The Mental Representation in Mental Rotation

Its Content, Timing and Neuronal Source

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Part of this work is also included in published articles. Specifically, the preliminary study was published as Liesefeld and Zimmer (2011) and experiments 1b and 2 are published as Liesefeld and Zimmer (2012). For these articles I am the first author. In order to warrant a smooth reading, the respective passages are not marked in the text. Furthermore, in keeping with the practice of these articles, in the main text I consistently employ "we" instead of "I".

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“For let no one hope to decide the question whether it is the earth or heaven that really revolves in the diurnal motion, until he has first comprehended the nature of spontaneous rotation.”

—Francis Bacon (1620).
The new organon.

“To form monsters and join incongruous shapes and appearances costs the imagination no more trouble than to conceive the most natural and familiar objects.”

—Hume (1748)
An enquiry concerning human understanding.

“I am crushed, I am carrying the whole world on my back in the process of trying to visualize my turning around and making myself see in terms of “right” what I saw in terms of “left” and vice versa.”

—Vladimir Nabokov (1974).
Look at the harlequins!

Contents

List of Tables

List of Figures

List of Abbreviations

°	Degree
€	Euro
%	Percent
α	Rate of Type I Error (Rejection of a True Null Hypothesis)
η_p^2	Effect Size for ANOVAs with Repeated Measurements (Partial η^2)
ε	Greenhouse-Geisser Epsilon
µV	Microvolt
χ^2	Test Statistic from Chi-Square Distribution
3D	Three-Dimensional
AC-PC line	Intercommissural (Anterior-Posterior Commissure) Line
ANOVA	Analysis of Variance
BA	Brodmann's Area
CCW	Counterclockwise
cf.	Compare
CW	Clockwise
dB/8ve	Decibel per Octave
Dep	(Amount of/Mismatch in) Orientation-Dependent Information
df	Degrees of Freedom
d_z	Effect Size for Paired t-Tests
EEG	Electroencephalography
e.g.	For Example
EOG	Electroocculogramm
EPI	Echo Planar Imaging
ERP	Event-Related Potential
F	Test Statistic from F-Distribution
fMRI	Functional Magnetic Resonance Imaging
FWHM	Full-Width at Half Maximum
Hz	Hertz
HRF	Haemodynamic Response Function
Indep	(Amount of/Mismatch in) Orientation Independent Information
IPC	Inferior Parietal Cortex
kΩ	Kilohm
IPS	Intraparietal Sulcus
M	Match
MANOVA	Multivariate Analysis of Variance
mm	Millimeter
MNI	Montreal Neurological Institute
ms	Millisecond
p.	Page
p	Probability of Equally Extreme Test Statistic, Given Null Hypothesis is True
p_{corr}	Greenhouse-Geisser Corrected p-Value
PET	Positron Emission Tomography
pMd	Dorsolateral Premotor Cortex
pp.	Pages
r	Pearson Product-Moment Correlation Coefficient
RMB	Renminbi (Chinese Yuan)

ROI	Region of Interest
s	Second
SPL	Superior Parietal Lobule
SPM	Statistical Parametric Mapping (fMRI Analysis Software)
t	Test Statistic from Student’s t-Distribution
T	Tesla
T_1	T_1-Weighted Image (Especially for Differentiating Fat From Water)
V3-5	Visual Areas 3-5
V5/MT	Human Visual Motion Area MT (Middle Temporal Visual Area)
V. Complex	Visually Complex (Stimulus Type)

