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Abstract

Mental rotation is a complex cognitive process involving a number of simpler cognitive processes. Most notably, mental rotation relies on storage and active maintenance of a mental image and manipulation of this image. People differ considerably in their mental rotation skills. Prior research has shown that the amplitude of an ERP component associated with mental rotation (termed rotation related negativity (RRN)) reflects a subjects´ performance in the mental rotation task. However, we do not know whether a subject who shows good performance is skilled in storage or rather manipulation of mental images. The aim of this study was to reveal the contribution of both sub-processes to the association between RRN and performance in mental rotation. In order to achieve this, in each subject we recorded ERPs during a mental rotation task and a task that measured visual short term memory efficiency. We found that performance in both tasks was strongly correlated. Additionally, we found an association between the ERPs in both tasks. Thus, we were able to confirm the strong connection of manipulation and storage related processes in mental rotation. Furthermore, we found that after correction of RRN for storage related ERPs the remaining activity still significantly predicted performance in mental rotation. Therefore, we conclude that mental rotation performance seems to rely mainly on manipulation related cognitive processes rather than storage related processes.

1) Theoretical Background

1.1) Mental Imagery

Understanding the cognitive processes underlying mental imagery represents an intriguing challenge in research of human cognition. Mental imagery plays an important role in nearly all everyday activities. Even thinking about simple questions (such as, whether one has enough milk in the fridge) typically evokes a mental image (of one´s fridge and the milk cartons inside). As defined by Kosslyn and Thomson (2003), visual mental imagery constitutes a process where a visual short-term memory (STM) representation is present (or active) but the stimulus is not actually being viewed. They describe visual imagery as *"seeing with the mind´s eye"* (Kosslyn 2003). According to Kosslyn et al. (1995), imagery processes also play an important role in the visual perception as such. This might especially be the case when imagery compensates for incomplete visual inputs (Kosslyn 1995).

However, mental imagery is not limited to visual mental imagery. It can also operate on all other sensory modalities – auditory, somatosensory, olfactory, or gustatory. A specific type of imagery is motor imagery – an imaginary execution of movements. Mental imagery also is involved in various complex cognitive operations - such as, spatial reasoning, concrete and abstract reasoning, learning, memory and language comprehension.

Visual mental imagery itself is not restricted to simple imagination of visual pictures but includes various more or less complex cognitive processes. Kosslyn et al. (1995) define four major abilities in processing mental images:

-*Image generation.* Mental images are generated by the activation of information stored in long-term memory or newly created by imagination.

-*Image retention.* Once generated, the mental images must be held active in STM.

-*Image inspection*. Images held in short-term memory can be inspected. Inspection also enables to extract specific information from a complex image.

-*Image transformation.* Mental images can be manipulated in mind in a similar way real objects are manipulated. For example, in mind objects can be shifted, rotated, reconfigured, etc.

This thesis focuses on a specific visual mental imagery process, namely mental rotation, which is rotation of an object in mind. This includes imagery of an object and its transformation in space. Therefore, mental rotation is considered as spatial cognitive ability (Vitouch 1997). Spatial skills significantly contribute to general cognitive ability (intelligence) and are included in many intelligence tests (e.g. Wechsler Adult Intelligence Scale, (Wechsler 1997)).

The ability of mental imagery has been attributed to a system called working memory (Baars 2010). The working memory system is an important theoretical construct, which is assumed to be crucial for practically every human cognitive process. One of the most influential models of working memory has been postulated by Baddeley and Hitch (1974) and Baddeley (1986) and since then has been modified and extended by the authors themselves as well as many other researchers (e.g. (Baddeley 2003)). In the next section the theoretical framework of working memory is introduced.

1.2) Working Memory

1.2.1) The working memory model

In early memory theories, memory was described as a three-component model (review in e.g. Eysenck and Keane (2005)). Multi-store approaches postulated that memory is divided into a sensory storage, a short-term storage and a long-term storage. It turned out that the three-component model was an oversimplification. Baddeley and Hitch (1974) introduced a different model of the human short-term memory store, which they called the working memory (WM) model. This new model abandoned the concept of a unitary short-term store in favor of a multicomponent system. Additionally, the new WM model did not only describe memory per se, but also integrated the short-term memory system into complex human cognition (Baddeley 2000). According to this model, WM is responsible for temporary storage as well as active processing of information and it is basically involved in all complex cognitive tasks. Baddeley et al. (2000) define WM as a *"broad framework of interacting processes that involve the temporary storage and manipulation of information in the service of performing complex cognitive activities"* (Baddeley 2000).

The original WM model assumed three sub components of WM – a phonological/verbal storage (termed phonological loop), a visual-spatial storage (termed visuospatial sketchpad) and a supervisory control system (termed central executive). In 2000, Baddeley extended the model by introducing a fourth component – the episodic buffer (Baddeley 2000). Figure 1 (all figures are provided in Appendix) is a schematic demonstration of the WM framework developed by Baddeley (2003) and shows the different WM components and their relation to each other.

Components of working memory and their neural correlates

WM “traces” can be found in many brain locations (Bear 2007). Experimental studies support the assumption that the different WM components are associated with different brain areas (see, e.g. (Jonides 1993; Smith 1997; Smith 1998; Bear 2007)). In the next, the different WM components and their neural correlates are outlined. Since the present study focuses on visual imagery, the visuospatial sketchpad is described in more detail while the other components are only briefly introduced.

The visuospatial sketchpad

The visuospatial sketchpad is responsible for storage and manipulation of visual and spatial information (e.g. (Vecchi 1995; Bruyer 1998; Baddeley 2003)). Based on a review of prior research, Jiang et al. (2000) state that representations of objects in visual WM consist of coarse rather than detailed mental copies. Additionally, they summarize that the capacity of visual STM is limited to about four to five items (Jiang 2000). According to Luria and Vogel (2011) one item is represented by an object, in which distinct visual features are grouped together (Luria 2011). However, Baddeley et al. (2011) argue that the visuospatial sketchpad might contain both feature and object levels of representations, which are hierarchically ordered (Baddeley 2011). Spatial information is assumed to be based on spatial configurations that specify the location of individual items. Additionally, relational information between individual items is represented within spatial WM (Jiang 2000). Concerning the capacity of spatial WM, Simons et al. (1996), for example, found that subjects performed almost perfectly in a spatial WM task with five locations (Simons 1996). However, spatial WM capacity can be increased by having a constant spatial configuration across encoding and retrieval (Jiang 2000).

The visuospatial sketchpad is assumed to subserve visual imagery (e.g. (Kosslyn 1995; Carlesimo 2001; Baddeley 2003; Zimmer 2008)). However, visuospatial WM is also crucial in other cognitive processes, such as spatial orientation, geographical knowledge, or understanding of complex systems, such as machinery (Baddeley 2003).

Distinction between visual and spatial short-term memory. The visuospatial sketchpad is assumed to be responsible for visual (object) and spatial WM. However, various experiments using different methods (such as, neuropsychological tests, patient case studies and neuroimaging experiments) indicate that object and spatial WM systems are functionally distinct (for review see e.g. (Della Sala 1999)). For example, dual task interference experiments found that remembering objects is disrupted by object processing tasks but not by spatial processing tasks, whereas remembering location is disrupted by spatial processing tasks but not by object processing tasks (e.g. (Hecker 1997)). Patient studies support this distinction in visuospatial STM. For example Carlesimo et al. (2001) reported a patient with a lesion in the right frontal and parietal cortex who suffered from a strong impairment in temporary storage of spatial but not of object information (Carlesimo 2001). Neuroimaging studies revealed that processing in visuospatial STM is generally associated with activity in prefrontal and posterior brain regions (e.g. (Agam 2009)). Preferential engagement of the right hemisphere has often been reported (e.g. (Jonides 1993; Smith 1997; Smith 1998; Baddeley 2000)). Results from neuroimaging studies also support the assumption that object information (such as color, shape, or texture) and spatial information are processed in different brain areas (e.g. (Smith 1999; Carlesimo 2001; Sala 2003; Zimmer 2008)). Based on a review, Zimmer (2008) states that spatial information seems to be processed in the parietal cortex, whereas object information seems to be processed in the inferotemporal, the lateral temporal-occipital and the fusiform cortex (Zimmer 2008). In general, spatial processing seems to require dorsal (occipitio-parietal) areas of the brain (so called dorsal stream), whereas visual-object processing seems to require ventral (occipito-temporal) brain areas (so called ventral stream) (e.g. (Smith 1999; Carlesimo 2001; Sala 2003)). Additionally, the prefrontal cortex (PFC) might also show a dorsal-ventral dissociation for spatial and object WM – such as the dorsolateral PFC might be involved in spatial WM and the ventrolateral PFC in object WM (as reviewed by

(Levy 2000)). Although Oliveri et al. (2001) argue, based on a TMS study, that the dorsolateral PFC might be necessary for WM computations in general, regardless whether spatial or object information is processed (Oliveri 2001).

However, a complete separation of brain structures associated with object and spatial WM might not be possible. Sala et al. (2003) state that the distinction between neural correlates of spatial and object WM is manifested by a graduated activation pattern rather than an absolute division. In a series of fMRI experiments, they found that both forms of WM activate similar pattern of brain areas (Sala 2003). They argue that object processing also includes spatial aspects and hence object WM might be distributed across dorsal and ventral areas of visual and prefrontal cortices (Sala 2003).

Distinction between storage and manipulation processes in visuospatial WM. Visuospatial WM is assumed to be responsible for manipulation and storage of visuospatial information (e.g. (Vecchi 1995; Bruyer 1998; Baddeley 2003)). The neural correlates of visuospatial WM can be aligned to manipulation related processes and storage related processes. However, research on the actual neural systems that underlie visuospatial storage and manipulation shows ambiguous results. Some authors argue that visuospatial manipulation processes are mainly associated with anterior brain regions, whereas visuospatial storage processes are related to more posterior areas (e.g. (Smith 1997; Smith 1999; Zimmer 2008; Ward 2010)). However, other authors argue that parts of the prefrontal cortex might be responsible for WM storage processes (e.g. (Jonides 1993; Petrides 1995; Petrides 2005)).

Smith and Jonides (1998 and 1999), for example, found that manipulation of visuospatial information is associated with activation in the right superior posterior parietal cortex, the right premotor cortex and the dorsolateral PFC. Storage of visuospatial information was found to be associated with activation in the right inferior posterior parietal area, the anterior occipital area and the ventrolateral PFC (Smith 1998; Smith 1999). Gruber and van Cramon (2003), on the other hand, found that visuospatial WM is associated with bilateral activation in the cortices along posterior parts of the superior frontal sulcus and along the intraparietal sulcus. In a fMRI study, they could not find a dissociation between neural correlates of visuospatial storage and visuospatial manipulation processes (Gruber 2003). However, Postle (2006) argues, based on an extensive review, that activation in prefrontal areas is not related to WM storage processes but rather to executive processes - such as, mediation of interference and distraction, attention and selection, flexible control, transformation, response preparation, motivation and reward expectation. He states, that *'the retention of information in working memory is associated with sustained activity in the same brain regions that are responsible for the representation of that information in non-working memory situations'* (Postle 2006). Thus, for the visuospatial sketchpad this means, that according to Postle, storage of visual and spatial information relies on brain areas that are also involved in spatial and visual perception (i.e. parietal cortex and inferotemporal, lateral temporal-occipital and fusiform cortex (Zimmer 2008)) and manipulation/transformation of visuospatial information relies on brain areas associated with executive functioning- (i.e. the PFC (Postle 2006)).

The phonological loop

According to Baddeley, the phonological loop consists of a passive transient phonological store for verbal and auditory information and an articulatory rehearsal process, in which information is refreshed via subvocal articulation (e.g. (Baddeley 1998; Baddeley 2000; Baddeley 2003)). By this definition, the phonological loop is responsible for passive storage and active manipulation of verbal information. The phonological loop is assumed to play a crucial role in acquisition of the native language in children as well as in acquisition of foreign languages (Baddeley 1998). In general, this component is mainly associated with activation in the left hemisphere (see, e.g. (Smith 1997; Smith 1998; Henson 2000)). Neuroimaging and lesion case studies support the assumption of an anatomical dissociation of storage and manipulation processes within the phonological loop (e.g. (Henson 2000)). Storage of phonological information is mainly associated with activation of the left posterior parietal cortex (Awh 1996; Smith 1998), especially the supramarginal gyrus (Paulesu 1993; Henson 2000). Manipulation of phonological information, on the other hand, is mainly associated with activation of anterior regions of the left hemisphere, such as the Broca´s area, the left supplementary motor area (Paulesu 1993; Awh 1996; Smith 1998) and the left premotor cortex (Paulesu 1993; Awh 1996; Smith 1998; Henson 2000).

The episodic buffer

This component has recently been added to the WM model by Baddeley (Baddeley 2000). The episodic buffer is responsible for binding information together in order to form integrated episodes. This component integrates information from the phonological loop and the visuospatial sketchpad and establishes links to long-term memory (Baddeley 2000; Baddeley 2003; Baddeley 2011). In a fMRI study, Gruber and von Cramon (2003) investigated the neural substrate of the episodic buffer. They found a specific activation in the right middle frontal gyrus and the presupplementary motor area, as well as bilateral activation in the opercular cortex and the cortex along anterior and middle parts of the intraparietal sulcus (Gruber 2003). Other fMRI studies reported activation of the right PFC, a region assumed to play a special role in integration of cross-modal information (Prabhakaran 2000; Zhang 2004). However, Baddeley et al. (2011) argue that the episodic buffer may be consist of a widely distributed neural system with different subsystems responsible for different types of binding, such as visual or verbal binding (Baddeley 2011).

The central executive

The central executive is assumed to be a superordinate system that coordinates other components of WM by allocating attention. In the Baddeley's WM model, the central executive represents a key component of WM, while the other systems are its slave systems (e.g. (Baddeley 2003)). However, the central executive itself seems to involve separate components. Miyake et al. (2000), for example, found evidence for distinct major executive cognitive processes – attention shifting, information updating and response inhibition (Miyake 2000). Central executive functions are assumed to be linked with activity of the PFC (e.g. (Smith 1998; Smith 1999; Bear 2007; Chudasama 2011)), especially its dorsolateral division (Smith 1997).

1.2.3) EEG correlates of visuospatial working memory

It has been shown that engagement of WM can be traced by event related potentials (ERPs) of the electroencephalogram (EEG) (e.g. (Klaver 1999; Gevins 2000; Vogel 2004; Vogel 2005; Morgan 2008)). A number of ERP studies found that processing in WM typically elicits a prolonged slow negative wave (as reviewed by (Kok 2001)). For example, Klaver et al. (1999) identified a negative slow wave during memorization of visual information which appeared contra-lateral to an object that had to be memorized (i.e. the contra-lateral negative slow wave, CNSW). In their task, subjects had to memorize a test object and subsequently match it to a probe object. Memory load was varied by the number of objects that had to be memorized- i.e. the subject had to memorize either one test object (low memory load) or two test objects (high memory load). The CNSW was maximal at occipital electrodes with an onset latency of 300 ms after the test objects were presented (Klaver 1999). Whereas in low memory load trials the negativity continued until the offset of the object, in high memory load trials the CNSW disappeared so that the ERP amplitude was similar to trials where no memorization was required. Klaver et al. interpreted this as a neural marker of reaching WM processing limits.

Vogel and Machizawa (2004) also found that the CNSW is sensitive to WM load during maintenance of visual object information (i.e. colors of figures). They found that the CNSW amplitude increased with increasing task demand (i.e., the number of items that had to be memorized). Moreover, individual differences in WM capacity were associated with CNSW amplitude. When a subject reached his/her capacity limits, the CNSW amplitude did not further increase. Thus, good performers showed higher CNSW amplitudes in high memory load trials than poor performers.

Prime and Jolicoeur (2009) showed that the offset latency of the CNSW was sensitive to WM task duration. The offset latency of the CNSW increased when the duration of storage related WM processes increased (Prime 2009).

Other studies also found a negative slow wave during storage of visuospatial information (e.g. (Morgan 2010)). This wave is maximal at parieto-occipital electrodes and seems to be content-specific, so that visual-spatial WM elicits higher amplitudes than visual-object WM (Morgan 2010).

Gevins et al. (2000) assessed the influence of visuospatial WM load on the amplitude of the late positive component (LPC, or P3) – a positive ERP component which occurs about 300-500 ms after stimulus onset (Luck 2005). They found that higher ability subjects showed higher LPC amplitudes than lower ability subjects. However, they did not find an interaction of LPC amplitude and task load, which means that higher LPC amplitudes in good performers were observed across all task conditions. However, the authors argue that the general task difficulty in their study was rather high compared to other studies. Since the LPC amplitude is associated with the amount of attention that is focused on a task (Gevins 1996) they argue that higher ability subjects might have greater attention capacity to allocate to the task (Gevins 2000). Nittono et al. (1999) found very similar results for the association between LPC and WM capacity (Nittono 1999).

In sum, processing in visuospatial WM is associated a slow negative wave (e.g. (Kok 2001)). Additionally, it seems that the amplitude of this negative slow wave increases when WM load is increased. When a subject reaches his/her WM capacity limits this seems to be associated with ceiling ERP amplitudes (Nittono 1999; Vogel 2004; Vogel 2005).

1.3) Mental Rotation

Mental rotation represents a specific type of visual mental imagery (see e.g. (Cooper 1973; Kosslyn 1995; Vitouch 1997; Eysenck 2005; Baars 2010)). Kosslyn et al. (1995) classify mental rotation under mental image transformations. Basically, two types of mental rotation are distinguished. So-called two-dimensional mental rotation refers to rotating a two-dimensional object (e.g., rotation of an alphanumeric characters). So-called three-dimensional mental rotation refers to rotating a three-dimensional object (e.g., rotation of a cube presented in a perspective drawing) (e.g. (Jordan 2001)).

In general, it is assumed that the process of mental rotation requires consecutive mental transformations while storage of the actual position/orientation of the object is being constantly updated (e.g. (Hyun 2007)). This means, that mental rotation includes short-term storage and manipulation of a visual image. This clearly links mental rotation with working memory (e.g. (Kosslyn 1995; Eysenck 2005; Hyun 2007; Prime 2009)). Hyun et al. (2007) have shown that mental rotation relies on visual STM rather than spatial STM. The necessary executive processes (such as attention, planning of subtasks to achieve goal, inhibition of distracters, or updating of WM contents) are assumed to be performed by the central executive (Eysenck 2005).

In a pioneering study, Cooper and Shepard (1973) investigated the amount of time subjects need to solve a two-dimensional mental rotation task. In this task, subjects had to decide whether rotated alphanumeric characters (i.e., the letters ‘F’, ‘G’, ‘J’, ‘R’, ‘e’, ‘j’, ‘k’, ‘m’ and the numbers ‘2’, ‘5’, ‘4’ and ‘7’) were displayed in the canonical form or mirror-reversed. Cooper and Shepard found that the more the character was rotated from the upright position, the more time subjects needed to solve the task. The authors suggested that subjects carry out a "continuous" rotation of an inner representation of the visual image and thus this rotation takes longer when rotation angles increase. In other words, the authors drew an analogy between mental rotation and physical object rotation (Cooper 1973).

1.3.1) Neural correlates of mental rotation

Mental rotation represents the most extensively studied mental-image transformation process (Milivojevic 2003). Researchers have applied a wide variety of experimental methods in order to assess the neural systems underlying mental rotation. In the next, the most relevant of these studies are presented. They are ordered according to the experimental method employed.

Mental rotation and EEG

Investigating mental rotation with event related potential (ERP) analysis of the electroencephalogram (EEG) has a long history, beginning with studies of Wijers et al. and Perronet and Farah in 1989. Most ERP studies used mental rotation of characters in the frontal plane (i.e. two-dimensional mental rotation) as the experimental task. This is due to the fact that ERPs require many repetitions in order to obtain a good signal to noise ratio of the averaged signal (Luck 2005). Two-dimensional mental rotation of characters can be solved quickly, keeping the total duration of experiments acceptable also with many task repetitions. On the contrary, three-dimensional mental rotation tasks usually require more time to find a solution and cannot be as easily studied with ERPs as two-dimensional mental rotation tasks

(Schendan 2009). Nevertheless, there are ERP studies which employed a three-dimensional mental rotation task (e.g. (Vitouch 1997; Lamm 1999; Schendan 2009)).

ERP recordings during two-dimensional mental rotation of characters revealed that this cognitive operation is associated with a specific ERP wave - the so called rotation related negativity (RRN) (e.g. (Perronet 1989; Wijers 1989; Heil 2002)). This negativity is considered as an electrophysiological correlate of the mental rotation process (e.g. (Wijers 1989; Heil 2002)). The RRN is a slow negative wave in the interval of 350-800 ms after stimulus onset that overlaps with a large positive component (i.e. the P3 component, or LPC) (Perronet 1989; Wijers 1989). Therefore, no negativity per se is visible in the resulting ERP wave. Instead, a decrease of the P3 amplitude is observable and this decrease becomes more negative with increasing angular deviation of the stimulus. Thus, the more mental rotation is necessary, the more negative is the ERP amplitude (Heil 2002). This effect is shown in Figure 2. Often, to visualize the RRN clearly a difference ERP is calculated between mental rotation condition and control condition. The RRN and its modulation with rotation magnitude is largest over parietal electrodes (Rösler 1997).

