0	(Right Insula)
29	5.8	579	33.0	-93.0	-1.0	(Right Inferior Occipital Gyrus)
30	4.2	257	29.0	45.0	19.0	(Right Middle Frontal Gyrus)
31	5.7	314	27.0	-97.0	-3.0	(Right Inferior Occipital Gyrus)
32	4.3	901	25.0	-49.0	-25.0	(Right Cerebellum)
33	5.0	441	15.0	-49.0	-17.0	(Right Cerebellum)
34	3.6	228	13.0	-5.0	3.0	(Right Thalamus)
35	3.6	288	13.0	-19.0	-35.0	(Right dmpfc)
36	4.2	683	11.0	45.0	15.0	(Right Anterior Cingulate Gyrus)
37	4.9	562	9.0	39.0	43.0	(Right Superior Medial Gyrus)
38	4.6	539	9.0	23.0	39.0	(Right Middle Cingulate Gyrus)
39	4.4	309	9.0	13.0	5.0	(Right Nucleus Caudatus)
40	5.6	627	9.0	11.0	53.0	(Right SMA)
41	5.0	398	9.0	5.0	59.0	(Right SMA)
42	4.3	914	7.0	-65.0	-35.0	(Right Cerebellum)
43	4.7	702	7.0	-65.0	-21.0	(Cerebellar Vermis)
45	4.7	807	5.0	-49.0	-9.0	(Cerebellar Vermis)
46	4.3	515	3.0	-19.0	-21.0	(Brain Stem)
47	4.2	278	1.0	-71.0	-33.0	(Cerebellar Vermis)
48	-4.4	317	-1.0	-73.0	55.0	(Left Precuneus)
49	3.8	302	-3.0	49.0	31.0	(Left Superior Medial Gyrus)
50	3.6	322	-5.0	43.0	21.0	(Left Superior Medial Gyrus)
51	5.4	764	-5.0	11.0	47.0	(Left SMA)
52	4.9	461	-7.0	-7.0	59.0	(Left Paracentral Lobule)
53	3.8	392	-7.0	-25.0	51.0	(Left Paracentral Lobule)
54	4.7	424	-9.0	23.0	3.0	(Left Nucleus Caudatus)
55	4.2	230	-9.0	-73.0	-41.0	(Left Cerebellum)
56	3.7	432	-21.0	11.0	1.0	(Left Putamen)
57	6.3	550	-21.0	-95.0	-11.0	(Left Inferior Occipital Gyrus)
58	4.2	635	-27.0	-11.0	1.0	(Left Putamen)
59	4.8	240	-29.0	29.0	1.0	(Left Insula)
60	4.1	309	-29.0	-5.0	-29.0	(Left ParaHippocampal Gyrus)
61	4.4	446	-29.0	-27.0	51.0	(Left Postcentral Gyrus)
62	6.0	887	-29.0	-93.0	-5.0	(Left Middle Occipital Gyrus)
63	4.8	339	-31.0	-71.0	-11.0	(Left Fusiform Gyrus)
64	4.4	746	-37.0	25.0	3.0	(Left Inferior Frontal Gyrus (p. triangularis))
65	4.8	507	-37.0	-1.0	45.0	(Left Frontal Eye Fields)
66	4.7	345	-37.0	-25.0	53.0	(Left Postcentral Gyrus)

67	4.4	296	-37.0	-53.0	-13.0	(Left Fusiform Gyrus)
68	4.6	248	-37.0	-77.0	-5.0	(Left Inferior Occipital Gyrus)
69	4.1	394	-39.0	-65.0	-29.0	(Left Cerebellum)
70	4.2	237	-41.0	-11.0	51.0	(Left Precentral Gyrus)
71	4.7	556	-41.0	-21.0	45.0	(Left Postcentral Gyrus)
72	4.4	592	-41.0	-31.0	19.0	(Left Rolandic Operculum)
73	4.3	226	-41.0	-65.0	5.0	(Left Middle Occipital Gyrus)
74	4.2	204	-43.0	-59.0	9.0	(Left Middle Temporal Gyrus)
75	4.7	660	-47.0	-1.0	37.0	(Left Frontal Eye Fields)
76	4.4	275	-49.0	19.0	3.0	(Left Inferior Frontal Gyrus (p. triangularis))
77	3.8	532	-49.0	-25.0	-3.0	(Left Middle Temporal Gyrus)
78	4.5	526	-51.0	-47.0	13.0	(Left Middle Temporal Gyrus)
79	4.9	539	-53.0	5.0	3.0	(Left Rolandic Operculum)
80	3.9	217	-53.0	-59.0	39.0	(Left Angular Gyrus)
81	4.4	233	-55.0	9.0	13.0	(Left Inferior Frontal Gyrus (p. Opercularis))
82	4.5	224	-57.0	3.0	17.0	(Left Precentral Gyrus)