Abstract

What is rotated in mental rotation? The implicitly or explicitly most widely accepted assumption is that the rotated representation is a visual mental image. We here provide converging evidence that instead mental rotation is a process specialized on a certain type of spatial information. As a basis, we here develop a general theory on how to manipulate and empirically examine representational content. One technique to examine the content of the representation in mental rotation is to measure the influence of stimulus characteristics on rotational speed. Experiment 1a and 1b show that the rotational speed of university students (10 men, 10 women and 10 men, 11 women, respectively) is influenced exclusively by the amount of represented orientation-dependent spatial-relational information but not by orientation-independent spatial-relational information, visual complexity, or the number of stimulus parts. Obviously, only explicit orientation-dependent spatial-relational information in an abstract, nonvisual form is rotated. As information in mental-rotation tasks is initially presented visually, a nonvisual representation during rotation implies that at some point during processing information is recoded. Experiment 2 provides more direct evidence for this recoding. While university students (12 men, 12 women) performed our mental-rotation task, we recorded their EEG in order to extract slow potentials, which are sensitive to working-memory load. During initial stimulus processing, slow potentials were sensitive to the amount of orientation-independent information or to the visual complexity of the stimuli. During rotation, in contrast, slow potentials were sensitive to the amount of orientation-dependent information only. This change in slow potential behavior constitutes evidence for the hypothesized recoding of the content of the mental representation from a visual into a nonvisual form. We further assumed that, in order to be accessible for the process of mental rotation, orientation-dependent information must be represented in those brain areas that are also responsible for mental rotation proper. Indeed, in an fMRI study on university students (12 men, 12 women) the very same set of brain areas was specifically activated by both the amount of mental rotation and of orientation-dependent information. The amount of orientation-independent information/visual complexity, in contrast, influenced activation in a different set of brain areas. Together, all activated areas constitute the so-called mental rotation network. In sum, the present work provides a general theory and several techniques to examine mental representations and employs these techniques to identify the content, timing, and neuronal source of the mental representation in mental rotation.

1. Mental Rotation

1.1 The Mental Rotation Effect

Is the character displayed in Figure 1.1A a normal or a mirrored version of an *R*? What about the *R* in Figure 1.1B?

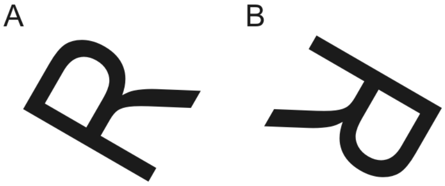

Figure 1.1. *Two trials of a mental rotation experiment.*

If you tried to answer these questions, your decision very probably took longer for the character in Figure 1.1B than for that in Figure 1.1A. Whether you noticed this or not, the comparison between the presented character and your long-term memory entry of an *R* took longer for the *R* rotated further from upright. In general, the time to decide whether two objects are the same or mirror images of each other is an (almost) linear function of the angular disparity between the two objects (see the rotation time patterns in the preliminary experiment as well as Experiment 1a, 1b and 3 reported here). The usual interpretation of this *mental rotation effect* is that in order to compare two stimuli that differ in absolute orientation, a visual mental image of one stimulus has to be rotated into alignment with the other stimulus (for a review see, e.g., Shepard & Cooper, 1982).

This interpretation implicates that the rotated object on its way from one orientation into the other moves through intermediate orientations. In a direct test of this hypothesis, Cooper and Shepard (Cooper, 1976; Cooper & Shepard, 1973) asked participants to mentally rotate one stimulus (in the following the *original stimulus*) at a predetermined speed. At unpredictable times during rotation either a matching or a mismatching second stimulus (in the following *comparison stimulus*) was shown. The time it took to compare the two stimuli depended on the (predicted) orientation of the mental representation of the original stimulus at comparison stimulus onset and not on the original stimulus' initial orientation. Instead of starting the rotation from the original stimulus' original orientation, participants apparently rotated their current mental representation of the original stimulus into alignment with the comparison stimulus. Critically, these results show that the orientation of the rotated mental representation at comparison stimulus onset depends on how far the representation was already rotated at this point in time. This constitutes strong evidence that the mental representation moves through intermediate orientations during mental rotation. Other and at first glance more efficient manipulation algorithms that would lead to the same outcome (a rotated representation) are conceivable. Matrix transformations would in a one step process transform a mental representation of the original stimulus from the initial into the target orientation. However, in contrast to the empirical results, matrix transformations do not take longer for larger rotational angles and do not go through intermediate orientations. These two characteristic result patterns of mental-rotation tasks consequently are the strongest evidence for the claim that mental rotation is an analog process similar to a real, physical rotation.