ERP recordings of three-dimensional mental rotation also identified an increasing parietal negativity with increasing rotation angle (Schendan 2009). However, Schendan and Lucia found that the linear modulation of ERP amplitude with rotation angle was not observable before 400 ms, indicating a later onset of mental rotation ERP effects in three-dimensional mental rotation compared to two-dimensional mental rotation (Schendan 2009).

Some ERP studies report a right-hemispheric dominance of the RRN (e.g. (Vitouch 1997; Yoshino 2000; Milivojevic 2003)), while others found no reliable hemispheric differences (e.g. (Heil 1998; Lamm 1999; Beste 2010)).

Several studies found that the RRN is associated with individual abilities in mental rotation. Using a three-dimensional mental rotation task (3DW task (Gittler 1990), Lamm et al. (1999) found a wider distribution of RRN over the scalp in poor compared to good performers. Additionally, poor performers showed negative potentials at fronto-medial sites, which did not occur in good performers (Lamm

1999). Vitouch et al. (1997) also used rotation in three dimensions and reported that poor performers show topographically wider distribution of activity over the right hemisphere compared to good performers who show more symmetrical activity (Vitouch 1997). This might be surprising since the right hemisphere is assumed to be particularly involved in spatial processing. Vitouch et al. (1997) speculate that some sort of preactivation prior to the actual task execution may be present in good performers, which results in lower task-specific amplitudes. Additionally, it might be that the demands of the task were not sufficient enough to ‘challenge’ the highly skilled subjects and thus little cortical activation was necessary for good performers to solve the task (Vitouch 1997).

In contrast, for two-dimensional character rotation Beste et al. (2010) reported that ERP amplitude modulation was more confined within the parietal region in poor performers than in good performers who showed a wider activation pattern. The authors explain this finding by the possibility that the recruitment of larger neural networks in good performers might represent a more efficient neural strategy that enables better mental rotation performance (Beste 2010).

Furthermore, mental rotation ability was found to be related to the amplitude of the RRN. Several studies found that higher RRN amplitudes are associated with worse mental rotation performance (e.g. (Rösler 1997; Vitouch 1997; Lamm 1999; Lamm 2005; Riecansky 2008; Beste 2010)). In particular, Riecansky and Jagla (2008) found that the amplitude of the RRN significantly predicted individual task performance. Again, higher RRN amplitudes were associated with poorer performance. However, this effect was only observable when ERPs were aligned to response time of subjects rather than stimulus onset, indicating that late, rather than early processing is crucial for task solution (Riecansky 2008). Those findings were interpreted in accordance with the neural efficiency hypothesis (for review, see e.g. (Neubauer 2005)). This hypothesis postulates that poor performers have to engage more intense brain activity (or more processes) compared to good performers who display a more efficient processing. The results of PET studies of Haier et al. (1988, 1992) were one of the first to support this hypothesis. They have shown that the brain glucose metabolic rate during execution of the Raven´s Advanced Progressive Matrices test was negatively correlated with test scores. Additionally, they found that practice in a two dimensional rotation task significantly reduced glucose metabolic rate (Haier 1988; Haier 1992). The authors concluded that higher abilities - either due to higher intellect or due to more practice – correlate negatively with brain activity. Additionally it has been found that task demands also influence the relationship between brain activity and performance (Vitouch 1997; Gevins 2000). When task demand is increased also subjects with high abilities have to allocate more resources to solve the task. Therefore, the investment of cortical effort may be linked to both, individual skills and task demands (Vitouch 1997).

Mental rotation and neuroimaging

Numerous studies used functional magnetic resonance imaging (fMRI) and positron emission tomography (PET) to assess the neural systems underlying mental rotation.

For example, in a fMRI study, Shelton and Pippitt (2006) showed that mental rotation and observation of an object rotation were associated with activation in similar brain regions. However, they also found differences - especially in the activity of parietal and frontal regions. More specific, they found that the inferior parietal cortex and the dorsolateral PFC were activated stronger in mental rotation than in visual perception of object rotation (Shelton 2006).

Zacks (2008) conducted a review and meta-analysis of thirty-two neuroimaging studies, including fMRI and PET studies. He concluded that mental rotation consistently activated the superior parietal, frontal and inferotemporal cortex (Figure 3). The activity was observed bilaterally in most areas; however, there was a tendency for stronger activation of the parietal cortex in the right hemisphere and, in contrast, stronger activation of the frontal cortex in the left hemisphere (Zacks 2008). Additionally, it seems that different kinds of stimuli used for mental rotation do not evoke a qualitatively different neural activation pattern (e.g. (Jordan 2001; Suchan 2006)). For example, Jordan et al. (2001) found very similar neural activation patterns for mental rotation of two-dimensional and three-dimensional figures. Also Suchan et al. (2006) found similar neural activity for mental rotation of three-dimensional cubes and mental rotation of two-dimensional matrices when WM load was high.

Posterior parietal and occipital cortex. A large number of studies reported activation in the superior parietal cortex and adjacent areas. Activity was somewhat more consistently observed in the right hemisphere. The meta analysis revealed that significant activation was centered in the intraparietal sulcus and extended into the transverse occipital sulcus, which included Brodmann´s areas 7, 39, 40 (areas inside the parietal cortex) and 19 (an area inside the occipital cortex) (Zacks 2008). Zacks argues, that the finding of strong involvement of the superior parietal cortex indicates a key role of this area in mental rotation. The superior parietal cortex showed significant activation also in transformation specific contrasts, i.e. contrasts in activation with large vs. small rotation angles. Thus, increase in rotation angle is related to increased activity in this area.

Motor cortex. Additionally, several studies reported bilateral activation in the precentral sulcus, an area associated with motor planning and execution. The meta-analysis revealed that the medial superior area of the precentral sulcus, the supplementary motor area (SMA), showed significant activation in transformation specific contrasts. This means, that with increasing rotation angle, the neural activity in these areas increased. Zacks argues that this activation might reflect the use of motor imagery in mental rotation, i.e. humans might imagine moving objects with their hands). For omnibus contrasts (i.e. mental rotation vs. a control task not involving mental rotation) activation was present in the lateral inferior area of the precentral sulcus, which includes the primary motor cortex (M1) and the lateral premotor cortex (PM).

Prefrontal cortex. In the meta-analysis, transformation-specific activation was revealed in the lateral inferior prefrontal cortex. Zacks argues that activation in this region might also be related to the use of motor imagery in mental rotation (Zacks 2008).

Zacks speculates that motor areas might be active due to two reasons:

1) Activation in these regions might reflect an incidental feature in mental rotation tasks since most tasks use a motor response (such as pressing a button to indicate task solution). Therefore, activation in motor areas might reflect the demands of planning and executing a motor response.

2) Activation in motor areas might reflect the use of a motor strategy in the mental rotation task. Various studies have discussed the issue whether motor strategies are used in mental rotation or not (e.g. (Kosslyn 1998; Kosslyn 2001; Wraga 2003; Lamm 2007)). Zacks hypothesizes that motor strategies might manifest as motor imagery processes which interact with visuospatial processes and argues that the use of a motor strategy might be rather task dependent than general. For example, tasks involving mental rotation of body parts were found to evoke stronger activation in motor areas than tasks involving mental rotation of objects (e.g. (Kosslyn 1998)). Furthermore, mental rotation of body parts seems to have a transfer effect on the use of the motor strategy in subsequent tasks. During mental rotation of objects Wraga et al. (2003) found greater activity in the precentral cortex in subjects that previously rotated hands compared to those who previously rotated objects (Wraga 2003). Additionally, training subjects to imagine turning an object with their hand was shown to result in stronger activation of motor areas during mental rotation tasks (Kosslyn 2001).

Mental rotation and TMS

Transcranial magnetic stimulation (TMS) of the human cortex confirmed involvement of the parietal cortex in mental rotation (e.g. (Harris 2003; Parsons 2003; Feredoes 2006)). In particular, Harris and Miniussi (2003) identified the right superior posterior parietal lobe as essential for performing a mental rotation task. They delivered short train of four pulses at 20 Hz in different time windows while subjects performed mental rotation of alphanumeric characters. They found that in the time window 400 ms - 600 ms after onset of the stimulus repetitive TMS of the right superior parietal lobe interfered with mental rotation. The findings support the assumption that this region is responsible for spatial transformations (Harris 2003). Feredoes and Sachdev (2006) conducted a TMS study with three-dimensional stimuli in order to replicate the findings of Harris and Miniussi (2003) with more complex stimuli. They used the same stimulation protocol as Harris and Miniussi (i.e. train of four pulses at 20 Hz). The results confirmed the crucial involvement of the right posterior parietal cortex in mental rotation and showed that this area is also involved in mental rotation of three-dimensional stimuli. Additionally, Feredoes and Sachdev (2006) found an involvement of the left posterior parietal cortex, but only at rotation angles that exceeded 180 deg. The authors argued that this involvement of left hemisphere might be due to adopting verbal or symbolic strategies in more complex rotation procedures (Feredoes 2006).

TMS studies also assessed primary motor cortex (M1) involvement in mental rotation (e.g. (Ganis 2000; Bode 2007; Tomasino 2007)). In mental rotation of body parts, the left primary motor cortex seems to play a crucial role (Ganis 2000; Tomasino 2007) whereas right M1 does not (Tomasino 2007).

1.3.2) Mental rotation: contribution of storage and manipulation in WM

Mental rotation is a working memory task, engaging both the processes of storage (including active maintenance) and manipulation of the stored information (Hyun 2007; Prime 2009). Hyun and Luck (2007) showed in a dual task experiment that mental rotation interfered with visual (object) STM processes and that this interference increased with increasing rotation angle. However, recruiting spatial STM did not interfere with mental rotation. Thus, the authors concluded that mental rotation requires object STM (Hyun 2007). In an ERP study, Prime and Jolicoeur (2009) assessed the latency of the contralateral negative slow wave (CNSW) - a component associated with maintenance of information in STM. The results showed that onset and offset of the CNSW was modulated by rotation angle- with higher rotation angles leading to longer latencies of the CNSW. This indicates that the duration for which an image is maintained in visual STM is related to the degree to which the image has to be rotated in order to reach the final orientation. Hence, the results of the study support the assumption that mental rotation is accomplished by transforming a representation held in visual STM (Prime 2009).

It is not clear yet, whether increasing engagement of mental rotation increases demands on both manipulation and storage processes. A related intriguing question is the role of storage vs. manipulation in individual differences in mental rotation ability. It remains unclear whether individuals with high mental rotation skills are skilled in manipulation, or rather storage of information in STM. Findings from neuroimaging studies indicate that visuospatial storage is associated with activity of the parietal cortex (e.g. (Smith 1998; Smith 1999; Postle 2006; Zimmer 2008)), which has been identified as a crucial brain region for mental rotation also (e.g. (Harris 2003; Parsons 2003; Feredoes 2006; Zacks 2008)). Furthermore, ERP studies found that visuospatial storage processes are associated with a slow posterior negativity, which increases with increasing task demand (e.g. (Gevins 2000; Vogel 2004; Vogel 2005)). Hence, similar ERP effects are observable during mental rotation and visuospatial storage processes. Thus, there might be a possibility that RRN reflects storage rather than manipulation processes.

Therefore, the aim of this study was to reveal the contribution of storage vs. manipulation to RRN and establish their respective roles in individual differences in mental rotation skills. In order to do this we built upon the results of an ERP study of Riecansky and Jagla (2008), who have shown that the RRN amplitude significantly predicted individual performance in a mental rotation task of characters (Riecansky 2008). We recorded ERPs in two tasks – a mental rotation task and a visual STM task. For mental rotation, a slightly modified version of Cooper and Shepard´s mental rotation task was used, requiring mental rotation of characters in the frontal plane. The visual STM task was developed specifically for the scope of this experiment and is termed orientation change detection (OCD) task. In this task, subjects had to memorize the position of a shortly displayed probe stimulus and subsequently, after a delay of about 3 s, match it to an identical test stimulus, which was rotated clockwise or counter-clockwise from the probe stimulus. During the maintenance interval between the two stimuli, a dot mask was presented. During this maintenance interval, the precise orientation of the stimulus had to be actively held in STM in order to perform task successfully. Capacity of visual STM storage was determined in this task as a deviation threshold for successful discrimination. Due to the specific design of the OCD task, we assume that the active STM maintenance of stimulus orientation is similar to STM processes engaged in mental rotation. Therefore, activity recoded in the maintenance phase of the OCD task was compared to RRN. In particular, we asked whether ERPs related to visual STM maintenance in the OCD task would explain the association between RRN and mental rotation performance. As usual in character mental rotation, performance was indexed by response time (RT) (e.g. (Cooper 1973)). This is due to the fact that response accuracy is very high in this task, which makes this performance measure unreliable.

2) Hypotheses

i. Performance in the mental rotation of characters correlates with visual STM capacity. Subjects with short RT in the mental rotation task tend to have lower OCD threshold.

ii. RRN amplitude predicts individual performance in the mental rotation task. We expect to replicate previous findings (Riecansky 2008) that shorter RT in the mental rotation task is associated the smaller amplitude of RRN if EEG signals are aligned to RT.

iii. We expect that the RRN reflects both manipulation and storage in WM. Amplitude of ERPs recorded during the maintenance phase of the OCD task is significantly associated with the amplitude of RRN.

iv. We expect that increasing the magnitude of mental rotation increases demands of manipulation rather than storage in WM. In other words, engagement of visual STM should be rather constant and should not increase considerably with increasing rotation angle. Therefore, we expect that modulation of RRN with increasing rotation angle is not significantly associated with ERP amplitude recorded in the OCD task.

v. We expect that mental rotation performance is related to manipulation rather than storage in STM. If this is the case, adjusting RRN for the ERP associated with visual STM maintenance should have little impact on the association between RRN and mental rotation task performance. In contrast, if the association between RT and RRN is strongly decreased after OCD-related ERPs have been regressed out from RRN, we can conclude that performance in mental rotation is mainly based on storage related processes.

3) Methods

3.1) Subjects

Forty-one right-handed healthy volunteers participated in the experiment (24 females, 17 males). The mean age of the participants was 25.8 years (range: 19 to 37 years, SD = 3.5). Most participants were undergraduate students of the University of Vienna. To assure that the subjects could participate in the experiment, a brief oral interview was held to scan for mental health problems, intake of psychotropic drugs, or neurological problems. Handedness was assessed using the Edinburgh Inventory (Oldfield 1971). Informed consent was obtained from all volunteers. All subjects had normal or corrected-to-normal vision.

3.2) Experiment

The experiment consisted of two different tasks. Both tasks were developed and run by ePrime 2.0 software (Psychology Software Tools, Inc.; http://www.pstnet.com). The stimuli were presented on a CRT monitor and subjects gave their response by pressing the keys ‘J’ and ‘F’ by the right or left index finger according to the matched response on a standard computer keyboard.

3.2.1) Mental rotation task

The mental rotation (MR) task was a slightly modified version of the task used by Cooper and Shepard (1973). We used the letters ‘R’, ’J’, ’G’, ’F’, ‘L’, ‘a’, ‘h’, ‘e’, ‘f’ and ‘r’, which were presented on the screen either canonical, or mirror reversed. Additionally, the letters were rotated clockwise in one of three possible angles (90 deg, 135 deg and 180 deg). We also included a 0 deg rotation condition with characters displayed in upright position, which served as a baseline control condition. The subjects´ task was to decide whether the stimulus was mirror reversed or canonical. The character was presented on the screen for as long as the subject gave a response. The matching of response key (“F” or “J”) to response (mirror-reversed or canonical) was counterbalanced. In total, the task consisted of 320 trials and after each 20 trials a break was included. The break ended when subjects pressed ‘1’ on the computer keyboard. Previous to each stimulus a fixation cross was presented in order to avoid eye movements. Figure 4 shows an example of a rotated stimulus from the MR task.

3.2.2) Orientation change detection task

The second task, called orientation change detection (OCD) task, was designed in order to measure visual short term memory (STM) capacity. The task represented a delayed match-to-sample task and was specifically designed for the scope of this experiment. The first stimulus, which was a rotated letter (‘E’) was presented on screen for 500 ms and was called the ‘probe stimulus’. The orientation of the stimulus was 45 deg, 135 deg, 270 deg or 315 deg. After 520 ms, a mask, which consisted of random black and white dots, appeared on the screen. This dot mask was presented for 3000 ms. During this interval the subjects had to hold the exact position of the probe stimulus in mind. After the delay interval, the ‘test stimulus’ was presented.

This was the same letter (‘E’) but presented in a slightly different angular deviation. The subjects´ task was to decide whether the test stimulus was rotated clockwise or counter-clockwise with respect to the probe stimulus. The test stimulus was displayed on the screen until the subject gave his/her response. The angular difference between the probe and the test stimulus was 2 deg, 4 deg, 6 deg or 8 deg. The biggest angle of 8 deg represented the easiest form of the task and the smallest angle of 2 deg the most difficult. The different deviation angles were presented in random order. This is referred to as the method of constant stimuli (see e.g. (Laming 1992)). The orientation change detection threshold, i.e. the angle at which the subject could reliably detect the difference between the probe and the test stimulus, was assessed by fitting a sigmoid curve to performance accuracy (for exact computation of detection thresholds, see section 4.1.2). Again, the matching of response key (‘F’ or ‘J’) to response (clockwise or counter-clockwise) was counterbalanced. The task consisted of 160 trials, and again, each 20 trials a break was included which was terminated by pressing the button ‘1’ on the computer key. Figure 5 shows an example of one trial of the OCD task.

Before beginning of the experiment, the subjects practiced both tasks. For the OCD task, the subjects were given as much time as they needed to feel confident in performing the task. For the MR task, the performance of each subject was monitored during the practice trials and the subjects were encouraged to continue practicing until they achieved at least 18 correct responses in a block of 20 trials. We did this to ensure that each subject understood the task instructions.

The duration of the experiment was approximately one hour, in which each task (OCD task and MR task) took about half an hour. Including preparation for EEG recordings and practice trials, the duration of one experiment session was approximately three hours.

3.2.3) EEG recording

The experiment took place in an experiment chamber, which was a sound attenuated and air conditioned separate room. The EEG-signal was recorded from 61 Ag / AgCl electrodes using an application cap (*EASYCAP GmbH; Herrsching, Germany*) with equidistant electrode placement. The electrodes were referenced to noncephalic sternovertebral reference. This is a joint lead from two electrodes, one placed over the sternal end of the right clavicula and the other over the processus spinosus of the vertebra prominens (7th vertebra), linked with an adjustable voltage divider (potentiometer). The potentiometer was adjusted individually so that signal components of the electrocardiogram (ECG) became minimized in the EEG recording. Bipolar derivation from the two electrodes was used to record ECG. Eye movements and blinks were monitored by recording the electrooculogram (EOG) using bipolar vertical (VEOG) and horizontal (HEOG) montages. VEOG was recorded from two electrodes placed above and below the midline of the left eye. HEOG electrodes were placed on the outer canthi of each eye. A ground electrode was placed on the forehead. The EOG and ECG recordings were used for later removal of artifacts from the EEG data. Underneath each electrode, the skin was scratched using a sterile needle and the electrodes were filled with degassed electrolyte to minimize skin potential artifacts and to keep electrode impedance < 4 Ω. The electrodes were connected to a DC - amplifier (Ing. Zickler Ges.m.b.H.) and analog filtered in the range of 0Hz - 95 Hz. A sampling rate of 250 Hz was used for digital-analog conversion.

4) Data Analysis

4.1) Processing of Behavioral Data

4.1.1) Mental rotation task

In the MR task, response accuracy of all trials and response time (RT) in correct response trials were analyzed. For the analysis of response accuracy, the incorrect responses (errors) were counted for each subject and rotation angle. The number of errors in the 0 deg rotation condition was considered as a baseline value, since no rotation of the stimulus was necessary in this condition. This baseline was subtracted from the number of errors registered at other rotation angles in order to obtain a score that relates only to MR. Two subjects were excluded due to the fact, that they made too many errors, indicating unreliable task performance. Thirty-nine subjects remained for the analysis.

For the analysis of RT, mean RT was computed for each angle of rotation (0 deg, 90 deg, 135 deg and 180 deg) for each subject. Again, mean RT at 0 deg served as a baseline. Therefore, mean RT for 0 deg was subtracted from the mean RT for each other angle of rotation. All statistical analyses of response accuracy and RT were conducted with such baseline-corrected data. Two subjects had RTs that were much slower compared to other subjects and were excluded from RT analysis. One additional subject was excluded because he showed no increase in RT with increasing rotation angle (see Results), casting doubts of his compliance with task instructions and strategy. Thirty-six subjects remained for the analysis.