**Table 4:** Regions that shows significant sustained activation. Peak extraction from activation clusters was performed using and watershed algorithm. Value corresponds to z-value, positive values stand for activation and negative values for deactivation. Number of voxels corresponds to cluster size. Coordinates are reported in MNI. MNI coordinates were labeled with SPL Anatomy toolbox and Neurosynth.

label	value	voxels	peak_x	peak_y	peak_z	anatomical label
2	4.1	472	63.0	-31.0	13.0	(Right Superior Temporal Gyrus)
3	5.0	230	61.0	-23.0	43.0	(Right Supramarginal Gyrus)
4	5.3	541	59.0	-19.0	33.0	(Right Postcentral Gyrus)
5	5.0	429	59.0	-33.0	37.0	(Right Supramarginal Gyrus)
6	4.8	580	55.0	19.0	-3.0	(Right Inferior Frontal Gyrus (p. opercularis))
7	4.7	275	55.0	3.0	35.0	(Right Precentral Gyrus)
8	4.3	285	53.0	11.0	11.0	(Right Inferior Frontal Gyrus (p. opercularis))
9	5.3	901	53.0	-33.0	47.0	(Right Supramarginal Gyrus)
10	5.4	893	51.0	-55.0	-15.0	(Right Area MT+)
11	5.7	1135	47.0	7.0	27.0	(Right Inferior Frontal Gyrus (p. opercularis))
12	4.3	252	47.0	7.0	47.0	(Right Precentral Gyrus)
13	4.8	269	47.0	-23.0	37.0	(Right Postcentral Gyrus)
14	4.5	330	45.0	43.0	17.0	(Right Middle Frontal Gyrus)
15	4.8	382	45.0	35.0	19.0	(Right Middle Frontal Gyrus)
16	4.4	258	45.0	-65.0	-29.0	(Right Cerebellum)
17	5.4	1549	45.0	-65.0	-9.0	(Right Inferior Temporal Gyrus)
18	5.1	361	43.0	-33.0	41.0	(Right Supramarginal Gyrus)
19	4.7	739	41.0	29.0	-7.0	(Right Inferior Frontal Gyrus (p. orbitalis))
20	3.9	302	39.0	51.0	1.0	(Right Middle Frontal Gyrus)
21	4.5	452	39.0	5.0	-11.0	(Right Insula)