1.2 What is Mental Rotation Good For?

Humans are highly skilled in manipulating rigid objects in order to solve problems. Using tools, for example, is one application of this ability. In some instances, manually trying out such manipulations and failing to achieve the expected goal induces no great costs. This is the case for the manipulation of small, easily replaceable objects. However, in many other instances, such failure might waste much energy, time or other resources (e.g., moving a heavy stone), or a rare opportunity (e.g., during hunting) or is even dangerous (e.g. cutting the tree branch one is sitting on). In all these cases, the ability to mentally simulate an action prior to performing it becomes a clear advantage in the struggle for survival.

Although this ability might have originally evolved for such situations, humans, creative as they are, regularly go beyond these practical applications of mental simulations. For example, in Einstein's thoughts "the words or the language, as they are written or spoken, do not seem to play any role", but rather "certain signs and more or less clear images which can be 'voluntarily' reproduced and combined" (Hadamard, 1945, p. 142). This is expressed in Einstein's famous avowal that his "particular ability does not lie in mathematical calculation, but rather in visualizing effects, possibilities and consequences." In order to decipher the double-helical structure of the DNA, Watson and Crick augmented their simulation ability by external models. Using such aids, Watson realized that "an adenine-thymine pair held together by two hydrogen bonds was identical in shape to a guanine-cytosine pair" (Watson, 1968, p. 123). When he came into the laboratory the next morning, Crick was "flipping the cardboard base pairs about an imaginary line" (Watson, 1968, p. 128). Mental simulations are known to have driven the invention of the self-starting, reversible induction motor and the polyphase system of electrical distribution by Tesla, the discovery of the molecular structure of benzene by Kekulé (Shepard & Cooper, 1982, pp. 6-7) and the mental rotation effect by Shepard and Metzler (Shepard &

Cooper, 1982, p. 7). More common applications of the simulation ability are, for example, to prepare for rearranging heavy furniture in a room, suitcases in a trunk or broken bones in a human body (cf. Shepard & Cooper, 1982, p. 2).

Furthermore, mental simulation is important in scholarly disciplines like geometry, engineering design and stereochemistry, in navigation and in the planning of movements like grasping. Many intelligence tests include subtests that purportedly demand mental simulation (e.g., block design, paper folding, paper form board, surface development and of course cube comparison as well as figure, card and flag rotation) and since recently mental rotation is even considered a relatively general and independent contributor to human intelligence on par with both general verbal and perceptual aptitude (W. Johnson & Bouchard, 2005).

Obviously, the mental simulation of manipulations of rigid objects in space is of utmost importance for the success of the human species. There exist six degrees of freedom of rigid motion in space. Three degrees are translational and three are rotational. All transformations of rigid bodies in space are reducible to combinations of translations and rotations (cf. Shepard & Cooper, 1982). Many spatial features of objects as perceived from a specific viewpoint remain invariant under translation but not under rotation, thereby rendering the ability to mentally rotate objects more important than the ability to mentally translate them. Indeed, mental rotation seems to be the critical bottle-neck of human mental simulation ability (see also Chapter 8.7.2).

1.3 Classification of Mental-Rotation Tasks

Since the first experimental study on mental rotation (Shepard & Metzler, 1971), many different types of this task were developed (see Figure 1.2). Naturally, these types of tasks share certain attributes. In all mental-rotation tasks two stimuli must be compared. Participants compare features of one (*original*) stimulus to subsequently encoded features of a second (*comparison*) stimulus. On most or all trials, these two stimuli differ in orientation. This *angular disparity* determines the amount of to-be-performed rotation. Participants decide whether the original stimulus matches the comparison stimulus irrespective of angular disparity. Mismatching comparison stimuli usually are mirror images of the respective original stimulus. As the mental rotation effect tends to disappear, whenever other than mirror images are employed as mismatching comparison stimuli (i.e., stimuli that mismatch in some other feature), this characteristic appears to be critical for mental rotation to occur (for reviews, see Corballis, 1988; but see also, Förster, Gebhardt, Lindlar, & Siemann, 1996; Shepard & Cooper, 1982). As a consequence, stimuli employed in mental-rotation tasks are usually asymmetrical, because the mirror image of a symmetrical stimulus is the stimulus itself.