4.1.2) Orientation change detection task

First, the correct responses for each test stimulus angular disparity (2 deg, 4 deg, 6 deg and 8 deg) were counted in order to compute the proportion of correct responses for each angle. This was done for all orientations of the probe stimulus (45 deg, 135 deg, 270 deg or 315 deg) together. The number of correct trials for each angle was divided by the total number of trials for that angle (which was always 80). Performance of each subject was then fitted with a logistic sigmoid curve using the formula:

$$y = 0.5 + 0.5 * (1 / (1 + (x / a) ^\wedge b)),$$

where x is the angular deviation and y is the proportion of correct responses. Theoretically, *y* can take values between 0.5 and 1. 0.5 represents the probability of being correct by chance (in deciding whether the test stimulus was rotated clockwise or counter-clockwise) and 1 indicates that every response was correct. This fit yielded two parameters (*a* and *b*). The first parameter (*a*) indicated the angle at which the subject achieved a proportion of correct responses equal to 75%. The second parameter (*b*) represented the slope of the function. Figure 6 shows an example of this analysis for one subject. The value of parameter a, was taken as an orientation change detection threshold (OCD threshold) for a given subject and represented the measure of task performance in the OCD task.

In two subjects, fitting of the logistic function was not successful due to the fact that their error scores did not follow the expected trend, making their judgments unreliable. These subjects were excluded from the analysis. From the remaining thirty-four subjects, two had an OCD threshold that was too high with respect to other subjects. The OCD threshold in these subjects was higher than 8 deg, which means they never reached the 75% correct performance level. These two outlier subjects were also excluded. Eventually, thirty-two subjects remained in the analysis. The data of these subjects were used for the statistical analysis of behavioral data.

4.2 Processing of ERP Data

The EEG signal was digital filtered in the range 01 Hz - 80 Hz. Off-line analysis of the EEG data was performed using EEGLAB 6.0.3b (Delorme 2004) integrated in Matlab 7.5.0 (The MathWorks). Coarse artifacts in the EEG signal, caused by body and eye-movements, muscle-activity or unstable electrode contacts were identified by visual inspection and removed. If necessary, bad channels were interpolated using spherical spline interpolation. To identify systematic artifacts related to eye-movements, eye-blinks, and ECG, independent component analysis (ICA) was performed on the data. ICA is a statistical procedure, which can separate a mixed signal into the original signals. With ICA, one can separate a mixed signal into statistically independent components (i.e. the source signals). Additionally, ICA provides an identification of the time courses and scalp topographies of activations. Therefore, artifactual signals – such as eye blinks - can be detected and separated from the EEG data (Jung 2000). ICA was run for each subject separately. The decision on which components to remove was based on visual inspection of components' activation time course and topographic pattern. Baseline (i.e. pre-stimulus interval of 300 ms) was subtracted in each trial for the whole time interval.

From this artifact free data, ERPs for each channel were obtained by averaging signals from single trials with respect to specific events. In the MR task, ERPs were computed for each angular stimulus deviation separately. ERPs were calculated with respect to stimulus onset and response time. RRN was calculated by subtracting the mean amplitude for 0 deg rotation (i.e. baseline condition) from the ERP amplitude of each rotation angle (90 deg, 135 deg and 180 deg). For signals aligned to stimulus onset, these difference ERPs were termed $\mathrm{RRN}_{\mathrm{on}}$ and for signals aligned to response time, the difference ERPs were termed $\mathrm{RRN}_{\mathrm{rt}}$. In the OCD task, ERPs were calculated across all probe stimulus orientation angles with signals aligned to the onset of the probe stimulus. We computed ERPs for each subject as well as grand mean ERPs (i.e. mean average amplitude of all subjects). For topographical and statistical analyses, we computed mean amplitudes within specific time intervals for each task and condition. For RRN_{on} we computed mean amplitude from 350 ms until 750 ms after stimulus onset. For RRN_{rt}, we computed mean amplitude from 600 ms until 200 ms before response time. Mean amplitudes were computed for each angular deviation. For the OCD task, we computed mean amplitude in the interval 2500 ms - 3500 ms after the onset of the probe stimulus (ERP_{OCD}). This time interval was a part of the maintenance phase, in which subjects actively held the representation of the probe stimulus in memory.

4.3 Statistical Analyses

Data were analyzed within the framework of the general linear model. The level of significance was set to 0.05. Greenhouse-Geisser correction was applied if necessary (Field 2009).

5) Results

5.1) Behavioral Data

5.1.1) Mental rotation task

Response Accuracy

Response accuracy in the MR task was very high across all stimulus conditions. Nevertheless, with increasing angle of stimulus rotation, i.e. with increasing task difficulty, a slight increase in error rate was observed. Mean number of errors (out of 80 trials for each rotation angle), as well as the standard deviation are shown in table 1 (tables are provided in Appendix). Figure 7 shows the increase in errors with increase of MR angle. We analyzed the effects of MR angle on response accuracy (i.e. errors) by computing a repeated measures ANOVA. We included sex as a between subjects factor. The statistical analysis revealed a significant effect of MR angle on response accuracy [$F(1.6, 49.02) = 51.01$, $p < 0.001$]. We found no significant effect of sex [$F(1, 30) = 1.06$, $p = 0.312$].

Response time

As expected, RT increased with increasing stimulus rotation angle (Figure 8). Mean RT, as well as the standard deviation are shown in table 2. Again, we analyzed the effects of MR angle on response time by computing a repeated measures ANOVA. As before, sex was included as a between subjects factor. The statistical analysis revealed a significant effect of MR angle on response time [$F(1.4, 40.54) = 138.01$, $p < 0.001$]. We found no significant effect of sex [$F(1, 30) = 2.22$, $p = 0.147$].

5.1.2) Orientation change detection task

Response accuracy in the OCD task increased with increasing angular difference between the test and the probe stimulus (figure 9). The OCD threshold, derived from fitting a logistic function to data of each subject (see methods), ranged from 1.7 to 7.6 deg with a mean of 3.6 deg and standard deviation of 1.4. Figure 10 shows the distribution of the OCD threshold values.

5.1.3) Association of performance between orientation change detection task and mental rotation task

Association between OCD threshold and MR response accuracy

We analyzed the effects of MR angle and sex on response accuracy (represented by the number of errors) in the MR task with the OCD threshold included as a covariate. We found a significant main effect of MR angle [F(1.6, 47.3) = 6.62, p = 0.005]. There was neither a significant effect of sex [F(1, 29) = 0.49, p = 0.491] nor a significant interaction between MR angle and sex [F(1.6, 47.3) = 0.01, p = 0.980]. We found no significant association between OCD threshold and MR errors [F(1, 29) = 0.95, p = 0.338]. Additionally, no significant interaction of OCD threshold with MR angle was found [F(1.6, 47.3) = 0.02, p = 0.966].

Association between OCD threshold and MR response time

For analysis of the effects on the RT in the MR task, MR angle was included as a within subject factor and sex as a between subject factor. The OCD threshold was included as a covariate. The statistical analysis revealed a significant main effect of MR angle [F(1.5, 43.2) = 11.611, p < 0.001]. Importantly, there was a significant effect of OCD threshold on RT [F(1, 29) = 6.536, p = 0.016]. There was no significant main effect of sex [F(1, 29) = 0.637, p = 0.431], nor a significant interaction between MR angle and sex [F(1.5, 43.2) = 2.47, p = 0.110]. No significant interaction was found between MR angle and OCD threshold [F(1.5, 43.2) = 1.287, p = 0.279].

This indicates that the association between MR RT and OCD threshold is of comparable magnitude for all rotation angles. This means that this association can be summarized by a single correlation coefficient. To do this, we computed mean RT (RT_{av}) according to the formula $RT_{av} = (RT_{90} + RT_{135} + RT_{180}) / 3$, where RT_{90}, RT_{135} and RT_{180} represent mean response time for given angle with mean response time for unrotated stimuli (0 deg) subtracted. We computed RT_{av} for each subject and calculated its association with OCD threshold. We computed a linear regression with OCD threshold as predictor of RT_{av} (R = 0.473, p = 0. 006). This association is shown in Figure 11.

Additionally, we computed a mean difference score of RT (RT_d) between the different rotation angles according to the formula $RT_d= (RT_{180} - RT_{90}) / 2$. This score represents the increase of RT with increasing rotation angle for each subject. We also calculated the association between this score and the OCD threshold. To do this, we computed a linear regression with OCD threshold as predictor of RT_d (R = 0.338, p = 0.063). This association is shown in Figure 12.

5.2) ERP Data

5.2.1) ERPs recorded during the mental rotation task

First we report ERPs recorded during the mental rotation task with signals aligned to stimulus onset. Figure 13 shows the ERPs at nine electrode positions in one subject and figure 14 shows the group average ERPs from 24 subjects. The ERPs are plotted for time interval from 300 ms before stimulus onset until 1500 ms after stimulus onset. The ERP for each angular deviation of the stimulus is shown in different color (see legend). Several deflections of the averaged signal, i.e. ERP components, are clearly visible. The first visible component is a deflection with positive polarity peaking at about 100 ms, termed P1. In the single subject ERPs, the P1 component is well visible at all nine electrode positions, though it is most prominent at posterior lateral electrodes. In the group mean, P1 can be seen only at posterior lateral leads. P1 is followed by a negative wave, N1 component with peak latency of approximately 150 ms. N1 is very prominent at posterior electrodes in the single subject ERPs, but has small amplitude in the group average. The following P2 component peaks at about 200 ms and is very prominent at anterior and central electrodes. At posterior electrodes the P2 component overlaps with the P3 component and thus cannot be clearly separated. A negative wave N2 follows the P2 component. The N2 peaks at approximately 300 ms and is present only at anterior and central electrodes. Next, a large positive wave P3 is maximal at posterior electrodes and peaks around 500 ms. At about 350 ms, ERPs for different rotation angles start to diverge and are separated up to about 750 ms. ERP amplitude is less positive (more negative), with increasing rotation angle. This slow negative shift is termed mental rotation related negativity (RRN; (Peronnet 1989)). The modulation of ERP amplitude with rotation angle is well visible in both single subject and group mean ERPs, particularly at posterior electrodes.

Figure 19 shows mean RRN_{on} amplitude in the interval 350-750 ms after stimulus onset for all recording channels. In these topographical plots, ERP amplitude is coded in color and its values are interpolated for the spaces between recording electrodes. Each plot represents the mean RRN_{on} for a different angle of rotation with the mean amplitude for 0 deg subtracted. The plots depict an increase in RRN amplitude with increasing rotation angle, which is maximal at posterior electrodes.

ERPs recorded during the mental rotation task with signals time-aligned to response time are presented in figures 15 and 16. ERPs are shown for one representative subject (figure 15) and for the group average (figure 16). Negative values on the time axis indicate time before manual response (which occurs in time 0). The RRN, i.e. more negative amplitude with increasing rotation angle, is clearly visible mainly at posterior electrodes at time interval from -600 ms to 0 ms. At about 120 ms before response until response time a decrease in ERP amplitude is evident at anterior and central electrodes. At posterior electrodes this decrease is delayed and starts closer to response (from about 50 ms). Figure 20 shows topographical plots of mean RRN_{rt} in the time interval from - 600 ms until - 200 ms before response time. For each angle, the mean ERP amplitude of the 0 deg rotation angle condition was subtracted. The effect of rotation angle and its topographical distribution was very similar to that seen in signals time-aligned to the stimulus onset (RRN_{on}). Also in this case, the effects of mental rotation are most prominent at posterior electrodes. There is a strong increase in negativity for increasing rotation angle from 135 deg to 180 deg.

The effect of rotation angle on ERP amplitude was statistically analyzed using mean RRN_{rt} amplitude in the time interval from of - 600 ms until - 200 ms as a dependent variable. Four electrodes were selected (figure 22) and a 3x2x2 ANOVA was computed with the independent variables rotation angle (90 deg, 135 deg and 180 deg), region (anterior vs. posterior), and hemisphere (left vs. right). For each stimulus condition, mean amplitude for 0 deg was subtracted. Figure 22 shows mean RRN_{rt} for all analyzed electrodes.

The statistical analysis revealed a significant main effect of rotation angle [$F(1.384, 31.838) = 15.943$, $p < 0.001$], reflecting the already mentioned modulation of ERP amplitude with rotation angle. We also found a significant main effect of region [$F(1,23) = 24.779$, $p < 0.001$]. ERP amplitude was more negative over the posterior electrodes than over anterior leads. There was no significant main effect of hemisphere [$F(1.23) = 0.443$, $p = 0.512$]. We found significant interactions between rotation angle and region [$F(1.514, 34.826) = 11.476$, $p < 0.001$] , as well as between rotation angle and hemisphere [$F(2, 46) = 7.024$, $p = 0.002$]. The decrease in ERP amplitude with increasing rotation angle was evident in posterior electrodes but there was little variation in amplitude at anterior recording sites (see figure 22). The significant interaction between hemisphere and amplitude was due to somewhat stronger decrease in ERP amplitude over the right hemisphere, but this is not clearly evident from figure 22.

5.2.2) ERPs recorded during orientation change detection task

Figure 17 shows the ERPs for one subject and figure 18 the group average ERPs for the OCD task. The ERPs are plotted for time interval from 300 ms before probe stimulus onset until 3600 ms after probe stimulus onset. At 500 ms after probe stimulus onset, the dot mask was presented on screen and the delay interval started. It ended at 3520 ms, when the test stimulus was displayed on the screen. First, a small positive P1 component appears with a peak latency of about 80 ms, visible in all electrodes. This component is followed by a more pronounced negative wave N1peaking at approximately 120 ms. The N1 is mainly visible at anterior and central electrodes. Subsequently a P2 wave follows with a peak latency of 200 ms and a prominent amplitude visible at all electrodes. About 300 ms the N2 component peak follows, which is again well pronounced at anterior and central electrodes. At posterior electrodes the N2 merges with P3. The P3 wave peaks approximately at 450 ms. Later on, the activity related to the onset of the mask is evident, which was presented on the screen 520 ms following the probe. In the maintenance period, from about 1000 ms after probe onset, a slow negative shift of ERP amplitude is visible in the single subject data as well as group average. This negative shift is more prominent at posterior electrodes.

Figure 21 shows a topographical plot of ERP_{OCD} amplitude in the interval 2500 ms - 3500 ms after probe onset, which is representative for the maintenance phase of the OCD task. The negativity was wide-spread with maximum at central electrodes.

5.2.3) Association between ERPs and performance in the mental rotation task

In order to investigate relationship between ERPs and RT in the MR task a linear regression was computed with the RRN_{rt} amplitude as a predictor and RT as the dependent variable. We separately considered two aspects of how ERPs and RT are modulated by mental rotation. First, a more general mental activation (or load) associated with mental rotation was analyzed by including mean values of RRN_{rt} amplitude and RT across all rotation conditions. I.e., the average ERP values (RRN_{av}) were computed according to the formula: $RRN_{av} = (RRN_{rt90} + RRN_{rt135} + RRN_{rt180}) / 3$. RRN_{rt90}, RRN_{rt135} and RRN_{rt180} represent, for given angle, mean RRN_{rt} amplitude within the time interval from - 600 ms until - 200 ms before response time with RRN_{rt} for 0 deg subtracted. Mean RT values were computed analogically as in the analysis of behavioral data (i.e. $RT_{av} = (RT_{90} + RT_{135} + RT_{180}) / 3$). Second, a more specific mental activity associated with mental rotation was analyzed using mean difference in both ERP amplitude and RT across rotation angles. Average ERP difference values (RRN_d) were computed as: $RRN_d = (RRN_{rt180} – RRN_{rt90}) / 2$. Again, mean difference RT values (RT_d) were computed analogically (i.e. ($RT_d= RT_{180} – RT_{90}) / 2$). The regressions were computed for each electrode.

Figure 23 shows Pearson’s correlation coefficients and their corresponding significance p-values (in log10 scale) for the association between RRN_{av} and RT_{av}. Additionally, the relationship between RRN_{av} and RT_{av} is shown at electrode Pz, where the strongest association was found (R = - 0.770). Over posterior leads, a negative correlation between RRN_{av} and RT_{av} was found. Hence, subjects with overall faster RT showed less negative ERP amplitude, i.e. a smaller RRN.

Figure 24 shows, for the relationship between RRN_d and RT_d , Pearson's correlation coefficients for each electrode, significance, as well as scatter plot at electrode Pz (again, the electrode with the highest correlation, R = - 0.554). Similarly to previous analysis, a high and significant correlation was observed over posterior electrodes. Additionally, however, a strong association between ERP and RT was also found over right parieto-temporal and right central regions. This means that negative amplitude modulation was associated with increase in RT. In other words, subjects who showed large difference in RT across rotation conditions showed large negative ERP amplitude modulation, i.e. large modulation of RRN.

5.2.4) Association between ERPs recorded during mental rotation task and orientation change detection task

Next, we were interested in the relationship between brain activity related to MR and visual STM-maintenance respectively. For this reason, a linear regression was computed with ERP_{OCD} as a predictor and the RRN_{rt} as a dependent variable. In order to consider different aspects of mental activity associated with mental rotation, again, two regressions were computed; one regression with RRN_{av} and one with RRN_{d} as a dependent variable. As before, regression was computed for each electrode. Figure 25 shows results for the association between ERP_{OCD} and RRN_{av}. Pearson's correlation coefficients and their significance for each electrode are shown. The highest correlation coefficient ($R = - 0.634$) was found at electrode Cz and the scatter plot for this electrode is shown too. A strong significant negative correlation was found at several leads with maximum at centro-parietal electrodes.

Figure 26 shows the result of regression analysis with ERP_{OCD} as predictor variable and RRN_{d} as dependent variable. As in the previous plot, Pearson's correlation coefficients and their significance for each electrode are shown. Plotted is also a scatter graph for electrode R16, which showed the highest correlation coefficient ($R = - 0.343$). There was only a weak and insignificant correlation between ERP_{OCD} and RRN_{d}, with highest values at right temporal electrodes. Thus, ERPs from the maintenance phase of the OCD task were no efficient predictor of the ERP amplitude changes associated with increasing rotation angle in mental rotation.

5.2.5) Contribution of visual STM maintenance and manipulation to the association between ERPs and RT in mental rotation

The ultimate aim of this study was to separate the sub-processes of mental rotation and determine their contribution to the association between ERPs and RT in mental rotation. In particular, we asked whether performance in MR was associated with processes related to visual STM manipulation or rather visual STM maintenance. In order to achieve this, we explored association between RT variance and the portion of variance in RRN that is not explained by the variation in ERP as recorded during the maintenance phase of the OCD task. Therefore, we used residuals of the regression of ERP_{OCD} amplitude on RRN_{rt} amplitude as a predictor and RT as a dependent variable. The variance of these residuals represents the variance in RRN that could not be explained by $ERP_{OCD.}$ This variance is assumed to be attributed to processes different from holding (maintaining) an active representation in visual STM.

Figure 27a shows the results of this regression for RRN_{av}. Comparison with figure 23 shows that correlation between RRN_{av} and RT_{av} is weaker at central electrodes. Correlation over posterior parietal and occipital regions was affected much less. This indicates that visual STM maintenance-related processes contribute to the association between RRN_{av} and RT_{av} over central regions, but not over posterior region. Thus, the association between RRN_{av} and RT_{av} over posterior regions seems to be related to visual STM manipulation. In order to quantify the change in correlation between RRN_{av} and RT_{av} before and after correcting for visual STM maintenance-related activity, a t-test for the difference in Pearson´s correlation coefficient was calculated (Field 2009). We assessed the difference in R in all 61 electrodes and set the level of significance to $p < 0.05$. For our sample size of $N = 24$, the corresponding critical t-value for one-tailed testing was 1.72. Figure 27b shows the results of this analysis. We found a significant change in correlation coefficients before and after correction for visual STM related activity in central and left centro-parietal electrodes. Thus, correction for visual STM related activity lead to significant change of correlation between RRN and RT in these electrodes. This indicates that here the association between mean RRN and RT seems to be based on processes related to visual STM activity.

Figure 28a shows the results of the regression using residual RRN_d. Regressing out the activity related to the maintenance phase of the OCD task did not lead to any obvious change in the correlation coefficients between RRN_d and RT_d. This suggests that the association between the negative amplitude modulation and RT increase in the mental rotation task seems to be mainly based on processes related to visual STM manipulation. Again, we assessed the difference in correlation coefficients before and after correcting for visual STM maintenance-related activity. Again, in all 61 electrodes with a level of significance of $p < 0.05$ and $N = 24$, which leads to a critical t-value for one-tailed testing of 1.72. The results of this analysis are shown in figure 28b. No electrode showed a significant change in R before and after correction for visual STM related activity. This result confirms that the association between the negative amplitude modulation and RT increase seems to be based on manipulation related processes rather than processes related to visual STM activity.