22	4.3	251	39.0	-77.0	15.0	(Right Middle Occipital Gyrus)
23	4.6	356	39.0	-81.0	3.0	(Right Middle Occipital Gyrus)
24	4.4	438	37.0	51.0	13.0	(Right Middle Frontal Gyrus)
25	4.0	381	37.0	35.0	31.0	(Right Middle Frontal Gyrus)
26	4.9	1060	37.0	-1.0	55.0	(Right Middle Frontal Gyrus)
27	5.2	882	37.0	-47.0	47.0	(Right Inferior Parietal Lobule)
28	4.0	224	33.0	-23.0	47.0	(Right Postcentral Gyrus)
29	4.8	225	33.0	-47.0	37.0	(Right Intraparietal Sulcus)
30	4.7	398	33.0	-53.0	57.0	(Right Superior Parietal Gyrus)
31	4.3	482	33.0	-71.0	25.0	(Right Middle Occipital Gyrus)
32	4.6	324	33.0	-81.0	7.0	(Right Middle Occipital Gyrus)
33	4.9	562	29.0	-5.0	57.0	(Right Frontal Eye Fields)
34	4.5	387	29.0	-45.0	-19.0	(Right Fusiform Gyrus)
35	4.3	587	29.0	-61.0	-19.0	(Right Cerebellum)
36	4.2	200	27.0	45.0	31.0	(Right Middle Frontal Gyrus)
37	4.3	351	27.0	-85.0	-21.0	(Right Cerebellum)
38	4.5	255	25.0	-63.0	55.0	(Right Intraparietal Sulcus)
39	4.8	423	25.0	-71.0	-47.0	(Right Cerebellum)
40	4.5	495	25.0	-75.0	-23.0	(Right Cerebellum)
41	5.0	957	23.0	-61.0	47.0	(Right Superior Occipital Gyrus)
42	4.4	206	21.0	63.0	-5.0	(Right Superior Occipital Gyrus)
43	4.5	383	17.0	11.0	61.0	(Right SMA)
44	3.8	305	15.0	-55.0	-45.0	(Right Cerebellum)
45	5.0	461	13.0	-71.0	-43.0	(Right Cerebellum)
46	4.0	218	11.0	-15.0	13.0	(Right Thalamus)
47	4.6	625	11.0	-23.0	-1.0	(Right Thalamus)
48	4.2	208	11.0	-29.0	-29.0	(Brainstem)
49	4.3	394	9.0	-1.0	65.0	(Right SMA)
50	4.7	356	7.0	15.0	61.0	(Right SMA)
51	4.1	740	7.0	-13.0	29.0	Right Temporal Gyrus)
52	4.4	458	7.0	-15.0	7.0	(Right SMA)
53	4.0	331	5.0	-65.0	-19.0	(Cerebellar vermis)
54	4.8	689	5.0	-81.0	-21.0	(Cerebellar vermis)
55	4.5	530	3.0	35.0	29.0	(Right Middle Cingulate Gyrus)
56	4.8	490	3.0	11.0	51.0	(Right SMA)
57	4.6	336	3.0	-79.0	-37.0	(Right Cerebellum)
58	4.7	544	1.0	21.0	43.0	(Left Superior Medial Gyrus)
59	4.4	494	1.0	-73.0	-13.0	(Cerebellar vermis)
60	4.7	414	-1.0	9.0	27.0	(Left Anterior Cingulate Cortex)
61	4.1	336	-1.0	-7.0	33.0	(Left Middle Cingulate Cortex)
62	3.8	413	-3.0	25.0	23.0	(Left Anterior Cingulate Cortex)
63	3.8	254	-5.0	-15.0	7.0	(Left Thalamus)
64	4.6	287	-5.0	-75.0	-41.0	(Left Cerebellum)
65	4.3	320	-7.0	-1.0	65.0	(Left SMA)
66	4.5	635	-9.0	1.0	-1.0	(Left Pallidium)

67	3.7	326	-11.0	-59.0	-45.0	(Left Cerebellum)
68	5.0	1025	-11.0	-77.0	-23.0	(Left Cerebellum)
69	3.5	220	-13.0	-17.0	7.0	(Left Thalamus)
70	3.6	276	-15.0	-3.0	21.0	(Left Caudate Nucleus)
71	4.0	273	-17.0	-45.0	-47.0	(Left Cerebellum)
72	5.0	812	-21.0	-63.0	51.0	(Left Superior Parietal Lobule)
73	5.5	943	-21.0	-73.0	-47.0	(Left Cerebellum)
74	4.5	498	-23.0	-79.0	-23.0	(Left Cerebellum)
75	4.8	471	-27.0	-5.0	55.0	(Left Frontal Eye Fields)
76	4.2	489	-27.0	-69.0	29.0	(Left Middle Occipital Gyrus)
77	4.9	668	-29.0	-65.0	-27.0	(Left Cerebellum)
78	4.0	397	-29.0	-85.0	3.0	(Left Middle Occipital Gyrus)
79	3.8	287	-31.0	-83.0	13.0	(Left Middle Occipital Gyrus)
80	3.8	346	-33.0	47.0	23.0	(Left Middle Frontal Gyrus)
81	4.3	352	-33.0	-55.0	-43.0	(Left Cerebellum)
82	4.2	446	-33.0	-59.0	-15.0	(Left Fusiform Gyrus)
83	4.2	479	-35.0	-43.0	41.0	(Left Inferior Parietal Lobule)
84	4.3	381	-35.0	-47.0	47.0	(Left Inferior Parietal Lobule)
85	4.1	350	-35.0	-83.0	-13.0	(Left Fusiform Gyrus)
86	3.6	250	-37.0	-9.0	49.0	(Left Frontal Eye Fields)
87	4.5	532	-39.0	-69.0	-3.0	(Left Middle Occipital Gyrus)
88	5.0	407	-39.0	-71.0	-25.0	(Left Cerebellum)
89	4.3	416	-41.0	-63.0	-33.0	(Left Cerebellum)
90	4.6	403	-41.0	-69.0	-9.0	(Left Area MT+)
91	4.4	266	-43.0	17.0	-3.0	(Left Insula)
92	4.9	703	-43.0	3.0	31.0	(Left Precentral Gyrus)
93	4.2	364	-47.0	-37.0	45.0	(Left Inferior Parietal Lobule)
94	4.3	210	-53.0	5.0	17.0	(Left Precentral Gyrus)
95	5.0	589	-59.0	-23.0	39.0	(Left Supramarginal Gyrus)