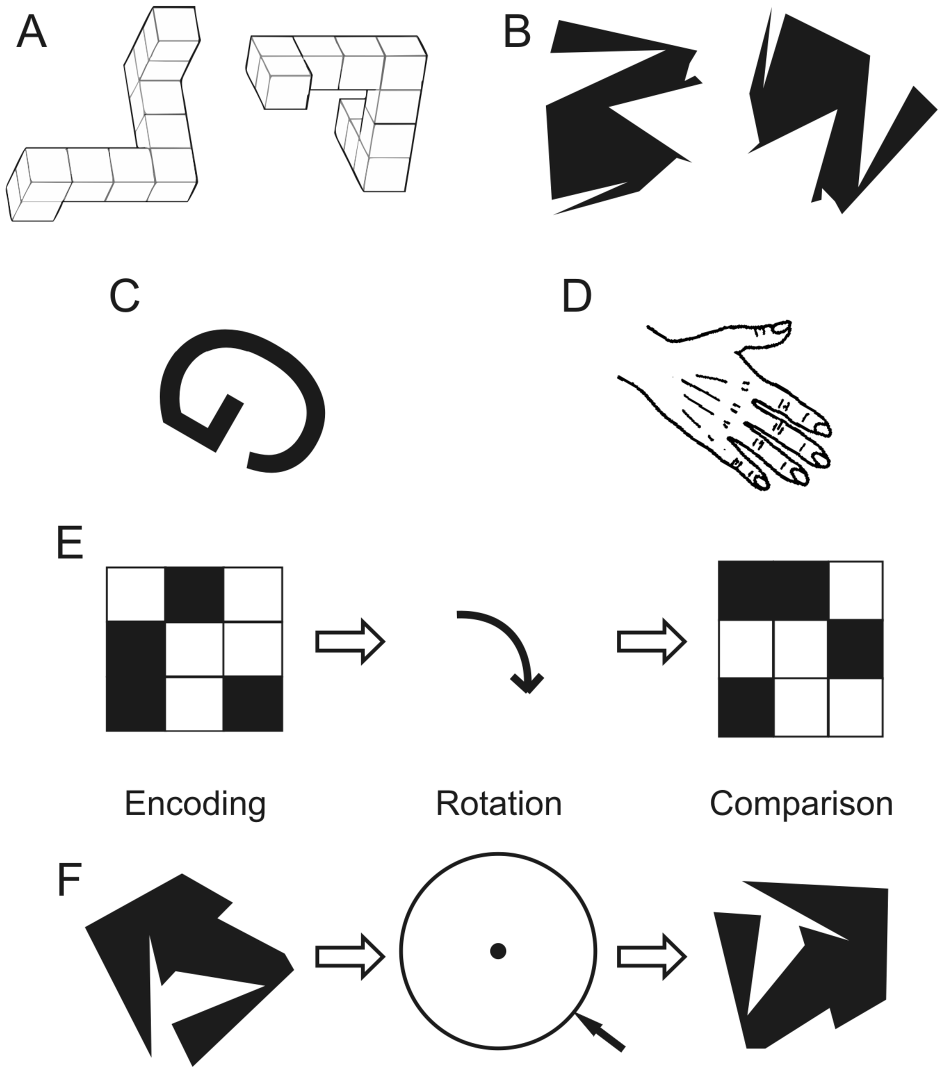

Figure 1.2. *The different types of mental-rotation tasks with typical stimuli. A and B: Comparison of simultaneously presented stimuli. C and D: Comparison of a stimulus with its long-term memory entry. E and F: Comparison of successively presented stimuli with a rotation cue shown in between. A, B, E and F show matching stimuli. C shows a normal (nonmirrored) G. D is a drawing of a right hand. Stimuli in A are copied from Peters and Battista (2008). Stimuli in B and F are redrawn from Vanderplas and Garvin (1959). The stimulus in D is copied from Parsons (1994). Stimuli and rotation cue in E are redrawn from Bethell-Fox and Shepard (1988). Rotation cue in F is redrawn from Folk and Luce (1987).*

On a relatively general level, the processing steps that take place in every mental-rotation task are:

1. Encoding of the original and/or comparison stimulus into a mental representation;
2. Determination of the angular disparity between original and comparison stimulus, that is, determination of the rotational angle;
3. Mental rotation proper;
4. Comparison of the now aligned mental representations of original and comparison stimulus;
5. Response selection.