6) Discussion

6.1) Behavioral Data

In accordance with prior research we observed that in a mental rotation task, response time increases with increasing angle of stimulus rotation from the upright position (e.g.(Cooper 1973)). We also observed that more errors were made with increasing rotation angle, a finding which also accords with prior studies (e.g. (Prime 2009)). However, error rates were generally low – the mean error rate for the biggest rotation angle of 180 deg was below 10%. This ceiling effect of accuracy makes the response accuracy a rather unreliable performance measure. Moreover, due to the low number of errors, signals from error trials could not be analyzed. RT, in contrast, represents a reliable performance index.

The OCD threshold served as a measure of visual STM capacity. The OCD task was specifically designed for this study in order to capture the putative visual STM part of mental rotation (i.e. subjects had to store the position of a character in addition to manipulate it). Due to the small differences between probe and test stimulus orientation, the task required focused attention of the subjects. This was intended in order to ensure the full attention of the subjects. For being able to solve the task the subjects had to actively focus on holding the exact position of the probe stimulus in mind until the test stimulus appeared. Subjects showed a mean OCD threshold of 3.6 deg, which falls within the range of tested deviations (i.e. 2 deg to 8 deg). This indicates that subjects followed task instructions appropriately and put adequate effort to solve the task. Therefore, we can be confident that the ERPs in the maintenance interval indeed reflect visual STM related brain activity.

The main aim of this study was to investigate the association between visual STM capacity and mental rotation performance. The behavioral results show that better visual STM performance goes along with faster RTs in mental rotation. Prior research has shown that mental rotation tasks require both, visual STM for information maintenance (i.e. holding the character at its actual position) and manipulation processes to mentally rotate a character (Carpenter 1999; Hyun 2007; Prime 2009). On the behavioral level, for example Hyun and Luck (2007) showed in a dual-task experiment that when mental rotation was performed during the maintenance interval of a visual WM task, performance in mental rotation declined. Additionally, they found that this interference increased with increasing rotation angles. However, this was only true when the WM task required storage of object features. When the WM task required storage of spatial information, no interference between the two tasks was observed. Thus, the authors concluded that visual (-object) STM is involved in mental rotation (Hyun 2007). In this respect, our finding of the significant correlation between performance data in the two tasks is not unexpected. Additionally, the correlation between change in response time with changing rotation angle and OCD threshold was close to significance. Therefore, we can state that the analysis of behavioral data showed a reliable association between performances in the two tasks. However, interestingly, this was only true for RT data. We found no significant association between OCD threshold and accuracy of mental rotation. This lack of association might be due to the ceiling effect of accuracy. This again confirms RT as a single reliable performance index in the mental rotation task.

Mental rotation is often discussed in relationship with sex differences in cognition. There is a firm evidence that men outperform women in spatial abilities (for a meta-analytic review, see (Voyer 1995)). However, for mental rotation, the male advantage is usually reported only for tasks requiring three-dimensional rotation. For two-dimensional mental rotation, most studies show no sex differences (see e.g. (Roberts 2003)). We included sex as a between subject factor in statistical analyses of mental rotation performance and also found no significant effects and interactions. Collins and Kimura (1997) argue that sex difference is related to task difficulty rather than spatial dimensionality. For mental rotation in two dimensions, they found male advantage in a task with high difficulty but no sex difference in a task with low difficulty. The authors argue that males might have higher spatial processing abilities in general which become more apparent when task demand is increased. Therefore, the absence of sex differences in two-dimensional mental rotation tasks might be due to a generally lower task demand in these tasks (Collins 1997).

The origins of sex differences in spatial skills, i.e. biological vs. environmental (or psycho-social), have been hotly debated. It has been argued that women show poorer skills in spatial processing tasks due to less experience with spatial processing. Gilger and Ho (1989) found that experience with spatial processing in childhood and adolescence was a significant predictor of mental rotation performance (Gilger 1989). Roberts and Bell (2000) tested developmental effects in mental rotation performance. They found that men performed better in a mental rotation task than women, whereas they found no difference between girls and boys. EEG spectral analysis revealed that brain activation differed between men and women but not between boys and girls (Roberts 2000). Those findings might support an environmental influence on mental rotation abilities, indicating that men might develop better spatial abilities over years, possibly due to a more extensive occupation with spatial stimuli. On the other hand, numerous studies on sex differences in spatial abilities found significant effects of testosterone level on spatial abilities (see e.g. (Gouchie 1991; Grimshaw 1995; Moffat 1996; Puts 2008; Vuoksimaa 2010). Additionally, associations between sex differences in spatial abilities and morphologic differences in the parietal lobe have been found (Koscik 2009). Those findings strongly indicate a biological origin of male advantage in spatial processing.

In sum, our main finding in the analysis of behavioral data was a strong association between visual STM efficiency (i.e. OCD threshold) and mental rotation performance (i.e. response time).Therefore, our findings confirm the need to disentangle the contributions from storage and manipulation processes in the analysis of mental rotation-related brain activity.

6.2) ERP Data

6.2.1) ERPs in mental rotation

As expected based on previous studies, we observed modulation of the ERP amplitude with the magnitude of mental rotation. In ERPs with signals aligned to stimulus onset the amplitude in the time interval from 350 ms until 750 ms was less positive (i.e., more negative) for higher stimulus angular deviation. This is attributed to increasing amplitude of the RRN which overlaps with the LPC (Peronnet 1989; Wijers 1989; Rösler 1990; Heil 2002)). Prior to the onset of LPC/RRN several earlier ERP processing components were visible in the ERP waves (see figure 14) – P1, N1, P2 and N2. These components are associated with early stimulus processing operations – such as perceptual encoding, discrimination and classification (Luck 2005). The early ERP components were not affected by the rotation angle. That is, ERP waves related to different angles of mental rotation did not separate until the onset of the LPC/RRN. The effects of mental rotation on ERPs were seen not only in group average ERP but also in ERPs of individual subjects. RRN was most prominent at posterior electrodes – a finding consistently reported in several previous studies (e.g. (Rösler 1997; Heil 2002; Beste 2010)).

The decrease in ERP amplitudes with increasing rotation angle (due to the increase in RRN) was also clearly evident in ERPs with signals aligned to RT. In addition, ERP amplitude modulations shortly before manual response were observed. There was a decrease in amplitudes, for ERP waves of all angular deviations, observable in anterior and central electrodes and somewhat later in posterior electrodes (figure 16). Most probably, these amplitude modulations reflect processes of motor preparation after decision has been made (Luck 2005).

6.2.2) Visual STM related ERPs

In ERPs recorded during the OCD task (figure 18) similar early processing components were seen as in ERPs of the mental rotation task aligned to stimulus onset (figure 14). In the OCD task however, late components of the ERP related to probe onset merged with early components of the ERP related to mask onset, which was presented with latency of 520 ms. Anyway, we were interested in the activity during the maintenance phase, which is related to holding the mental image of the probe stimulus in STM. During this phase we observed a slow negative shift of the ERP amplitude, which resembles processing negativities recorded in other paradigms recruiting STM (Rösler 1997; Morgan 2010)). This negativity was most prominent at central electrodes but had a wide-spread distribution. Compared to other studies which assessed STM processes, the peak negative amplitude was located more anteriorly. Studies which assessed neural correlates of object WM maintenance with EEG (e.g. (Rösler 1997; Vogel 2004; Vogel 2005; McCollough 2007), as well as fMRI consistently report involvement of posterior cortical areas (as reviewed by (Postle 2006; Zimmer 2008)). It could be speculated that since the stimulus material was the letter ‘E’, verbal processing might be recruited. It has been shown that processing in verbal WM is associated with activation in supplementary motor and premotor areas (e.g. (Paulesu 1993; Awh 1996; Smith 1998; Henson 2000)). Since this the first ERP study employing this particular OCD task, replications should prove consistency of our ERP findings.

6.2.3) Association between mental rotation related ERPs and visual STM related ERPs

We assessed the relationship of ERPs in the two tasks by computing a regression with visual STM-related ERPs as a predictor of RRN. This analysis revealed a significant correlation at centro-parietal electrodes for the mean RRN computed across all rotation angles (RRN_{av}). However, we did not find such significant association for the difference in RRN between rotation angles (RRN_d). This indicates that the increase in negativity with increasing rotation angle is not attributed to WM storage processes. Thus, in mental rotation, WM storage demands seem to be rather constant for all rotation angles. As Prime and Jolicoeur (2009) found, duration of STM storage is assumed to increase with increasing angles in mental rotation. Namely, Prime and Jolicoeur were able to show in a set of ERP studies that offset latency of the contralateral negative slow wave (CNSW), a component associated with STM maintenance, increased with increasing rotation angle. The authors concluded from this that duration of object storage in STM increased as the angle of rotation increased (Prime 2009). However, as the results of our study show, increase in rotation angle is not accompanied by increase in STM demand. Thus, the combined results of both studies indicate that for the mental rotation of characters storage processes are employed longer when rotation angles increase, but STM demand does not increase with increasing rotation angle. It would be interesting to study if this also holds for rotation of three-dimensional objects.

6.2.4) Association between RRN and performance in mental rotation

As a first point, we replicated the finding of Riecansky and Jagla (2008); subjects with stronger RRN showed longer RTs in the mental rotation task. In other words, RRN predicted individual performance. However, the actual aim of this study was to reveal the contribution of the two main WM sub-processes (i.e. storage and manipulation) to the association between RRN and mental rotation performance. Therefore, we adopted an approach where we adjusted the RRN for the individual differences in visual STM-related activity. We found that the correlation between RRN and response time at posterior electrodes did not change considerably when visual STM related activity was regressed out. In general, this was the case for both, the mean RRN amplitude (RRN_{av}) and the mean RRN amplitude difference (RRN_d). We only found a change at centro-parietal electrodes for RRN_{av}, where the association between RRN and RT decreased after RRN had been corrected for visual STM activity. For RRN_d, we found no significant change in correlation coefficients after correcting for the visual STM activity. These results indicate that the association between RRN and performance in mental rotation is in fact based on manipulation related processes rather than visual STM related processes.

7) Conclusion

The results of our investigation confirmed the association between WM storage and manipulation processes in mental rotation at the behavioral as well as the electrophysiological level. Our results show that increasing demands of mental rotation increase engagement of mental transformation but keep demands of storage in STM rather constant. Furthermore, we show that the association of the ERP amplitude with performance in mental rotation is mainly due to processes of mental transformation. This implies that individual skill in mental rotation is determined by subject's capacity to manipulate rather than store mental images. In sum, we were able to confirm our hypotheses. However, the implications of our findings are restricted to two-dimensional mental rotation of characters. Therefore, our results encourage investigations with three-dimensional mental rotation in order to show if our findings also hold for more complex forms of mental rotation.

8) References

Agam, Y., Hyun, J., Danker, J.F., Zhou, F., Kahana, M.J., Sekuler, R. (2009). "Early neural signatures of visual short-term memory." Neuroimage **44**(2): 531-536.

Awh, E., Jonides, J., Smith, E.E., Schumacher, E.H., Koeppe, R.A., Katz, S. (1996). "Dissociation of Storage and Rehearsal in Verbal Working Memory: Evidence from Positron Emission Tomopgraphy." Psychological Science **7**(1): 25-31.

Baars, B. J., Gage, N.M. (2010). Cognition, Brain, and Consciousness. Introduction to Cogntive Neuroscience. Burlington, San Diego, Oxford, Academic Press.

Baddeley, A. (2000). "The episodic buffer: a new component of working memory?" Trends in Cognitive Sciences **4**(11): 417-423.

Baddeley, A. (2003). "Working memory: looking back and looking forward." Nature Reviews Neuroscience **4**(10): 829-839.

Baddeley, A. D. (2000). "The episodic buffer: a new component of working memory?" Trends in Cognitive Sciences **4**(11): 417-423.

Baddeley, A. D. (2003). "Working memory and language: an overview." Journal of Communication Disorders **36**: 189-208.

Baddeley, A. D., Allen, R.J., Hitch, G.J. (2011). "Binding in visual working memory: The role of the episodic buffer." Neuropsychologia **49**: 1393-1400.

Baddeley, A. D., Gathercole, S. E., Papagno, C. (1998). "The phonological loop as a language learning device." Psychological Review **105**: 158-173.

Bear, F. M., Connors, B.W., Paradiso, M.A. (2007). Neuroscience. Exploring the Brain. Baltimore, Philadelphia, Lippincott Williams & Wilkins.

Beste, C., Heil, M., Konrad, C. (2010). "Individual differences in ERPs during mental rotation of characters: Lateralization, and performance level." Brain and Cognition **72**: 238-243.

Bode, S., Koeneke, S., Jäncke, L. (2007). "Different strategies do not moderate primary motor cortex involvement in mental rotation: a TMS study." Behavioral and Brain Functions **3**.

Bruyer, R., Scailquin, J.C. (1998). "The visuospatial sketchpad for mental images: Testing the multicomponent model of working memory." Acta Psychologica **98**: 17-36.

Carlesimo, G. A., Perri, R., Turriziani, P., Tomaiuolo, F., Caltagirone, C. (2001). "Remembering what but not where: Independence of spatial and visual working memory in the human brain." Cortex **36**: 519-534.

Carpenter, P. A., Just, M.A., Keller, T. A., Eddy W., Thulborn K. (1999). "Graded Functional Activation in the Visuospatial System with the Amount of Task Demand." Journal of Cognitive Neuroscience **11**(1): 9-24.

Chudasama, Y. (2011). "Animal Models of Prefrontal-Executive Function." Behavioral Neuroscience **125**(3): 327-343.

Collins, D. W., Kimura, D. (1997). "A Large Sex Difference on a Two-Dimensional Mental Rotation Task." Behavioral Neuroscience **111**(4): 845-849.

Cooper, L. A., Shepard, R.N (1973). Chronometric studies of the rotation of mental images. Visual information processing. W. G. Chase. New York, Academic Press**:** 75-176.

Della Sala, S., Gray, C., Baddeley, A., Allamano, N., Wilson, L. (1999). "Pattern span: a tool for unwelding visuo-spatial memory." Neuropsychologia **37**: 1189-1199.

Delorme, A., Makeig, S. (2004). "EEGLAB: an open source toolbox for analysis of single-trial EEG dynamics including independent component analysis." Journal of Neuroscience Methods **134**: 9-21.

Eysenck, M. W., Keane, M.T. (2005). Cognitive Psychology. A student´s handbook. Hove & New York, Psychology Press.

Feredoes, E. A., Sachdev, P.S. (2006). "Differential effects of transcranial magnetic stimulation of left and right posterior parietal cortex on mental rotation tasks." Cortex **42**: 750-754.

Field, A. (2009). Discovering statistics. Using SPSS. Los Angeles, London, New Dehli, Singapore, Washington DC, SAGE Publications.

Ganis, G., Keenan, J.P., Kosslyn S.M., Pascual-Leone, A. (2000). "Transcranial Magnetic Stimulation of Primary Motor Cortex Affects Mental Rotation." Cerebral Cortex **10**: 175-180.

Gevins, A., & Smith, M. E. (2000). "Neurophysiological measures of working memory and individual differences in cognitive ability and cognitive style." Cerebral Cortex **10**: 829-839.

Gilger, J. W., Ho, H.Z. (1989). "Gender differences in adult spatial information processing: Their relationship to pubertal timing, adolescent activities, and sex-typing of personality." cognitive Development **4**(2): 197-214.

Gittler, G. (1990). Dreidimensionaler Würfeltest (3DW). Ein Rasch-skalierter Test zur Messung des räumlichen Vorstellungsvermögens. Theoretische Grundlagen und Manual. Weinheim, Beltz Test.

Gouchie, C., Kimaru, D. (1991). "The relationship between testosterone levels and cognitive ability patterns." Psychoneuroendocrinology **16**: 323-334.

Grimshaw, G. M., Sitarenios, G., Finegan, J.A. (1995). "Mental rotation at 7 years: Relations with prenatal testosterone levels and spatial play experiences." Brain and Cognition **29**: 85-100.

Gruber, O., von Cramon, D.Y. (2003). "The functional neuroanatomy of human working memory revisited. Evidence from 3-T fMRI studies using classical domain-specific interference tasks." NeuroImage **19**: 797-809.

Haier, R. J., Siegel Jr., B.V., Nuechterlein, K.H., Hazlett, E., Wu, J.C., Peak, J., Browning, H.L., Buchsbaum, M.S. (1988). "Cortical glucose metabolic rate correlates of abstract reasoning and attention studied with positron emission tomography." Intelligence **12**(2): 199-217.

Haier, R. J., Siegel, B. Tang, C., Abel, L., Buchsbaum, M.S. (1992). "Intelligence and changes in regional cerebral glucose metabolic rate following learning." Intelligence **16**(3-4): 415-426.

Harris, I. M., Miniussi, C. (2003). "Parietal Lobe Contribution to Mental Rotation Demonstrated with rTMS." Journal of Cognitive Neuroscience **15**(3): 315-323.

Hecker, R., Mapperson, B. (1997). "Dissociation of visual and spatial processing in working memory." Neuropsychologia **35**(5): 599-603.

Heil, M. (2002). "The functional significance of ERP effects during mental rotation." Psychophysiology **39**: 535-545.

Heil, M., Rauch, M., Hennighausen, E. (1998). "Response preparation begins before mental rotation is finished: Evidence from event-related brain potentials." Acta Psychologica **99**: 217-232.

Henson, R. N. A., Burgess, N., Frith, C.D. (2000). "Recoding, storage, rehearsal and grouping in verbal short-term memory: a fMRI study." Neuropsychologia **38**: 426-440.

Hyun, J. S., & Luck, S. J. (2007). "Visual working memory as the substrate for mental rotation." Psychonomic Bulletin & Review **14**: 154-158.

Jiang, Y., Olson, I.R., Chun, M.M. (2000). "Organization of Visual Short-Term Memory." Journal of Experimental Psychology: Learning, Memory, and Cognition **26**(3): 683-702.

Jonides, J., Smith, E.E., Koeppe, R.A., Awh, E., Minoshima, S., Mintun, M.A. (1993). "Spatial working memory in humans as revealed by PET." Nature **363**(4630): 623-625.

Jordan, K., Heinze, H.J., Lutz, K., Kanowski, M., Jäncke, L. (2001). "Cortical Activations during the Mental Rotation of Different Visual Objects." NeuroImage **13**: 143-152.

Jung, T. P., Makeig, S., Humphries, C., Lee, T.W., McKeown M.J., Iragui V., Sejnowski, T.J. (2000). "Removing electroencephalographic artifacts by blind source separation." Psychophysiology **37**: 163-178.

Klaver, P., Talsma, D., Wijers, A.A., Heinze, H., Mulder G. (1999). "An event-related brain potential correlate of visual short-term memory." NeuroReport **10**: 2001-2005.

Kok, A. (2001). "On the utility of P3 amplitude as a measure of processing capacity." Psychophysiology **38**: 557-577.

Koscik, T., O´Leary, D., Moser, D.J., Andreasen, N.C., Nopoulos, P. (2009). "Differences in parietal lobe morphology: Relationship to mentalrotation performance." Brain and Cognition **69**: 451-459.

Kosslyn, S. M., Behrmann, M., Jeannerod, M. (1995). "The cognitive neuroscience of mental imagery." Neuropsychologia **33**(11): 1335-1344.

Kosslyn, S. M., Digirolamo, G.J., Thompson, W.L., Alpert, N.M. (1998). "Mental rotation of objects versus hands: Neural mechanisms revealed by positron emission tomography." Psychophysiology **35**: 151-161.

Kosslyn, S. M., Thompson, W.L. (2003). "When is early visual cortex activated during visual mental imagery?" Psychological Bulletin **129**(5): 723-746.

Kosslyn, S. M., Thompson, W.L., Wraga, M., Alpert, N.M. (2001). "Imagining rotation by endogenous versus exogenous forces: Distinct neural mechanisms." NeuroReport **12**(112519-2525).

Laming, D., Laming, J. (1992). "F. Hegelmaier: On memory for the length of a line." Psychological Research **54**(233-239).

Lamm, C., Bauer, H., Vitouch, O., Gstattner, R. (1999). "Differences in the ability to process a visuo-spatial task are reflected in event-related slowcortical potentials of human subjects." Neuroscience Letters **269**: 137-140.

Lamm, C., Fischmeister, F. P., Bauer, H. (2005). "Individual differences in brain activity during visuo-spatial processing assessed by slowcortical potentials and LORETA." Cognitive Brain Research **25**: 900-912.

Lamm, C., Windischberger, C., Moser, E., Bauer, H. (2007). "The functional role of dorso-lateral premotor cortex during mental rotation. An event-related fMRI study separating cognitive processing steps using a novel task paradigm." NeuroImage **36**: 1374-1386.