**Table 5:** Results of the ANOVA with factors "Time" and "Difficulty". ANOVA was performed to research transient moment-to-moment processing of brain regions involved in the vigilance task. Peak extraction from activation clusters was performed using and watershed algorithm. Value corresponds to z-values. Number of voxels corresponds to cluster size. Coordinates are reported in MNI. MNI coordinates were labeled with SPL Anatomy toolbox and Neurosynth.

label	value	voxels	peak_x	peak_y	peak_z	anatomical label
2	6.0	453	63.0	7.0	3.0	(Right Temporal Lobe)
3	4.5	330	63.0	-29.0	35.0	(Right Supramarginal Gyrus)
4	5.1	490	59.0	-27.0	13.0	(Rght Superior Temporal Gyrus)
5	5.3	332	57.0	-9.0	7.0	(Right Heschls Gyrus)
6	5.1	608	51.0	-49.0	-23.0	(Right inferior Temporal Gyrus)
7	5.3	542	51.0	-71.0	-17.0	(Right Fusiform Gyrus)
8	3.9	350	45.0	-13.0	43.0	(Right Precentral Gyrus)
9	6.0	475	37.0	-35.0	65.0	(Right Postcentral Gyrus)
10	5.3	213	29.0	-15.0	71.0	(Right Precentral Gyrus)
11	5.4	287	25.0	-63.0	-13.0	(Right Fusiform Gyrus)

12	6.6	363	25.0	-87.0	17.0	(Right Superior Occipital Gyrus)
13	6.6	375	25.0	-87.0	25.0	(Right Superior Occipital Gyrus)
14	5.5	491	21.0	-51.0	-1.0	(Right Lingual Gyrus)
15	5.9	281	21.0	-59.0	3.0	(Right Lingual Gyrus)
16	6.4	312	21.0	-73.0	-15.0	(Right Cerebellum)
17	5.5	217	19.0	-57.0	-11.0	(Right Lingual Gyrus)
18	5.2	526	17.0	-21.0	-7.0	(Right Hippocampus)
19	7.3	288	15.0	-69.0	-7.0	(Right Lingual Gyrus)
20	7.7	373	15.0	-87.0	-15.0	(Right Lingual Gyrus)
21	7.4	326	13.0	-91.0	1.0	(Right Calcarine Gyrus)
22	8.3	792	11.0	-71.0	3.0	(Right Lingual Gyrus)
23	8.2	473	11.0	-71.0	11.0	(Right Calcarine Gyrus)
24	5.7	358	11.0	-83.0	43.0	(Right Cuneus)
25	7.7	501	11.0	-89.0	17.0	(Right Cuneus)
26	4.1	200	9.0	-11.0	75.0	(Right SMA)
27	7.6	484	9.0	-81.0	-13.0	(Right Lingual Gyrus)
28	6.5	1129	7.0	-53.0	67.0	(Right Precuneus)
29	7.1	1027	7.0	-81.0	23.0	(Right Cuneus)
30	4.8	316	5.0	-37.0	51.0	(Right Middle Cingulate Gyrus)
31	7.9	397	5.0	-85.0	9.0	(Right Calcarine Gyrus)
32	4.6	628	3.0	-35.0	23.0	(Right Posterior Cingulate Gyrus)
33	6.3	469	1.0	-61.0	61.0	(Right Precuneus)
34	6.2	550	1.0	-71.0	55.0	(Right Superior Parietal Lobule)
35	5.6	284	1.0	-79.0	37.0	(Left Cuneus)
36	5.1	291	-1.0	-53.0	51.0	(Left Precuneus)
37	7.8	232	-1.0	-87.0	-1.0	(Left Calcarine Gyrus)
38	8.0	1605	-5.0	-77.0	3.0	(Left Lingual Gyrus)
39	6.5	315	-5.0	-91.0	15.0	(Left Cuneus)
40	7.5	489	-7.0	-73.0	-7.0	(Left Lingual Gyrus)
41	7.1	617	-7.0	-83.0	-13.0	(Left Lingual Gyrus)
42	7.1	371	-7.0	-93.0	3.0	(Left Calcarine Gyrus)
43	6.2	651	-9.0	-43.0	1.0	(Left Lingual Gyrus)
44	4.8	220	-11.0	-81.0	39.0	(Left Cuneus)
45	6.6	236	-11.0	-97.0	17.0	(Left Superior Occipital Gyrus)
46	5.5	505	-17.0	-53.0	-15.0	(Left Cerebellum)
47	6.0	338	-17.0	-55.0	1.0	(Left Lingual Gyrus)
48	6.3	538	-17.0	-79.0	-15.0	(Left Cerebellum)
49	6.3	585	-17.0	-87.0	23.0	(Left Superior Occipital Gyrus)
50	4.7	536	-41.0	-73.0	13.0	(Left Middle Occipital Gyrus)
51	5.5	426	-47.0	-69.0	-27.0	(Left Cerebellum)
52	6.2	337	-47.0	-71.0	-19.0	(Left Inferior Occipital Gyrus)
53	5.6	298	-55.0	-13.0	5.0	(Left Superior Temporal Gyrus)
54	5.7	281	-59.0	1.0	3.0	(Left Rolandic Operculum)
55	4.8	261	-61.0	-31.0	15.0	(Left Superior Temporal Gyrus)