Although all types of mental-rotation tasks share these task characteristics and processing steps, some characteristics and processing steps differ between the types of mental-rotation tasks.

1.3.1 Comparing simultaneously presented stimuli

In one type of mental-rotation tasks (Figure 1.2A and Figure 1.2B), on each trial two stimuli are shown next to each other. Participants' task usually is to decide whether the two stimuli are the same or mirror images of each other. Based on eye- fixation patterns Just and Carpenter (1976) developed a relatively detailed processing model which differentiates between three major processing stages:

1. Search.
   a. A segment of the original stimulus is encoded.
   b. The corresponding segment of the comparison stimulus is searched for. Search starts at the corresponding point of the field around the comparison stimulus, whereby fields are hypothetical imaginary symmetrical boundary boxes around the two stimuli.
   c. If there is no stimulus segment at this point, first the stimulus segment closest to this point is compared.
   d. As the angular disparity between stimuli increases, search time increases for two reasons.

        i. Corresponding stimulus segments are in successively dissimilar locations in the searched fields and therefore successively more time is dedicated to active search.
        ii. The probability that the wrong segment is selected and erroneously rotated increases.
2. Transformation and Comparison.
    a. The corresponding segments are mentally rotated towards each other in 50° steps.
    b. After each step a check is conducted whether the segments are within 25° of each other and if so, the rotation is finished.
3. Confirmation, strategy 1:
    a. A second pair of corresponding segments is encoded.
    b. The same rotation that was applied to the first pair is applied to this second pair of segments.
    c. After rotation, the corresponding segments are compared.
4. Confirmation, strategy 2:
    a. The relation between an arm and the central joint of each stimulus is encoded.
    b. This relation is directly (i.e., independent of angular disparity) compared between stimuli.

This model applies especially to the task and stimuli originally developed by Shepard and Metzler (1971; see Figure 1.2A). Just and Carpenter (1985) adapted the model to the rotation of other stimuli (cubes), but still within the same type of mental-rotation task (simultaneous-presentation).

1.3.2 Comparing a single stimulus to its long-term memory entry

When only one stimulus is shown on each trial, this stimulus can be considered the comparison stimulus and the representation of the original stimulus is drawn from long-term memory. This presupposes that a long-term memory entry of the stimulus exists. Consequently, the stimuli are learned prior to the proper mental-rotation task (e.g., Cooper, 1975; Koriat & Norman, 1985a) or are pre-experimentally known. Examples for frequently employed pre-experimentally known stimuli are alphanumeric characters (*character-rotation tasks*; Figure 1.2C) or drawings of human body parts (e.g., hands, Figure 1.2D). In these tasks, participants have to differentiate between normal and mirror-imaged characters or between left and right body parts. Their decision time follows an almost linear function of the stimulus disparity from upright (e.g., Cooper & Shepard, 1973). Reaction time for differentiating between left and right disoriented body parts additionally depends on physiological properties of the human body (e.g., Parsons, 1994). Note that differentiating between normal and mirror imaged characters or between left and right body parts can be translated into deciding whether the presented stimulus matches its long-term memory entry or whether the presented body part matches optionally a right or left body part. Therefore, single-stimulus mental-rotation tasks also require the comparison of two stimuli as do all mental-rotation tasks.

One crucial difference between single-stimulus and simultaneous-presentation mental-rotation tasks lies in the process of determining the angular disparity and thereby the correct rotational angle. For alphanumeric characters two possibilities are discussed (see also Chapter 2).