Levy, R., Goldman-Rakic, P.S. (2000). "Segretation of working memory functions within the dorsolateral prefrontal cortex." Experimental Brain Research **133**(1): 23-32.

Luck, S. J. (2005). An introduction to the event-related potential technique. Massachusetts, MIT Press.

Luria, R., Vogel, E.K. (2011). "Shape and color conjuction stimuli are represented as bound objects in visual working memory." Neuropsychologia **49**: 1632-1639.

McCollough, A. W., Machizawa, M.G., Vogel, E.K. (2007). "Electrophysiological measures of maintaining representations in visual working memory." Cortex **43**: 77-94.

Milivojevic, B., Johnson, B.W., Hamm, J.P., Corballis, M.C. (2003). "Non-identical neural mechanisms for two types of mental transformation: event-related potentials during mental rotation and mental paper folding." Neuropsychologia **41**: 1345-1356.

Miyake, A., Friedman, N.P., Emerson, M.J., Witzki, A.H., Howerter, A. (2000). "The Unity and Diversity of Executive Functions ant Their Contributions to Complex "Frontal Lobe" Tasks: A Latent Variable Analysis." Cognitive Psychology **41**: 49-100.

Moffat, S. D., Hampson, E. (1996). "A curvilinear relationship between testosterone and spatial cognition in humans: Possible influence of hand preference." Psychoneuroendocrinology **21**: 323-337.

Morgan, H. M., Jackson, M.C., Klein, C. Mohr, H., Shapiro, K.L., Linden, D.E.J. (2010). "Neural Signatures of Stimulus Features in Visual Working Memory- A Spatiotemporal Approach." Cerebral Cortex **20**: 187-197.

Morgan, H. M., Klein, C., Boehm, S.G., Shapiro, K.L., Linden, D.E.J. (2008). "Working memory load for faces modulates P300, N170, and N250r." Journal of Cognitive Neuroscience **20**(6): 989-1002.

Neubauer, A. C., Grabner, R.H., Fink, A., Neuper, C. (2005). "Intelligence and neural efficiency: Further evidence of the influence of task content and sex on the brain-IQ relationship." Cognitive Brain Research **25**(1): 217-225.

Nittono, H., Nageishi, Y., Kakajima, Y., Ullsperger, P. (1999). "Event-related potential correlates of individual differences in working memory capacity." Psychophysiology **36**: 745-754.

Oldfield, R. C. (1971). "The assessment and analysis of handedness: The Edinburgh inventory " Neuropsychologia **9**(1): 97-113.

Oliveri, M. T., P., Carlesimo, G.A., Koch, G., Tomaiuolo, F., Panella, M., Caltagirone, C. (2001). "Parieto-frontal Interactions in Visual-object and Visual-spatial Working Memory: Evidence from Transcranial Magnetic Stimulation." Cerebral Cortex **11**: 606-618.

Parsons, L. M. (2003). "Superior parietal corices and varieties of mental rotation." Trends in Cognitive Sciences **7**(12): 515-517.

Paulesu, E., Frith,C.D., Frackowiak, R.S.J. (1993). "The neural correlates of the verbal component of working memory." Nature **362**(6418): 342-345.

Peronnet, F., Farah, M.J. (1989). "Mental rotation: An event-related potential study with a validated mental rotation task." Brain and Cognition **9**(2): 279-288.

Perronet, F., Farah, M.J. (1989). "Mental rotation: An event-related potential study with a validated mental rotation task." Brain and Cognition **9**(2): 279-288.

Petrides, M. (1995). "Functional Organization of the Human Frontal Cortex for Mnemonic Processing." Annals of the New York Academy of Sciences **769**: 85-96.

Petrides, M. (2005). "Lateral prefrontal cortex: Architectonic anf functional organization." Philosophical Transactions of the Royal Society B **360**(1456): 781-795.

Postle, B. R. (2006). "Working memory as an emergent property of the mind and brain." Neuroscience **139**: 23-38.

Prabhakaran, V., Narayanan, K., Zhao, Z., Gabrieli, J.D.E. (2000). "Integration of diverse information in working memory within the frontal lobe." Nature Neuroscience **3**(1): 85-90.

Prime, D. J., Jolicoeur, P. (2009). "Mental rotation requires visual short-term memory: Evidence from human electric cortical activity." Journal of Cognitive Neuroscience **22**(11): 2437-2446.

Puts, D. A., McDaniel, M.A., Jordan, C.L, Breedlove, S.M. (2008). "Spatial ability and prenatal androgens: Meta-analyses of congenital adrenal hyperplasia and digit ratio (2D:4D) studies." Archives of Sexual Behavior **37**: 100-111.

Riecansky, I., Jagla, F. (2008). " Linking performance with brain potentials: Mental rotation-related negativity revisited." Neuropsychologia **46**: 3069-3073.

Roberts, J. E., Bell, M.A. (2000). "Sex Differences on a Mental Rotation Task: Variations in Electroencephalogram Hemispheric Activation Between Children and College Students." Developmental Neuropsychology **17**(2): 199-223.

Roberts, J. E., Bell, M.A. (2003). "Two- and three-dimensional mental rotation tasks lead to different parietal laterality for men and women." International Journal of Psychophysiology **50**: 235-246.

Rösler, F., Heil, M., Röder, B. (1997). "Slow negative brain potentials as reflections of specific modular resources of cognition." Biological Psychology **45**: 109-141.

Rösler, F., Schumacher, G., Sojka, B. (1990). "What the brain reveals when it thinks. Event-related potentials during mental rotation and mental arithmetic." The German Journal of Psychology **14**: 185-203.

Sala, J. B., Rämä, P., Courtney, S.M. (2003). "Functional topography of a distributed neural system for spatial and nonspatial information maintenance in working memory." Neuropsychologia **41**: 341-356.

Schendan, H. E., Lucia, L.C. (2009). "Visual object cognition precedes but also temporally overlaps mental rotation." Brain Research **1294**: 91-105.

Shelton, A. L., Pippitt, H.A. (2006). "Motion in the mind´s eye: Comparing mental and visual rotation." Cognitive, Affective, & Behavioral Neuroscience **6**(4): 323-332.

Simons, D. J. (1996). "In Sight, Out of Mind: When Object Representations Fail." Psychological Science **7**(5): 301-305.

Smith, E. E., Jonides, J. (1997). "Working Memory: A View from Neuroimaging." Cognitive Psychology **33**: 5-42.

Smith, E. E., Jonides, J. (1998). "Neuroimaging analyses of human working memory." Proceedings of the National Academy of Sciences of the United States of America **95**: 12061-12068.

Smith, E. E., Jonides, J. (1999). "Storage and Executive Processes in the Frontal Lobes." Science **283**(5408): 1657-1661.

Suchan, B., Botko, R., Gizewski, E., Forsting, M., Daum, I. (2006). "Neural substrates of manipulation in visuospatial working memory." Neuroscience **139**: 351-357.

Tomasino, B., Borroni, P., Isaja, A., Rumiati, R.I. (2007). "The role of the primary motor cortex in mental rotation: a TMS study." Cognitive Neuropsychology **22**(3/4): 348-363.

Vecchi, T., Monticellai, M.L., Cornoldi, C. (1995). "Visuo-spatial working memory: Structures and variables affecting a capacity measure." Neuropsychologia **33**(11): 1549-1564.

Vitouch, O., Bauer, H., Gittler, G., Leodolter,M., Leodolter,U. (1997). "Cortical activity of good and poor spatial test performers during spatial and verbal processing studied with slow potential topography." International Journal of Psychophysiology **27**: 183-199.

Vogel, E. K., Machizawa, M. G. (2004). "Neural activity predicts individual differences in visual working memory capacity." Nature **428**: 748-751.

Vogel, E. K., McCollough, A.W., Machizawa, M.G. (2005). "Neural measures reveal individual differences in controlling access to working memory." Nature **438**: 500-503.

Voyer, D., Voyer, S., Bryden, M.P. (1995). "Magnitude of Sex Differences in Spatial Abilities: A Meta-Analysis and Consideration of Critical Variables." Psychological Bulletin **117**(2): 250-270.

Vuoksimaa, E., Kaprio, J., Kremen, W.S., Hokkanen, L., Viken, R.J., Tuulio-Henriksson, A., Rose, R.J. (2010). "Having a Male Co-Twin Masculinizes Mental Rotation Performance in Females." Psychological Science **21**(8): 1069-1071.

Ward, J. (2010). The Student´s Guide to Cognitive Neuroscience. Hove, New York, Psychology Press.

Wechsler, D. (1997). Manual for the Wechsler Adult Intelligence Scale. San Antonio, Psychological Corporation.

Wijers, A. A., Otten, L. J., Feenstra, S., Mulder, G., Mulder, L. J. M. (1989). "Brain potentials during selective attention, memory search, and mental rotation." Psychophysiology **26**: 452-467.

Wraga, M., Thompson, W.L., Alpert, N.M., Kosslyn, S.M. (2003). "Implicit transfer of motor strategies in mental rotation." Brain and Cognition **52**: 135-143.

Yoshino, A., Inoue, M., Suzuki, A. (2000). "A topographic electrophysiologic study of mental rotation." Cognitive Brain Research **9**: 121-124.

Zacks, J. M. (2008). "Neuroimaging Studies of Mental Rotation: A Meta-analysis and Review." Journal of Cognitive Neuroscience **20**(1): 1-19.

Zhang, D., Zhang, X., Sun, X., Li, Z., Wang, Z., He, S., Hu, X. (2004). "Cross-Modal Temporal Order Memory for Auditory Digits and Visual Locations: An fMRI Study." Human Brain Mapping **22**: 280-289.

Zimmer, H. D. (2008). "Visual and spatial working memory: From boxes to networks." Neuroscience and Biobehavioral Reviews **32**: 1373-1395.

9) Appendix

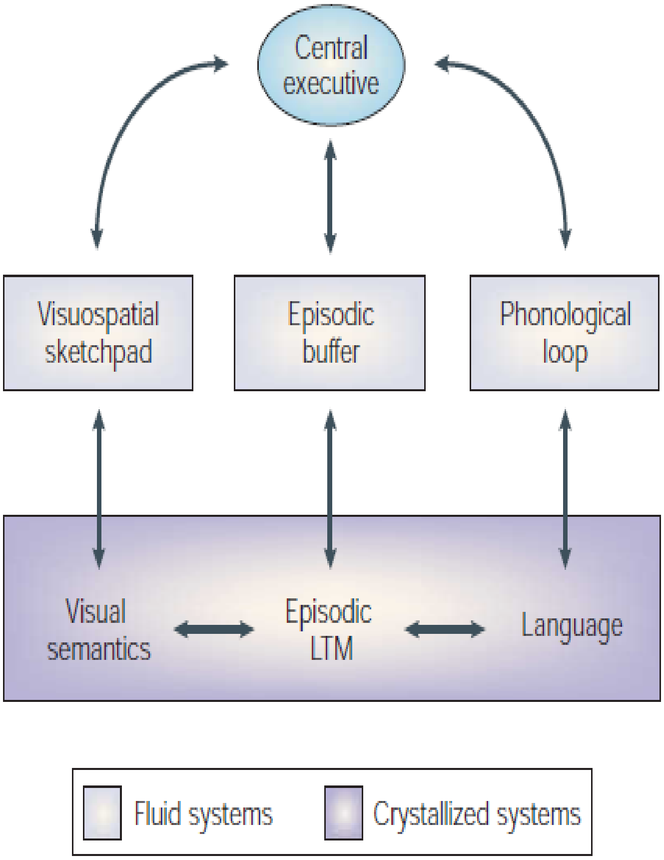


Figure 1

Recent version of the multi-component working memory (WM) model of Baddeley. The dark purple areas represent long term or crystallized knowledge. The episodic buffer provides an interface between the sub-systems of WM and long-term memory (Baddeley 2003).

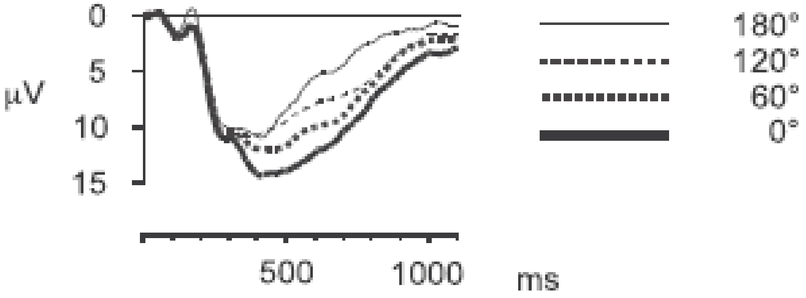


Figure 2

Example of the rotation related negativity (RRN) from an experiment of Heil et al. (1996). The figure presents the grand average ERPs recorded from electrode Pz (midline parietal). Negativity is plotted upwards. The decrease in amplitude starting at about 400 ms with growing rotation angle is well visible.

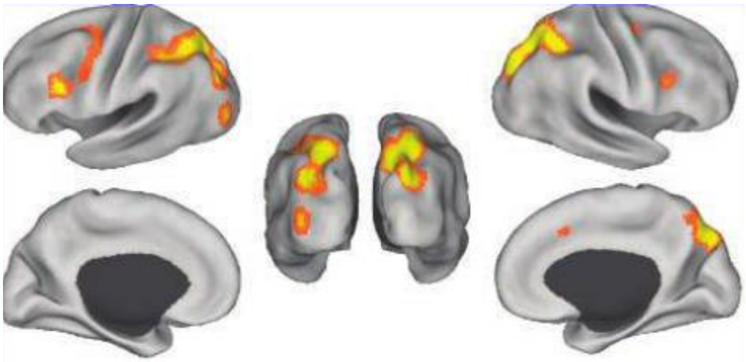


Figure 3

Meta-analysis of neuroimaging studies of mental rotation by (Zacks 2008). Regions that are significantly activated by mental rotation are shown in yellow. These include both, regions showing transformation specific activation (i.e. comparisons between different rotation conditions within a mental rotation task) and regions showing omnibus task-related activation (i.e. comparison between mental rotation tasks and control tasks not requiring mental rotation).

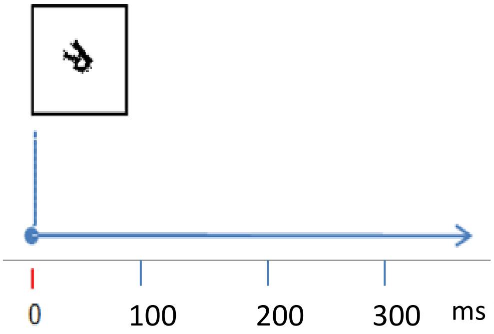


Figure 4

Example of one trial of the MR task. Here, the character is presented in canonical form and rotated 135 deg in clockwise direction.

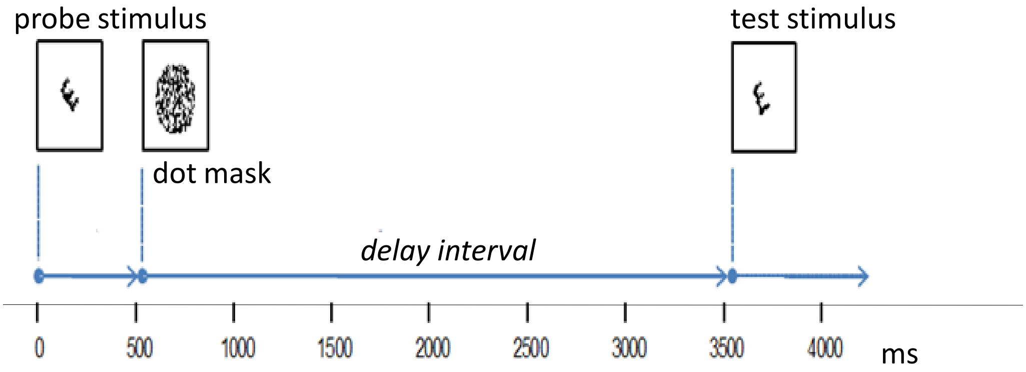


Figure 5

Example of one trial of the OCD task. The chronology (in ms) of probe stimulus, delay interval (i.e. dot mask) and test stimulus is presented.

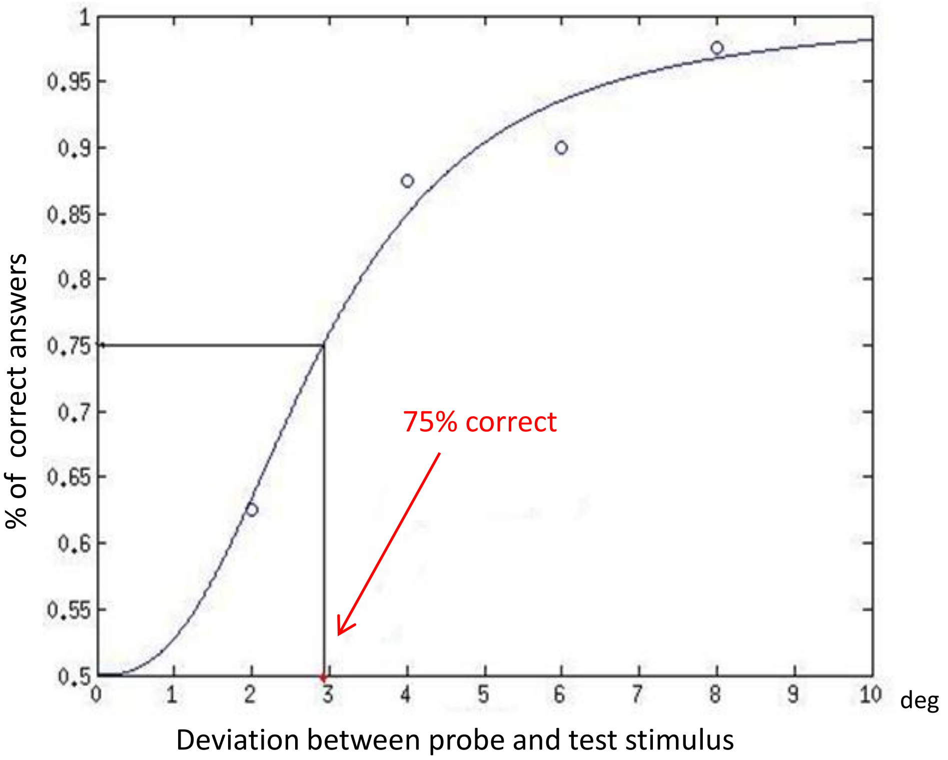


Figure 6

Psychometric function in the OCD task in one subject. Circles indicate the correct response rate for each angular deviation (2 deg, 4 deg, 6 deg and 8 deg). The OCD threshold is marked by a red arrow and for this subject was equal to 2.9 deg.

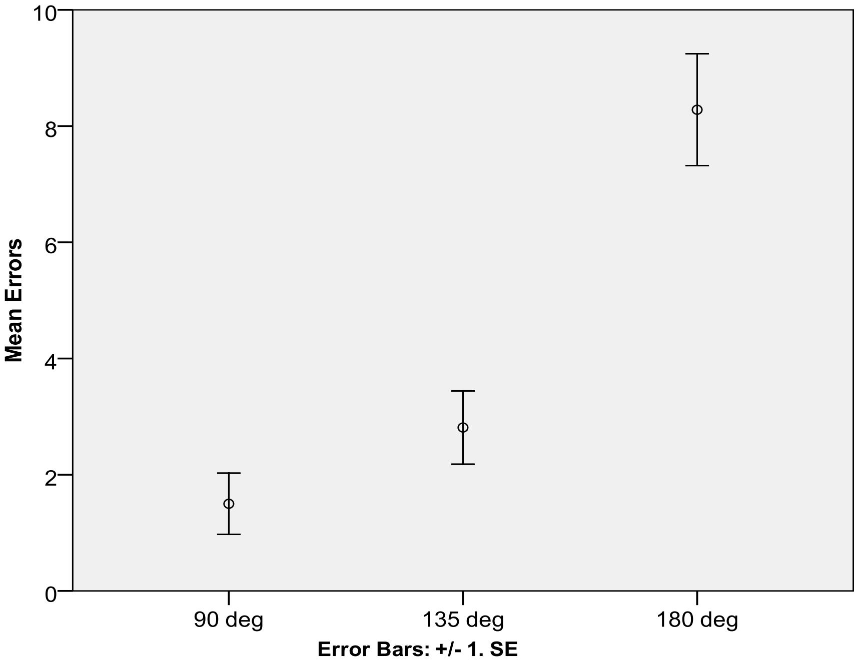


Figure 7

Mean errors and standard error for each angular deviation for the MR task.