**Table 6:** Results of the post-hoc t-test that was performed to examine transient activation after a subject correctly identified a target stimulus in *condition of hard discriminability*. Peak extraction from activation clusters was performed using and watershed algorithm. Value corresponds to z-values. Number of voxels corresponds to cluster size. Coordinates are reported in MNI. MNI coordinates were labeled with SPL Anatomy toolbox and Neurosynth.

label	value	voxels	peak_x	peak_y	peak_z	anatomical Label
2	-4.5	352	65.0	-17.0	27.0	(Right SupraMarginal Gyrus)
3	-4.5	336	61.0	1.0	33.0	(Right Postcentral Gyrus)
4	4.2	268	59.0	-61.0	-25.0	(Right Cerebellum)
5	-4.1	364	57.0	-23.0	33.0	(Right SupraMarginal Gyrus)
						(Right Superior Temporal
6	-4.2	441	57.0	-25.0	5.0	Gyrus)
7	-4.7	304	49.0	-21.0	63.0	(Right Postcentral Gyrus)
8	-5.0	283	47.0	-45.0	-17.0	(Right Inferior Temporal Gyrus)
9	-4.8	220	47.0	-77.0	5.0	(Right Middle Occipital Gyrus)
10	-4.7	310	43.0	-27.0	19.0	(Right Rolandic Operculum)
11	-5.3	792	43.0	-69.0	-1.0	(Right Middle Temporal Gyrus)
12	-4.2	279	41.0	-17.0	51.0	(Right FEF)
13	-4.9	499	41.0	-63.0	-11.0	(Right Inferior Occipital Gyrus)
14	-4.5	362	37.0	-81.0	1.0	(Right Middle Occipital Gyrus)
15	-4.6	263	35.0	-85.0	15.0	(Right Middle Occipital Gyrus)
16	-5.0	533	31.0	-77.0	23.0	(Right Middle Occipital Gyrus)
17	-5.3	366	29.0	-67.0	-9.0	(Right Fusiform Gyrus)
18	-4.7	319	25.0	-81.0	-7.0	(Right Fusiform Gyrus)
						(Right Superior Occipital
19	-4.3	256	23.0	-73.0	37.0	Gyrus)
20	-5.2	656	19.0	-49.0	-3.0	(Right Lingual Gyrus)
21	-5.3	568	17.0	-63.0	7.0	(Right Calcarine Gyrus)
22	-5.3	421	15.0	-79.0	-7.0	(Right Lingual Gyrus)
23	-5.2	213	13.0	-67.0	-5.0	(Right Lingual Gyrus)
24	-4.8	527	11.0	-69.0	19.0	(Right Calcarine Gyrus)
25	4.2	414	9.0	-39.0	-65.0	(Right Cerebellum)
26	-4.5	852	9.0	-83.0	15.0	(Right Cuneus)
27	-4.3	256	7.0	-17.0	51.0	(Right SMA)
28	4.2	383	7.0	-91.0	-23.0	(Right Cerebellum)
29	-3.9	374	5.0	-11.0	-1.0	(Right Thalamus)
30	4.2	372	1.0	-25.0	79.0	(Right Primary Motor Cortex)
31	-4.6	206	-3.0	-77.0	21.0	(Left Cuneus)
32	-5.3	766	-7.0	-81.0	-3.0	(Left Lingual Gyrus)
33	-6.0	529	-11.0	-61.0	-1.0	(Left Lingual Gyrus)
34	-4.6	209	-13.0	-67.0	9.0	(Left Calcarine Gyrus)
35	-5.2	686	-19.0	-87.0	27.0	(Left Superior Occipital Gyrus)
36	-4.7	295	-21.0	-51.0	-5.0	(Left Lingual Gyrus)
37	-5.3	399	-21.0	-73.0	-5.0	(Left Lingual Gyrus)