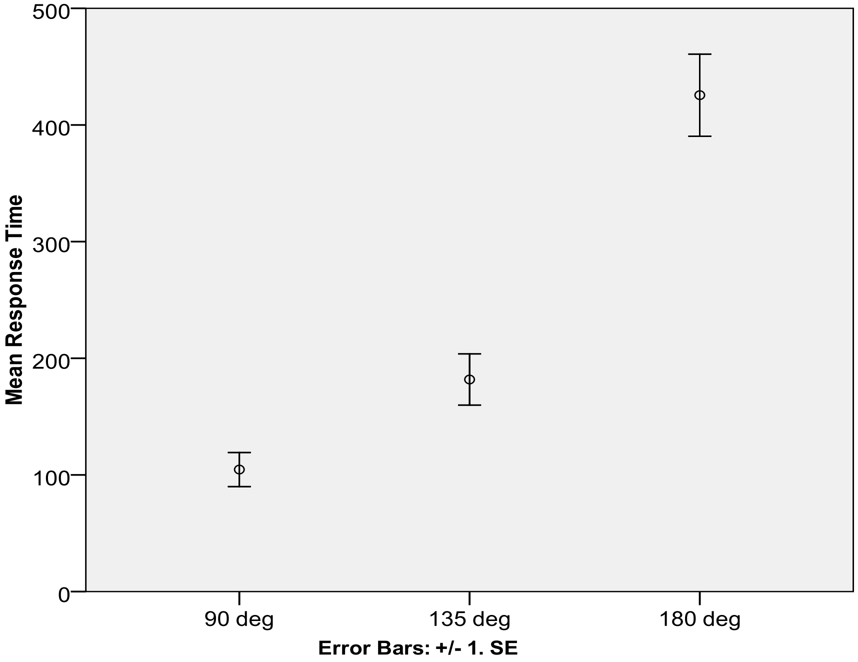


Figure 8

Mean RT and standard error for each angular deviation for the MR task.

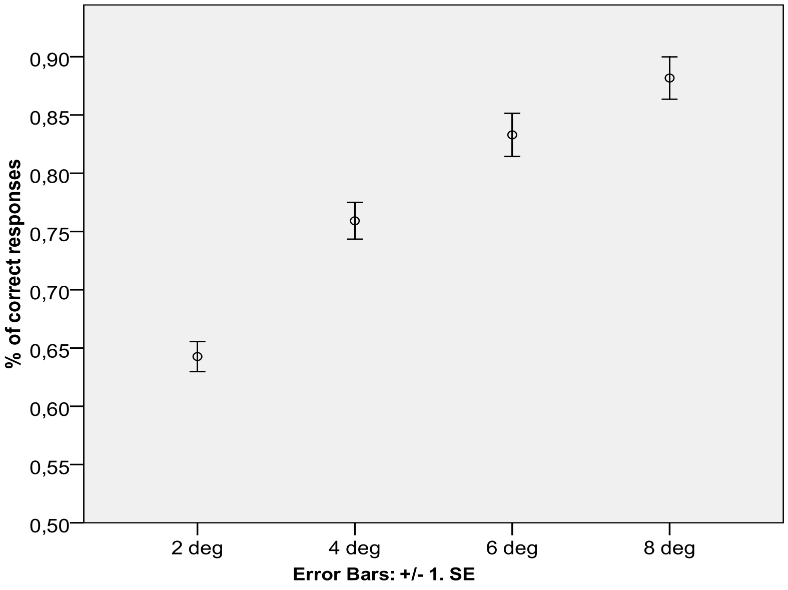


Figure 9

Mean percentage rate of correct responses and standard deviation for the OCD task.

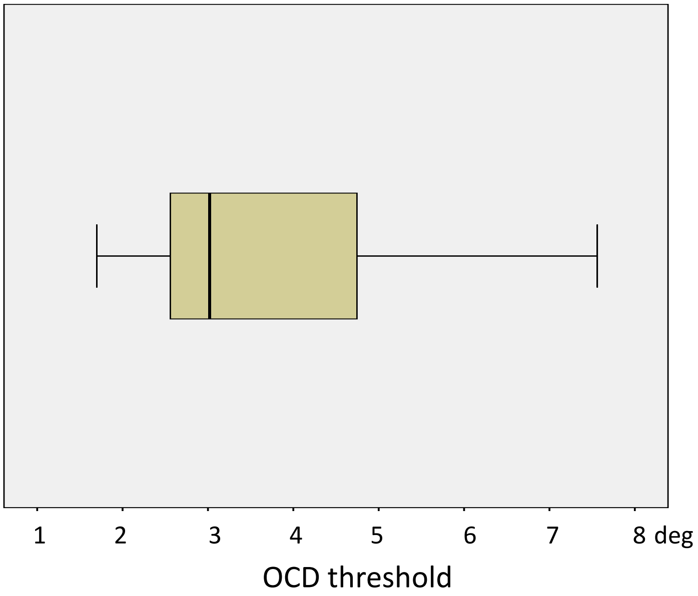


Figure 10

Distribution of the OCD threshold for N = 32 subjects. The y-axis depicts the threshold angle for reliable orientation discrimination.

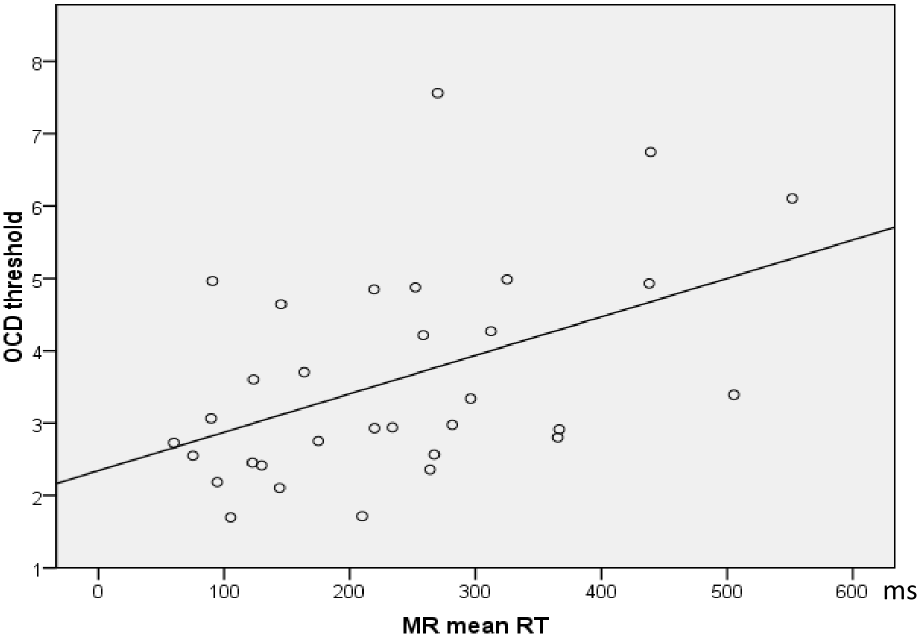


Figure 11

Scatter-plot for the association between OCD threshold and mean RT (RT_{av}) for the MR task. Mean RTs were computed across all angular deviations.

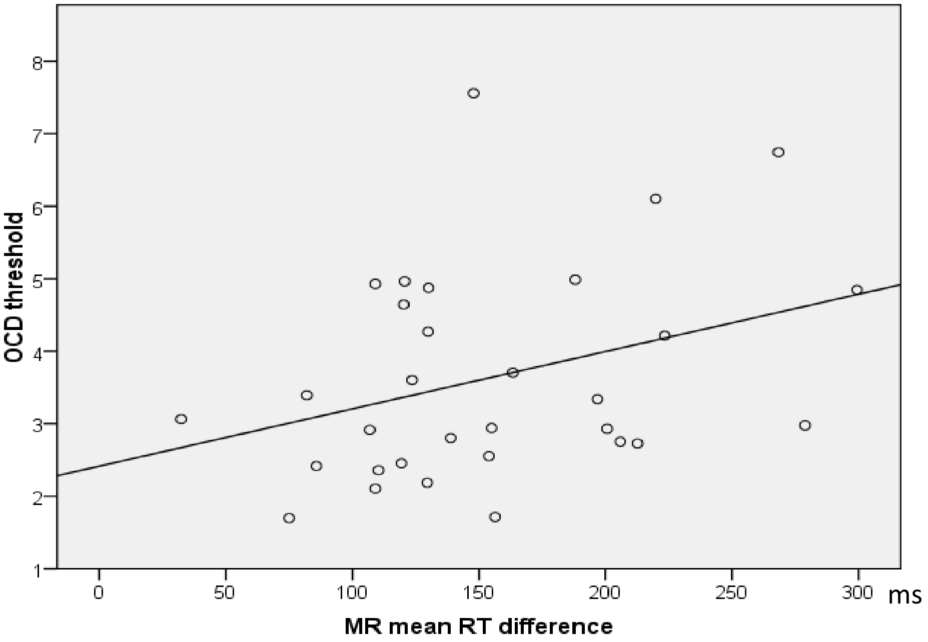


Figure 12

Scatter-plot for the association between OCD threshold and mean difference RT (RT_d) for the MR task.

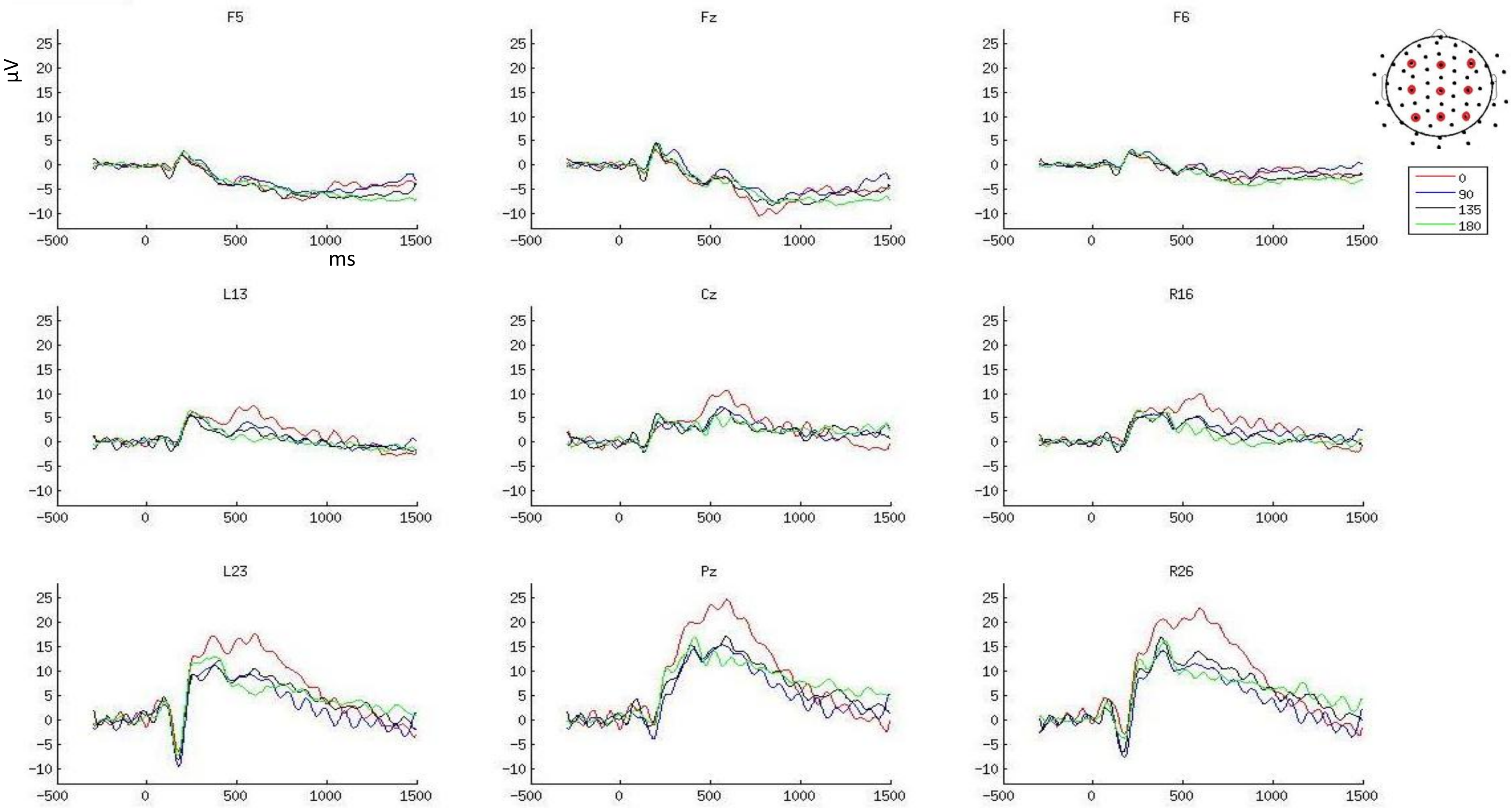


Figure 13

ERPs of the MR task aligned to stimulus onset in one subject. ERP waves for nine electrodes are shown. Positions of the electrodes are highlighted on the cartoon head. The ERPs of the different rotation angle conditions are shown in different colors (see legend).

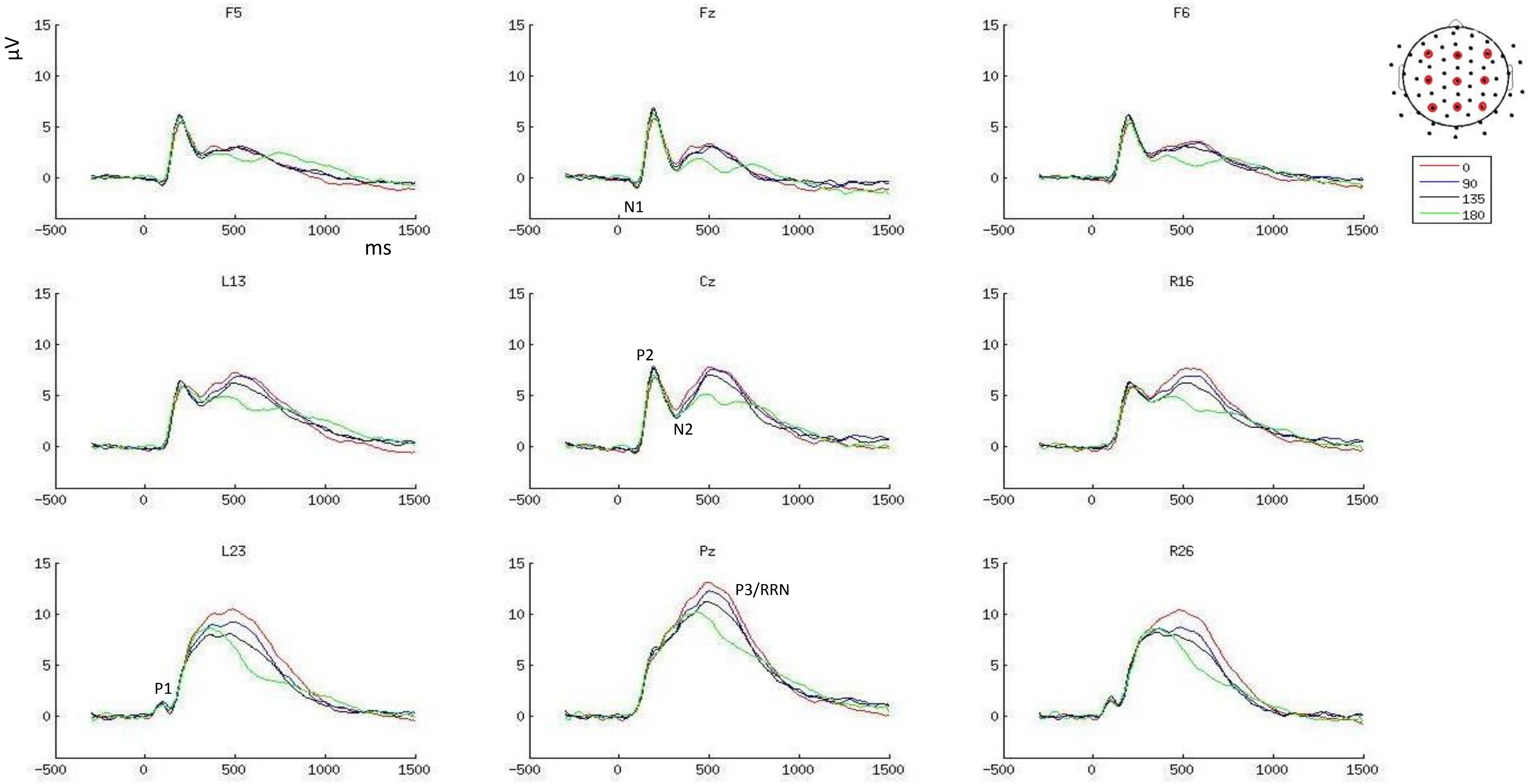


Figure 14

ERPs of the MR task aligned to stimulus onset for group average. ERP waves for nine electrodes are shown. Positions of the electrodes are highlighted on the cartoon head. The ERPs of the different rotation angle conditions are shown in different colors (see legend). ERP components are marked at peaks with prominent occurance.

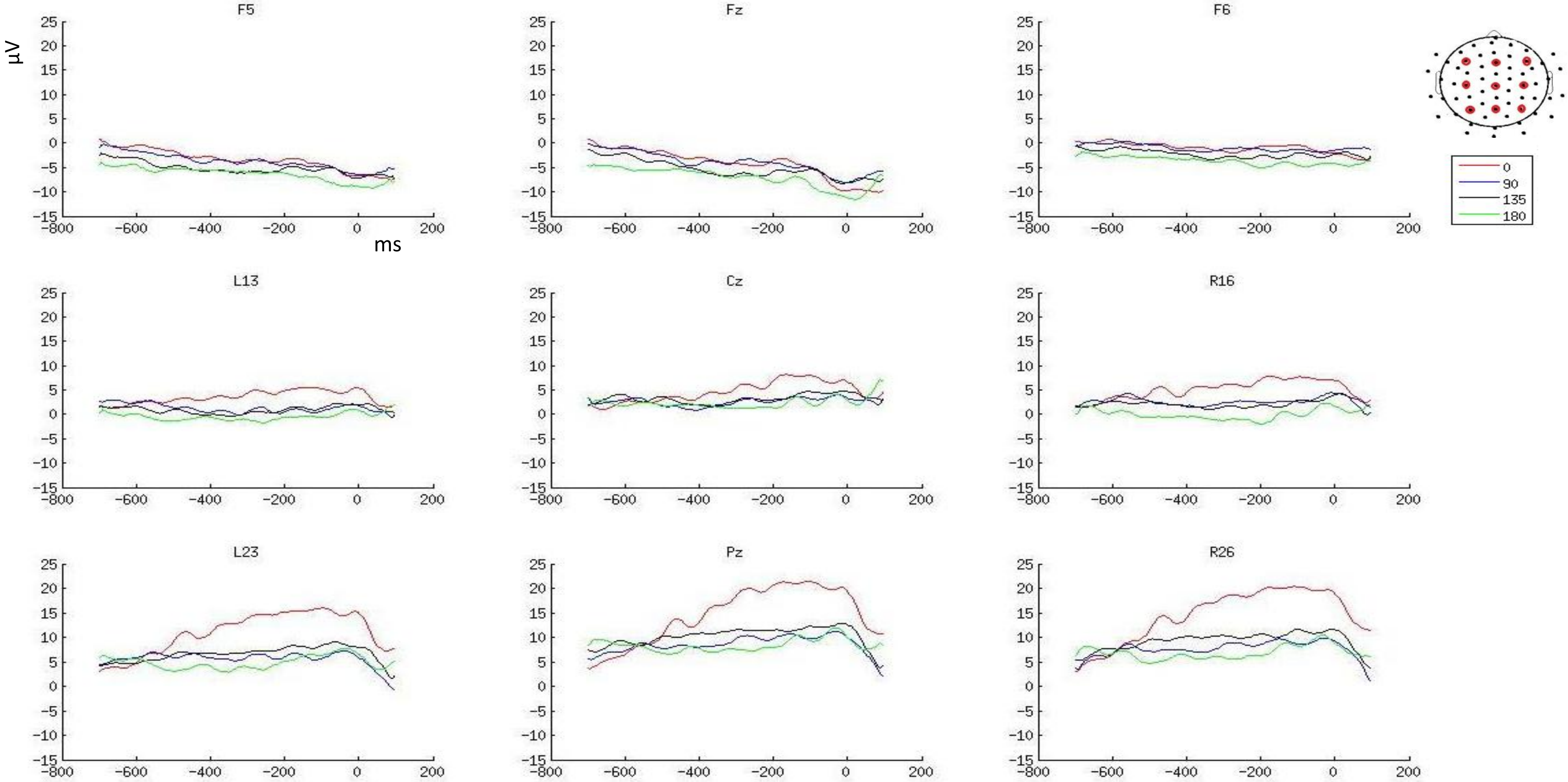


Figure 15

ERPs of the MR task aligned to response time in one subject. ERP waves for nine electrodes are shown. Positions of the electrodes are highlighted on the cartoon head. The ERPs of the different rotation angle conditions are shown in different colors (see legend).

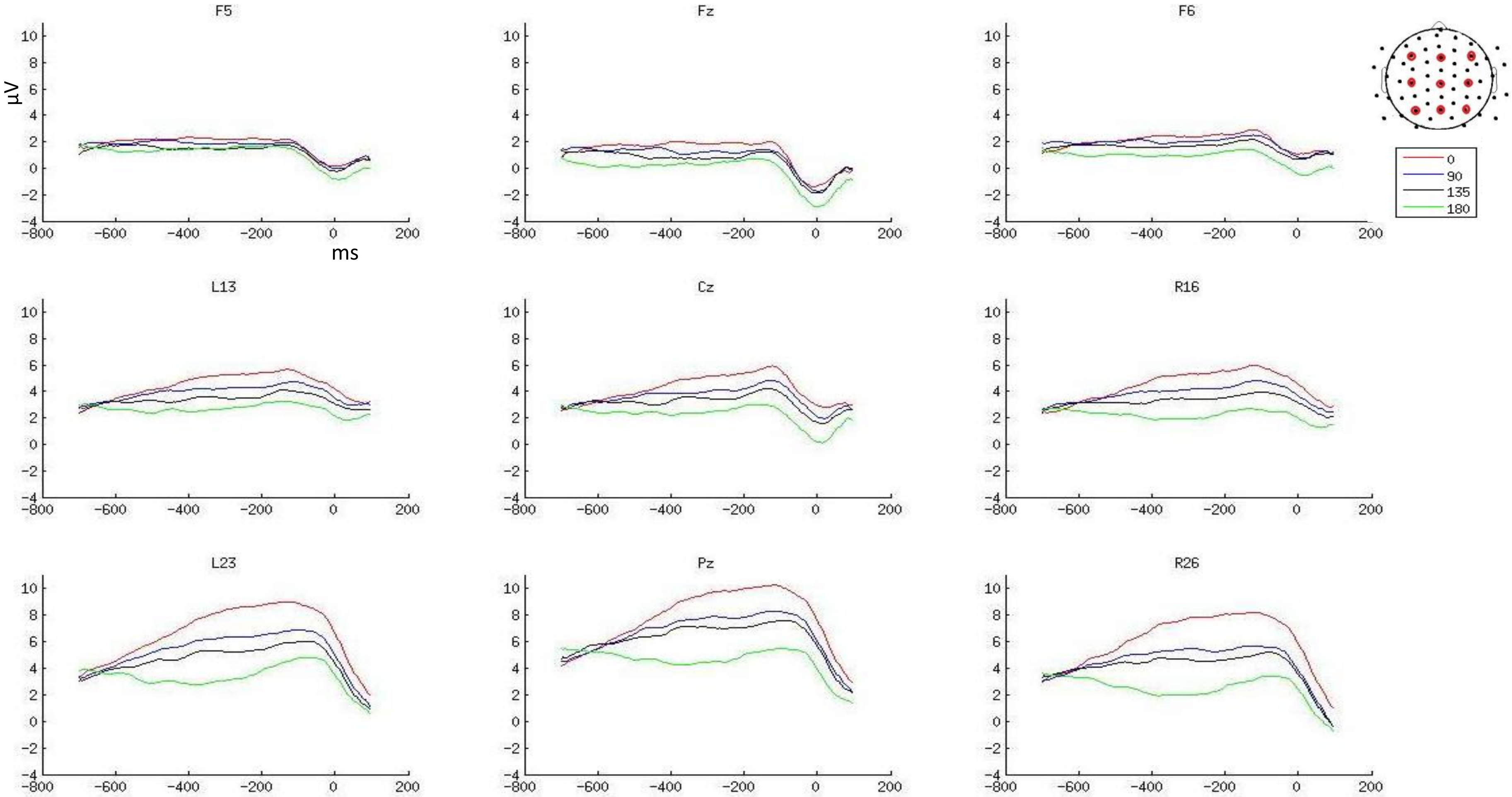


Figure 16

ERPs of the MR task aligned to response time for group average. ERP waves for nine electrodes are shown. Positions of the electrodes are highlighted on the cartoon head. The ERPs of the different rotation angle conditions are shown in different colors (see legend).

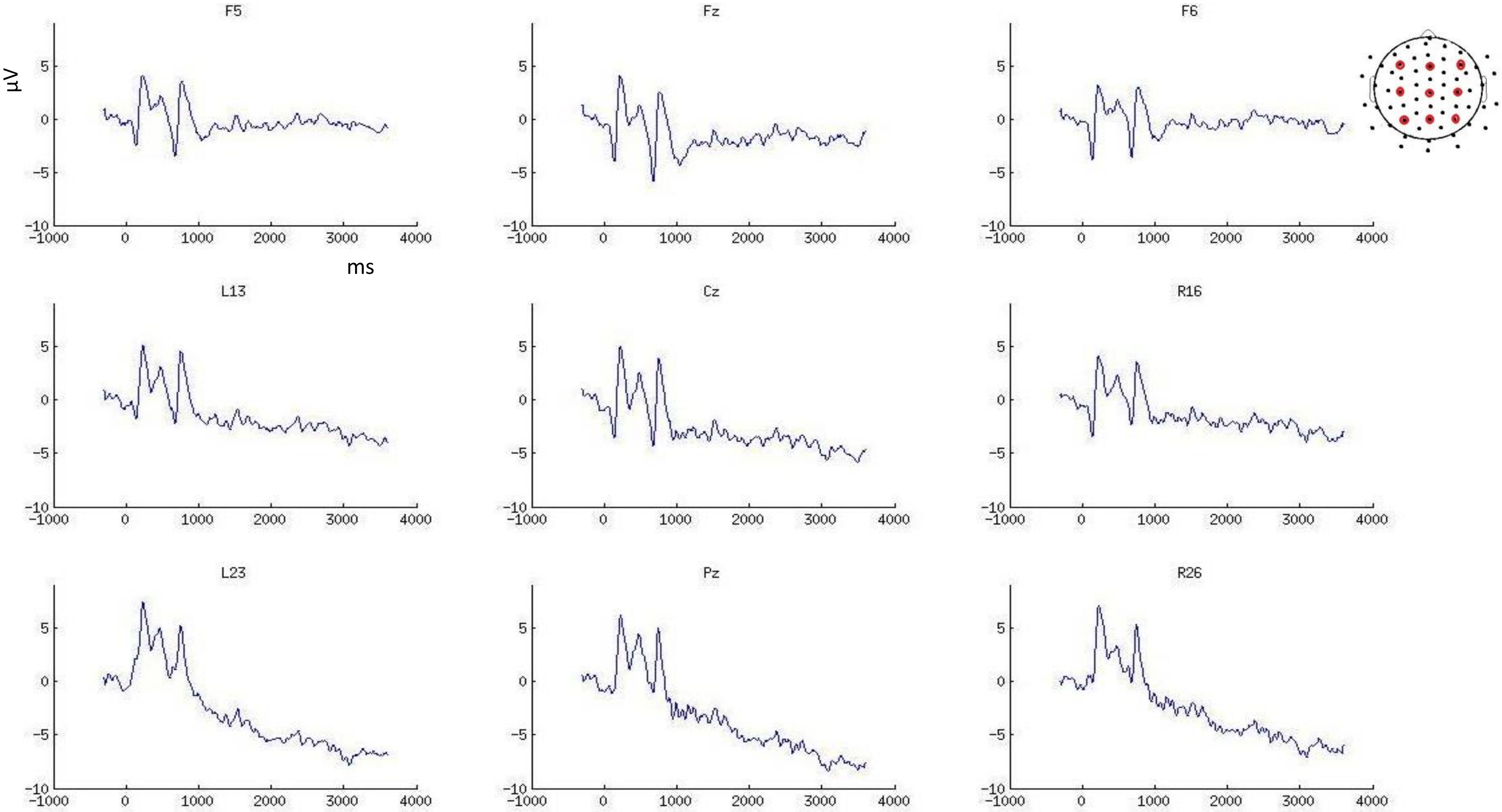


Figure 17

ERPs from the OCD task in one subject. ERP waves from probe stimulus onset until mask offset (3520 ms) for nine electrodes are shown. Positions of the electrodes are highlighted on the cartoon head.

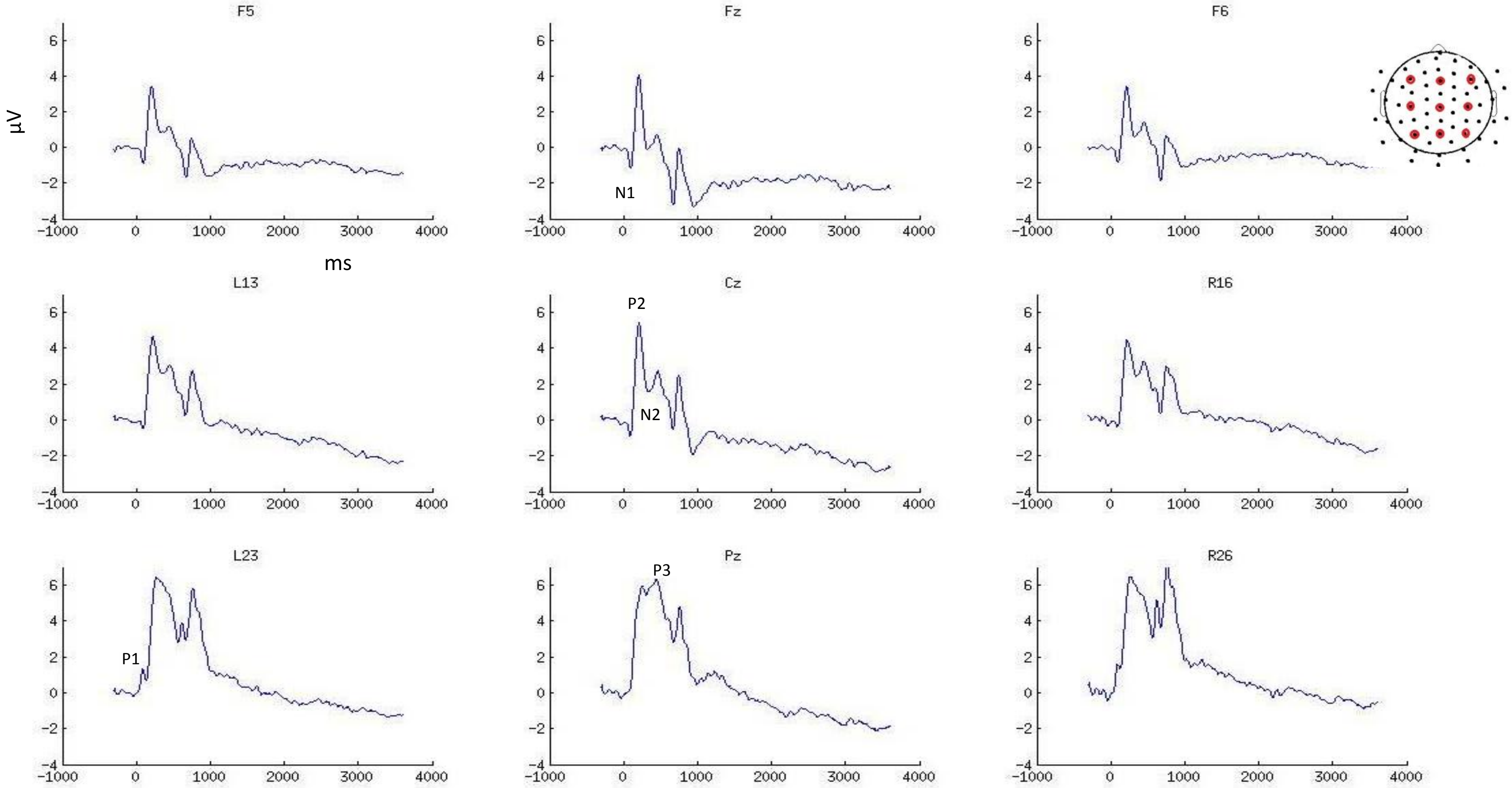


Figure 18

ERPs from the OCD task for group average. ERP waves from probe stimulus onset until mask offset (3520 ms) for nine electrodes are shown. Positions of the electrodes are highlighted on the cartoon head. ERP components are marked at peaks with prominent occurance.

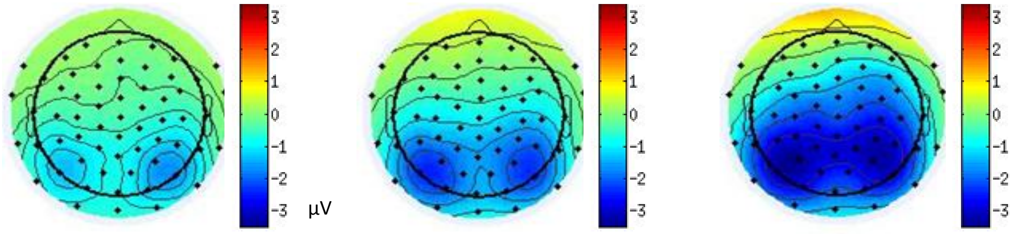


Figure 19

Topographical plot RRN$_{on}$. Group mean amplitude in the interval 350 ms – 750 ms after stimulus onset is plotted for 90 deg, 135 deg and 180 deg (from left to right). Mean amplitude for 0 deg stimulus condition is subtracted.

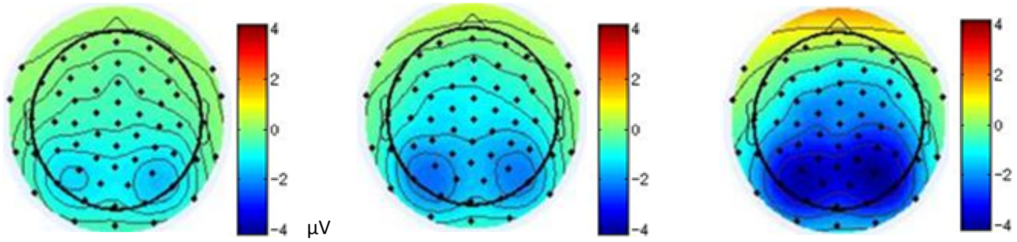


Figure 20

Topographical plot RRN$_{rt}$. Group mean amplitude in the interval 600 ms – 200 ms before response time is plotted for 90 deg, 135 deg and 180 deg (from left to right). Mean amplitude for 0 deg stimulus condition is subtracted

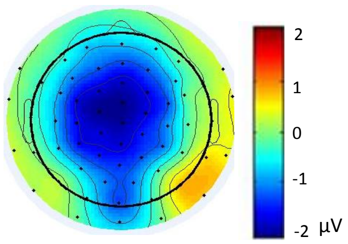


Figure 21

Topographical plot ERP$_{OCD}$. Group mean amplitude in the interval 2500 ms – 3500 ms after probe stimulus onset is plotted.

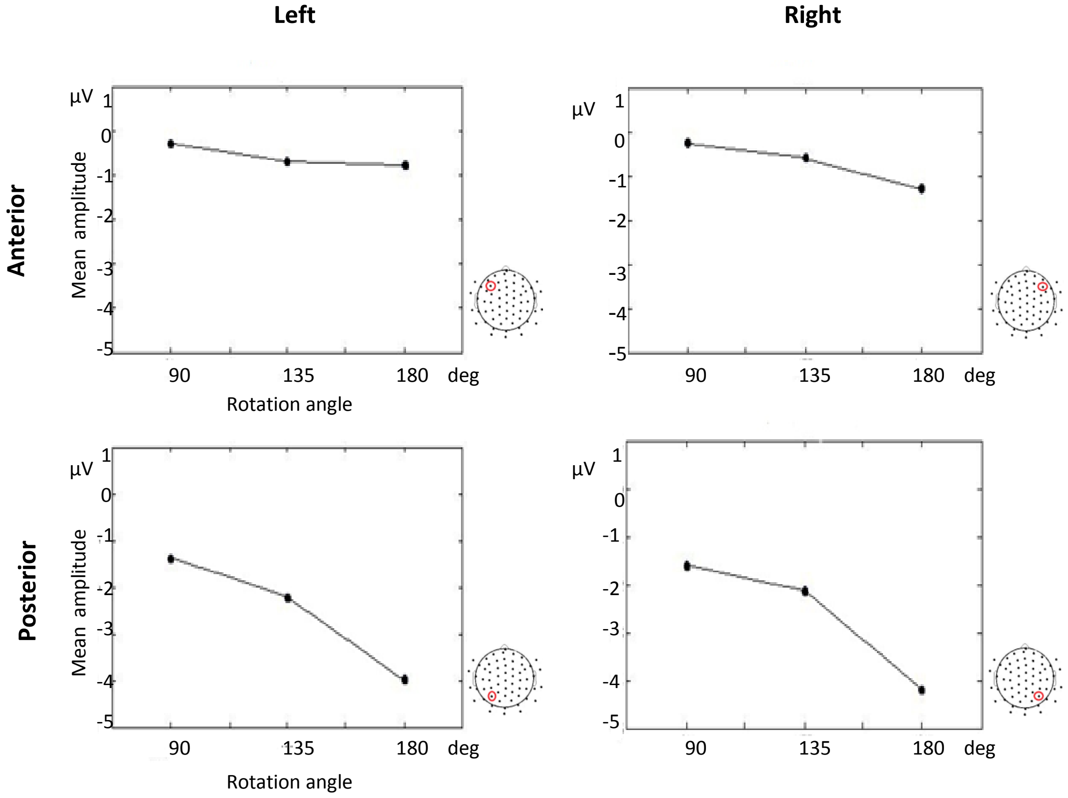


Figure 22

Change in mean amplitude as a function of rotation angle at four electrode locations. Each electrode location is encircled in red on the cartoon head.

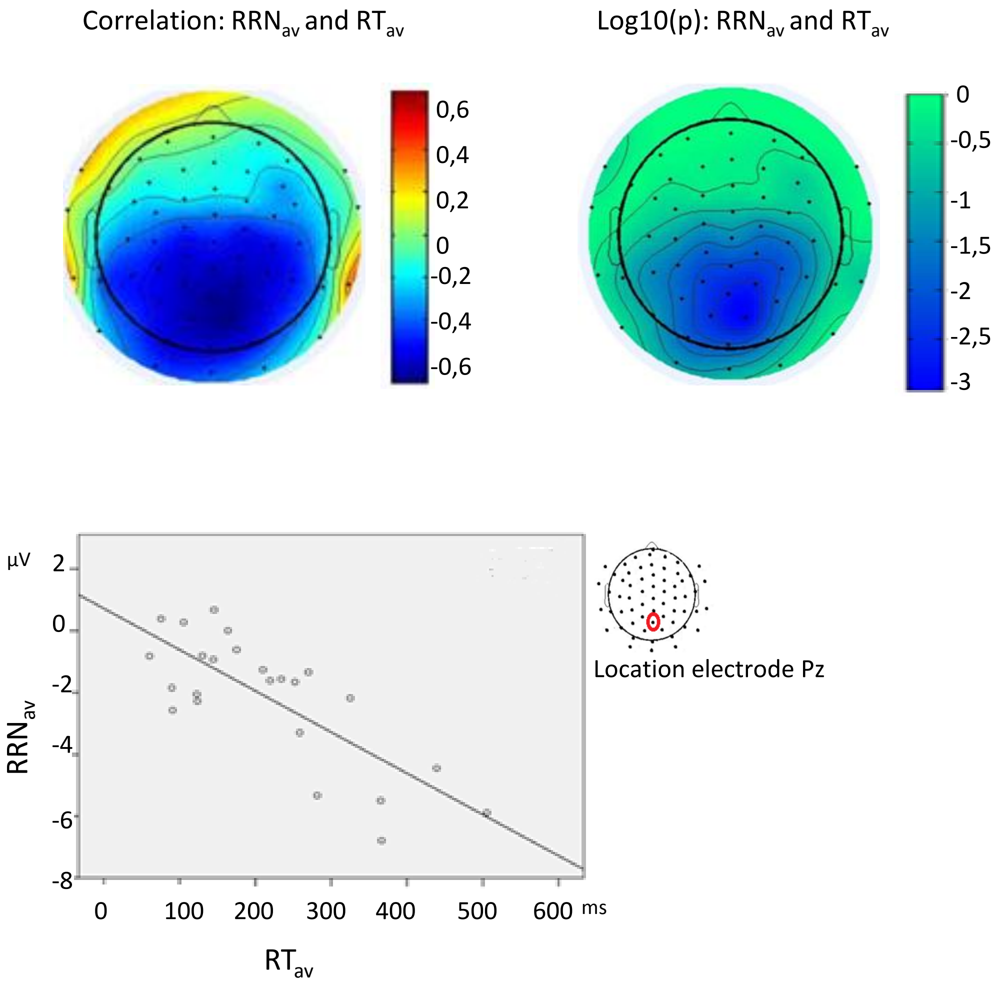


Figure 23

Pearson's correlation coefficients and corresponding p-values (log10 scale is used, i.e. the value of - 3 corresponds to $p = 0.001$) for the association between RRN_{av} and RT_{av} at all 61 electrodes in the group of 24 subjects. The scatter plot shows this the relationship at electrode Pz ($R = -0.770$, $p < 0.001$).