-4.8	371	-25.0	-79.0	23.0	(Left Middle Occipital Gyrus)
-4.9	247	-25.0	-87.0	-11.0	(Left Inferior Occipital Gyrus)
-4.2	222	-25.0	-93.0	17.0	(Left Middle Occipital Gyrus)
-4.8	306	-35.0	-59.0	-15.0	(Left Fusiform Gyrus)
-4.4	209	-37.0	-77.0	-9.0	(Left Inferior Occipital Gyrus)
-4.5	348	-43.0	-75.0	-3.0	(Left Inferior Occipital Gyrus)
-4.4	464	-43.0	-83.0	5.0	(Left Middle Occipital Gyrus)
-4.3	251	-59.0	-13.0	1.0	(Left Superior Temporal Gyrus)
-4.7	213	-61.0	1.0	21.0	(Left Postcentral Gyrus)
	-4.8 -4.9 -4.2 -4.8 -4.4 -4.5 -4.4 -4.3 -4.7	-4.8371-4.9247-4.2222-4.8306-4.4209-4.5348-4.4464-4.3251-4.7213	-4.8371-25.0-4.9247-25.0-4.2222-25.0-4.8306-35.0-4.4209-37.0-4.5348-43.0-4.4464-43.0-4.3251-59.0-4.7213-61.0	-4.8371-25.0-79.0-4.9247-25.0-87.0-4.2222-25.0-93.0-4.8306-35.0-59.0-4.4209-37.0-77.0-4.5348-43.0-75.0-4.4464-43.0-83.0-4.3251-59.0-13.0-4.7213-61.01.0	-4.8371-25.0-79.023.0-4.9247-25.0-87.0-11.0-4.2222-25.0-93.017.0-4.8306-35.0-59.0-15.0-4.4209-37.0-77.0-9.0-4.5348-43.0-75.0-3.0-4.4464-43.0-83.05.0-4.3251-59.0-13.01.0-4.7213-61.01.021.0

**Table 7:** Results of the post-hoc t-test that was performed to examine transient activation after a subject correctly identified a target stimulus in *condition of easy discriminability*. Peak extraction from activation clusters was performed using and watershed algorithm. Value corresponds to z-values. Number of voxels corresponds to cluster size. Coordinates are reported in MNI. MNI coordinates were labeled with SPL Anatomy toolbox and Neurosynth.

label	value	voxels	peak_x	peak_y	peak_z	anatomical label
2	4.9	420	53.0	-63.0	-25.0	(Right Cerebellum)
3	5.3	295	49.0	-83.0	-19.0	(Right Lateral Occipital Gyrus)
4	-4.0	252	47.0	-21.0	53.0	(Right Postcentral Gyrus)
5	-4.3	275	45.0	-11.0	49.0	(Right FEF)
6	-4.6	245	45.0	-63.0	17.0	(Right Area MT+)
7	-6.2	858	45.0	-79.0	11.0	(Right Middle Occipital Gyrus)
8	-4.9	618	33.0	-31.0	-19.0	(Right Fusiform Gyrus)
9	-5.4	307	33.0	-57.0	-11.0	(Right Fusiform Gyrus)
10	-5.4	457	31.0	-77.0	-9.0	(Right Fusiform Gyrus)
11	-5.1	557	31.0	-77.0	25.0	(Right Middle Occipital Gyrus)
12	-5.4	235	29.0	-63.0	-5.0	(Right Fusiform Gyrus)
13	-5.0	301	23.0	-47.0	-9.0	(Right Lingual Gyrus)
14	-5.1	274	21.0	-61.0	-3.0	(Right Lingual Gyrus)
15	-5.1	929	21.0	-69.0	29.0	(Right Cuneus)
16	-5.9	544	19.0	-63.0	11.0	(Right Calcarine Gyrus)
17	-4.4	478	13.0	-33.0	51.0	(Right Paracentral Lobule)
18	-4.7	204	13.0	-77.0	13.0	(Right Calcarine Gyrus)
19	-4.8	279	9.0	-63.0	19.0	(Right Calcarine Gyrus)
20	4.8	363	3.0	-23.0	11.0	(Right Thalamus)
21	5.4	372	1.0	-17.0	79.0	(Right Motor Cortex)
22	5.1	324	1.0	-49.0	73.0	(Right Superior Parietal Cortex)
23	5.2	737	1.0	-87.0	-21.0	(Right Cerebellum)
24	4.7	225	-1.0	5.0	75.0	(Left SMA)
25	-5.3	448	-5.0	-71.0	19.0	(Left Calcarine Gyrus)
26	-5.3	332	-9.0	-69.0	3.0	(Left Lingual Gyrus)
27	-5.8	561	-13.0	-59.0	-1.0	(Left Lingual Gyrus)
28	-5.3	253	-15.0	-49.0	-51.0	(Left Cerebellum)
29	-4.7	231	-15.0	-75.0	35.0	(Left Cuneus)
30	-5.8	336	-17.0	-45.0	-9.0	(Left Lingual Gyrus)
31	-5.3	371	-17.0	-65.0	9.0	(Left Calcarine Gyrus)

32	-4.8	209	-19.0	-73.0	-7.0	(Left Lingual Gyrus)
33	-5.7	623	-19.0	-81.0	29.0	(Left Superior Occipital Gyrus)
34	-5.6	546	-29.0	-49.0	-17.0	(Left Fusiform Gyrus)
35	-4.6	375	-33.0	-81.0	3.0	(Left Middle Occipital Gyrus)
36	-5.0	304	-37.0	-79.0	-9.0	(Left Area MT+)
37	-4.5	600	-37.0	-81.0	15.0	(Left Middle Occipital Gyrus)
38	4.8	517	-51.0	-75.0	-19.0	(Left Lateral Occipital Gyrus)

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## Abbreviations

6 DOF FLIRT	6 Degree of Freedom Rigid Body Transformation
Area MT+	Middle Temporal Area
Area LIP	Lateral Intraparietal Area
BOLD	Blood Oxygenated Level Dependent
FEF	Frontal Eye Fields
fMRI	functional Magnet Resonance Imaging
FWHM	Full Width at Half Maximum
GLM	General Linerar Model
НСР	Human Connectome Project
HRF	Hemodynamic Response Function
IFG	Inferior Frontal Gyrus
IPS	Intraparietal Sulcus
IPL	Inferior Parietal Lobule
ISI	Inter-Stimulus-Interval
ITI	Inter-Trial-Interval
PET	Positron Emission Tomography
MFG	Middle Frontal Gyrus
MNI	Montreal Neurological Institute
SMG	Supramarginal Gyrus
SPL	Superior Parietal Lobule
STG	Superior Temporal Gyrus
STS	Superior Temporal Sulcus
TMS	Transcranial Magnet Stimulation
ТРЈ	Temporoparietal Junction
TR	Repetition Time

## List of Figures

Figure 1: Localization of the dorsal and ventral frontoparietal attention systems	8
Figure 2: Core Regions of the dorsal frontoparietal attention system	9
Figure 3: Core Regions of the ventral frontoparietal attention system	11
Figure 4: Timing of the BOLD-runs	17
Figure 5: Illustration of Block, Event-related and Mixed Design	18
Figure 6: The Hemodynamic Response Function	20
Figure 7: Illustration of the 7Networks	26
Figure 8: Activations in condition of hard discriminability vs. zero	28
Figure 9: Deactivations in condition of hard discriminability vs. zero	28
Figure 10: Activations in condition of easy discriminability vs. zero	30
Figure 11: Deactivations in condition of easy discriminability vs. zero	30
Figure 12: Overlaps between sustained activation in dorsal and ventral	31
frontoparietal attention and the 7Networks	
Figure 13: Cortical renderings and axial slices of sustained activation	33
Figure 14: Axial slices of brain areas that showed sustained deactivation	33
Figure 15: Overlaps between transient activation and the 7Networks	34
Figure 16: Cortical renderings and axial slices of transient activation	36
Figure 17: Post-hoc t-test 1: Correct target identification in	37
condition of hard discriminability vs. condition of easy discriminability	
Figure 18: Post-hoc t-test 2: Correct target identification in	39
condition of hard discriminability vs. zero	
Figure 19: Post-hoc t-test 3: Correct target identification in	40
condition of easy discriminability vs. zero	
Figure 20: Overlaps between ANOVA and post-hoc t-tests	45
## List of Tables