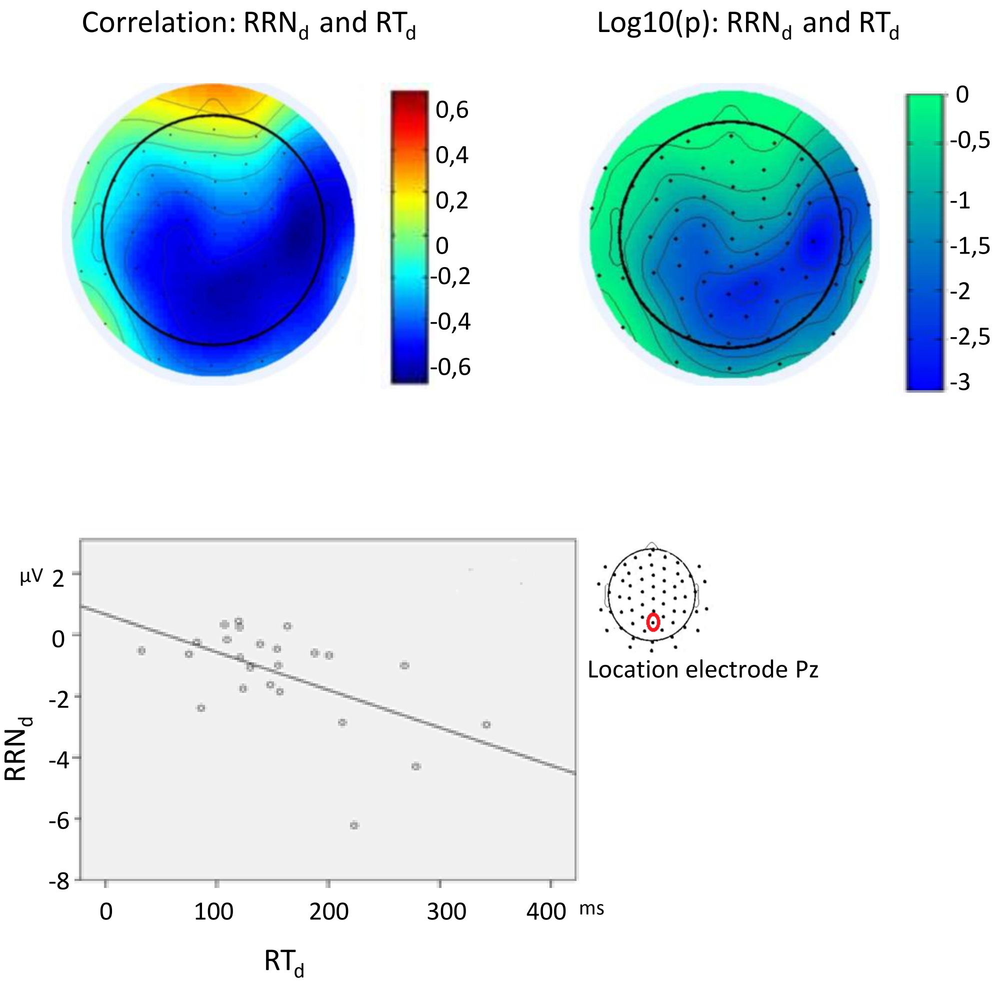
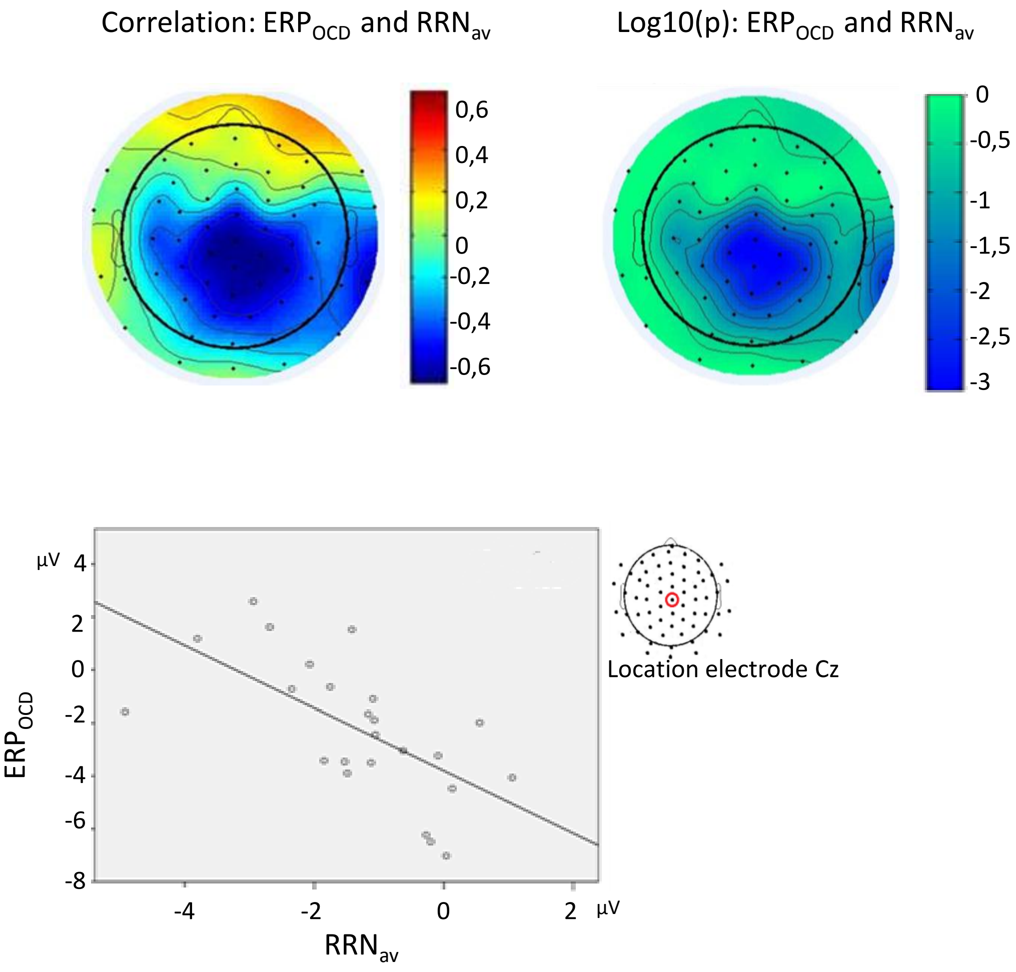


Figure 24

Pearson's correlation coefficients and corresponding p-values (log10 scale is used, i.e. the value of - 3 corresponds to p = 0.001) for the association between RRN$_d$ and RT$_d$ at all 61 electrodes in the group of 24 subjects. The scatter plot shows this the relationship at electrode Pz (R = - 0.554, p = 0.005).



Correlation: ERP_{OCD} and RRN_{av}

Log10(p): ERP_{OCD} and RRN_{av}

Figure 25

Pearson’s correlation coefficients and corresponding p-values (log10 scale is used, i.e. the value of - 3 corresponds to p = 0.001) for the association between ERP_{OCD} and RRN_{av} at all 61 electrodes in the group of 24 subjects. The scatter plot shows this the relationship at electrode Cz (R = - 0.634; p = 0.001).

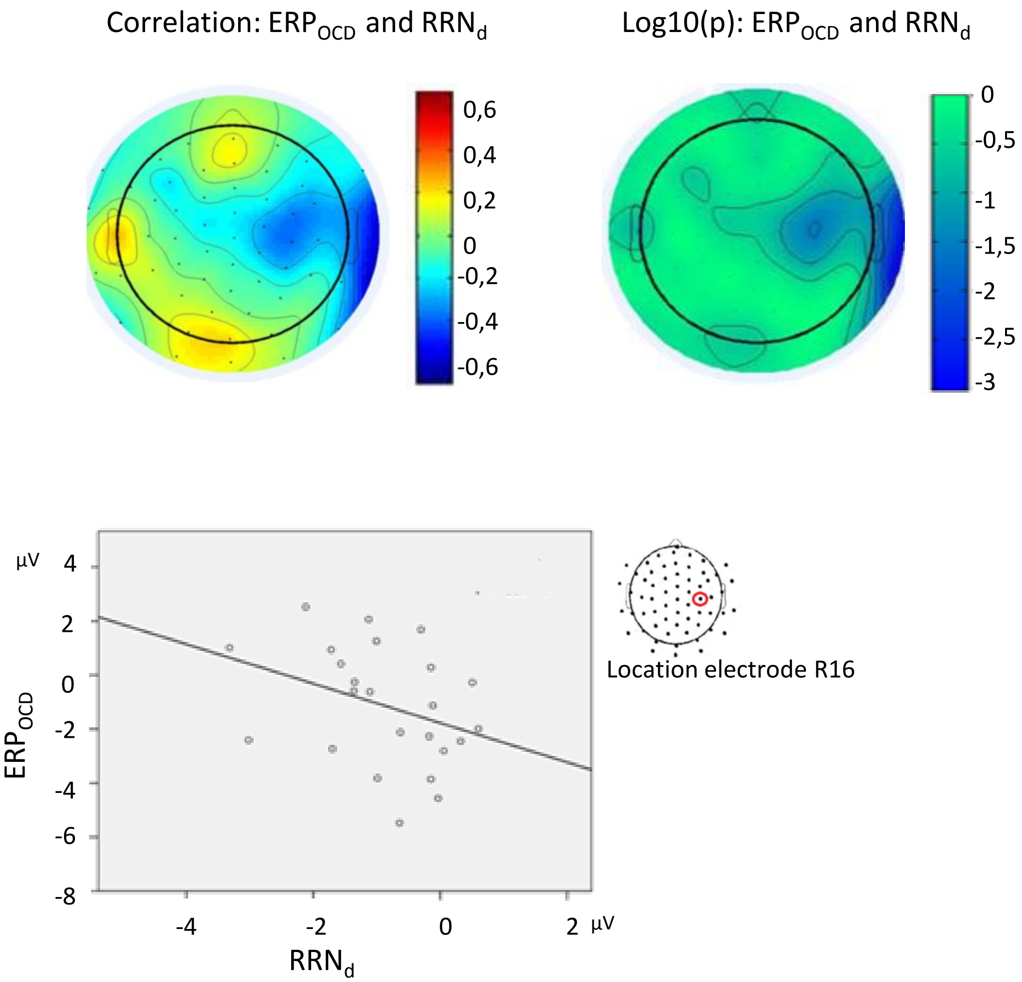


Figure 26

Pearson’s correlation coefficients and corresponding p-values (log10 scale is used, i.e. the value of - 3 corresponds to p = 0.001) for the association between ERP$_{OCD}$ and RRN$_d$ at all 61 electrodes in the group of twenty-four subjects. The scatter plot shows this the relationship at electrode R16 (R = -0.343; p = 0.101).

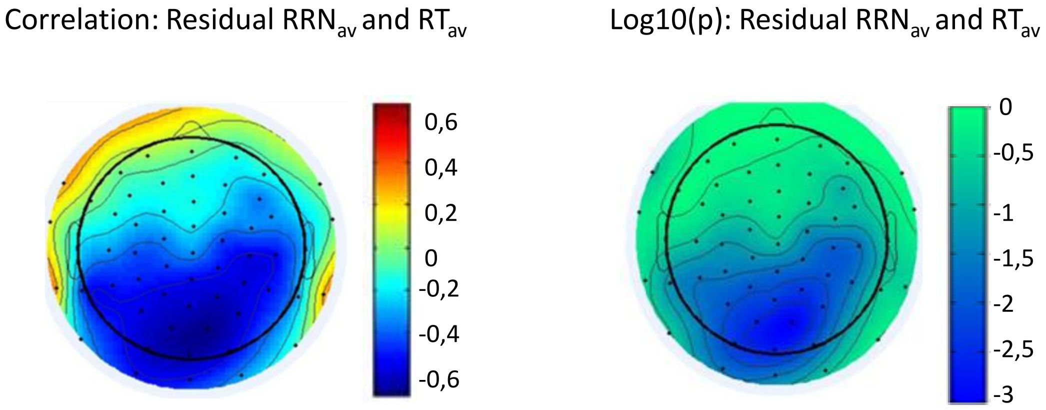


Figure 27a

Pearson's correlation coefficients and corresponding p-values (log10 scale is used, i.e. the value of - 3 corresponds to p = 0.001) for the association between residual RRN$_{av}$ and RT$_{av}$ at all 61 electrodes in the group of twenty-four subjects.

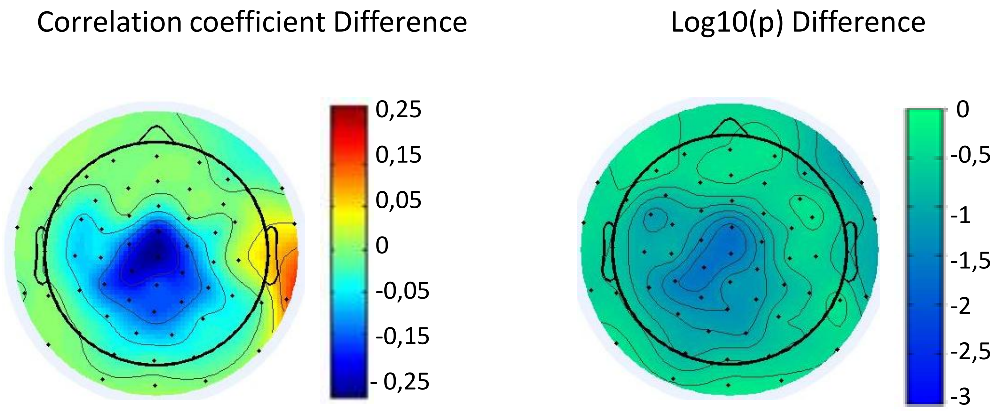
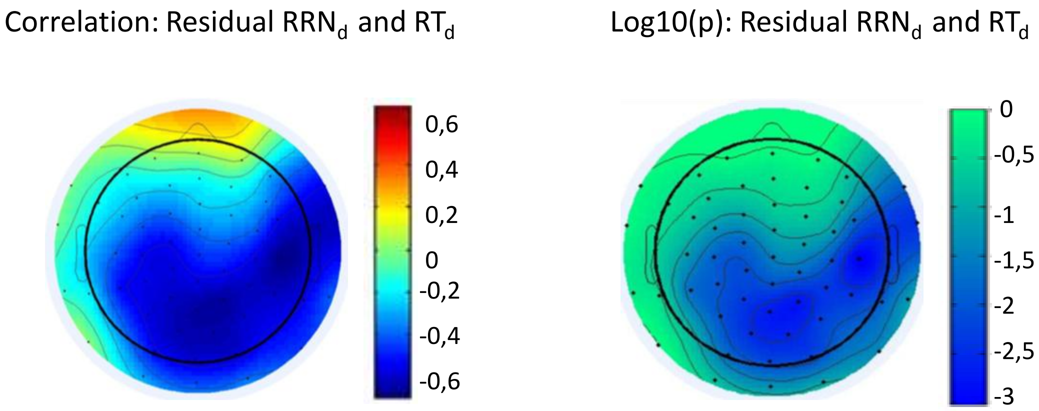


Figure 27b

Pearson's correlation coefficients and corresponding p-values (log10 scale is used, i.e. the value of - 3 corresponds to p = 0.001) for the difference in Pearson´s correlation coefficients between the association RRN$_{av}$ and RT$_{av}$ and residual RRN$_{av}$ and RT$_{av}$ at all 61 electrodes in the group of twenty-four subjects.

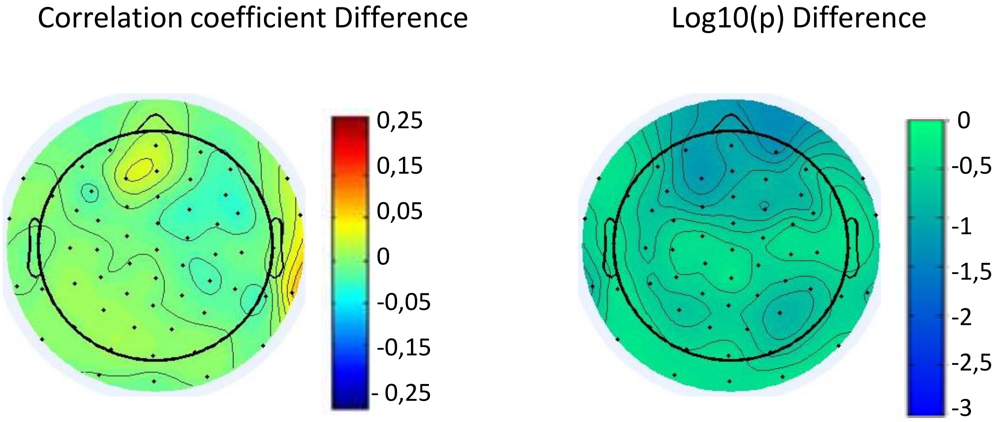


Correlation: Residual RRN_d and RT_d

Log10(p): Residual RRN_d and RT_d

Figure 28a

Pearson’s correlation coefficients and corresponding p-values (log10 scale is used, i.e. the value of - 3 corresponds to p = 0.001) for the association between residual RRN_d and RT_d at all 61 electrodes in the group of twenty-four subjects.



Correlation coefficient Difference

Log10(p) Difference

Figure 28b

Pearson’s correlation coefficients and corresponding p-values (log10 scale is used, i.e. the value of - 3 corresponds to p = 0.001) for the difference in Pearson´s correlation coefficients between the association RRN_d and RT_d and residual RRN_d and RT_d at all 61 electrodes in the group of twenty-four subjects.

Tables

MR angle	N	Mean Errors	Std. Deviation
90 deg	32	1,50	2,98
135 deg	32	2,81	3,57
180 deg	32	8,28	5,44

Table 1

Mean number of errors and standard deviation of errors for the MR task for each angular deviation of the character.

MR angle	N	Mean RT	Std. Deviation
90 deg	32	104,60	82,54
135 deg	32	181,80	123,93
180 deg	32	425,56	199,22

Table 2

Mean RT and standard deviation of RT for the MR task

Abstract in German

Die geistige Rotation einer mentalen Repräsentation wird als Mental-Rotation bezeichnet. Es wird angenommen, dass während des Prozesses der Mental-Rotation, eine mentale Manipulation (i.e. die Rotation an sich) bis zu einem geplanten Rotationsgrad durchgeführt wird, während gleichzeitig eine konstante Speicherung des mentalen Bildes in den jeweiligen Zwischenpositionen erfolgt. Die Fähigkeit Mental-Rotation durchzuführen, ist zwischen verschiedenen Personen unterschiedlich gut ausgeprägt. Bisherige Studien konnten zeigen, dass die Amplitude der sogenannten ‚rotation related negativity' (RRN; i.e. eine ereigniskorrelierte Potential (EKP)-Komponente welche mit Mental-Rotation assoziiert wird) die Leistung einer Testperson in einer Mental-Rotationsaufgabe vorhersagen kann. Allerdings ist unklar, ob Personen, welche gute Leistungen in Mental-Rotation zeigen, auch tatsächlich gut im Manipulieren (i.e. Rotieren), oder eher gut im Speichern der aktuellen Position des Objekts sind. Ziel dieser Studie war es daher, die beiden Subprozesse der Mental-Rotation zu trennen und herauszufinden welcher der Subprozesse wieviel zur Leistung in Mental-Rotations-Aufgaben beiträgt. Zu diesem Zweck wurden EKPs während einer Mental-Rotationsaufgabe und während einer Kurzzeitgedächtnis (KG)- Aufgabe aufgezeichnet. Anschließend wurden mittels linearer Regression die mit KG assoziierten EKPs aus der neuronalen MR Aktivität (i.e. RRN) herausregressiert. Dabei zeigte sich, dass die für KG bereinigte MR Aktivität immer noch signifikant die Reaktionszeiten der Versuchspersonen vorhersagen konnte. Somit kann man aus dieser Studie schließen, dass Leistung in Mental-Rotation hauptsächlich von der Fähigkeit des mentalen Rotierens an sich abhängt und weniger von KG Prozessen zur Speicherung der aktuellen Position.

Lebenslauf

Persönliche Information

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- WS 2004-SS 2009 Studium Publizistik und Kommunikationswissenschaft, Universität Wien
- seit WS 2005 Studium Psychologie, Universität Wien
- Juli-Sept. 2007 Praktikum bei Prenzl Komm- Psychiatrischer Verbund, Berlin
- Juli-Okt. 2009 6-Wochen-Praktikum auf der Gerontopsychiatrischen Station,Psychiatrische Abteilung, Sozialmedizinisches Zentrum-Ost/Donauspital, Wien
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