Table 1: Demographic data of the subjects	52
Table 2: Peak activation clusters in condition of hard discriminability vs. zero	53
Table 3: Peak activation clusters in condition of easy discriminability vs. zero	57
Table 4: Peak activation clusters of sustained activation	59
Table 5: Peak activation clusters of transient activation	61
Table 6: Peak activation clusters of transient activation/	63
condition of hard discriminability vs. zero	
Table 7: Peak activation clusters of transient activation/	64
condition of easy discriminability vs. zero	

## Zusammenfassung

Hintergrund: Die Fähigkeit die Aufmerksamkeit über einen längeren Zeitraum aufrecht zu erhalten, wie in etwa beim Steuern eines Autos auf einer Autobahn wird Vigilanz genannt. Basierend auf früheren Studien gibt es zwei Systeme im Gehirn welche die Kontrolle von Aufmerksamkeit unterstützen: das bilaterale dorsale und das rechts-lateralisierte ventrale frontoparietale Aufmerksamkeitssystem. Das dorsale System wird durch top-down Aufmerksamkeit aktiviert. D.h., wenn eine Person sich fokussiert und die Umgebung nach relevanten Stimuli absucht, basierend auf Zielen und Erwartungen. Das ventrale System wird durch bottom-up sensorische Stimuli aktiviert die Verhaltensrelevant sind und außerhalb des Fokus der Aufmerksamkeit erscheinen. Während der visuellen Suche, geht die Aktivität des dorsalen Systems mit der Unterdrückung der Aktivität des ventralen Systems einher. Ein Wechsel in der Aufmerksamkeit (bsp. eine Umorientierung in Richtung eines überraschend/plötzlich erscheinendes Stimulus), wird durch beide Systeme gesteuert. Aus früheren Studien geht hervor, dass anhaltende und transiente (vgl. "sustained" und "transient" activity) neuronale Aktivität mit unterschiedlichen Verarbeitungsmodi des Gehirns in Verbindung gebracht werden können. Task-bezogene, anhaltende Aktivität wird mit dem generellen Aufmerksamkeitsstatus assoziiert. Item-bezogene, transiente Aktivität wird mit der moment-zu-moment Verarbeitung von Stimuli verbunden. Methoden: Um die Rolle beider Aufmerksamkeitsnetzwerke näher zu untersuchen, wurden die fMRI-Daten von 23 Versuchspersonen die einen Vigilanz-Test mit zwei Schwierigkeitsgraden absolvierten, analysiert. Es wurde ein Mixed-Design verwendet um die separate Schätzung von anhaltender und transienter Aktivität von Gehirnregionen zu ermöglichen. Resultate: Die Resultate deuten darauf hin, dass anhaltende Aktivität in beiden Aufmerksamkeitssystemen während der Absolvierung des Vigilanz-Tests stattfindet (In leichter und schwieriger Version). Nur im TPJ (einer Kernregion des ventralen Systems) zeigte sich keine Task-bezogene Aktivität. Beide Aufmerksamkeitssysteme partizipierten in der Kontrolle der transienten Aktivität. Bedingt durch Limitationen der Studie, konnten keine Konklusionen darüber gemacht werden, ob transiente Aktivität in den Aufmerksamkeitssystemen durch die Schwierigkeit des Vigilanz-Tests beeinflusst wurde. In allen Konditionen und Verarbeitungsmodi konnte eine Lateralisierung zur rechten Hemisphäre seitens des ventralen Systems beobachtet werden. Insgesamt deuten die Ergebnisse darauf hin, dass beide Systeme zusammenarbeiten um anhaltende und transiente Aufmerksamkeit zu steuern.

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