1. Parallel rotation of two mental representations (e.g., Jolicoeur, 1990)
    a. Two mental representations of the presented comparison stimulus are rotated in parallel one into clockwise and the other into counterclockwise direction.
    b. As soon as one representation reaches upright it is compared to the respective long-term memory entry—determination of the angular disparity becomes superfluous.
2. Rotation after identification of orientation (e.g., Corballis, 1988)
    a. The comparison stimulus or at least its top is identified. Indeed, a stimulus can be identified at least to a certain degree without the need for rotation (e.g., Jolicoeur, Snow, & Murray, 1987).
    b. The orientation of the stimulus is identified as its disparity from upright (the disparity from the respective long-term memory entry)
    c. The correct rotational angle is calculated by simply reversing the sign of the value for this angular disparity.

1.3.3 Comparing successively presented stimuli

An alternative to training pre-experimentally unknown stimuli prior to the rotation part of an experiment is to present the original stimulus before the comparison stimulus on each trial (e.g., D. Cohen & Kubovy, 1993; Figure 1.2E and Figure 1.2F without the rotation cue). In these tasks, the original stimulus is encoded into working memory and mental rotation is performed when the comparison stimulus is shown. From onset of the comparison stimulus on, these tasks are therefore similar to the single-stimulus tasks with the only difference that the original stimulus is held in working memory instead of being retrieved from long-term memory. Stimuli employed in this type of task can but do not need to be pre-experimentally unknown (for successive-presentation mental rotation-tasks with pre-experimentally known stimuli, see, e.g., Cooper & Shepard, 1973 and the preliminary experiment of the present work). Simultaneous-presentation mental-rotation tasks can be considered special cases of successive-presentation tasks with an interstimulus interval of zero (cf. Farell, 1985). However, a critical effect of an interstimulus interval larger than zero is that participants cannot check back and forth between the two stimuli and consequently have to encode all relevant information while the original stimulus is shown.

A potential advantage of single-stimulus and successive-presentation above simultaneous-presentation mental-rotation tasks is that the original stimulus is retrieved from long-term or working memory instead of being visually encoded. Presenting only one stimulus at a time certainly reduces the number of performed saccades. Furthermore, retrieval from memory might proceed smoother and might allow for fewer strategies (but see Chapter 2) than visual encoding of this stimulus. Thereby the process of mental rotation is potentially measured a little more purely. However, there are still many processes which are difficult to separate from mental rotation proper, as for example, determination of the rotational angle (potentially including identification of the disoriented stimulus), encoding of the comparison stimulus and comparison of the two stimuli. This difficulty arises from the fact that all sub-processes (encoding, determination of the rotational angle, rotation, and comparison) take place within the same time-interval, namely while the comparison stimulus is shown on the screen.

An interesting consequence of the existence of the mental rotation effect is that the process of mental rotation can to a certain degree be mathematically isolated from other processing stages. Indicators of the process of mental rotation proper increase in value with the amount of mental rotation. Only the slope but not the intercept of the function relating any dependent variable to rotational angle reflects mental rotation proper. Some of the processes taking place in mental-rotation tasks—especially encoding, comparison and response selection—are not likely to influence dependent variables in an angle-dependent manner and therefore can be separated from the process of mental rotation proper. Consider that it takes some time to compare two identically oriented objects. This is not due to mental rotation proper (which should not take place in this case) but to the mentioned additional processes (which must also take place when mental rotation is necessary).

1.3.4 Rotation cues

Unfortunately, the mental rotation effect does not enable a differentiation between effects of mental rotation proper and effects of the identification of the correct rotational angle. As evident in the descriptions of mental-rotation tasks so far, the determination of rotational angle is a complex process. In fact, this process is not necessarily identical to the process of mental rotation proper. Time and effort spent on determining the rotational angle and mental rotation proper are however easily confused, because both processes purportedly become more difficult and time-consuming with increasing rotational angle. This complication can easily be alleviated by employing rotation cues that indicate the correct rotational angle (see Figure 1.2E and Figure 1.2F). Although, in principle, rotation cues can be employed in each of the three types of tasks, they are most often found in tasks with successive stimulus presentation (e.g., Bethell-Fox & Shepard, 1988; M. D. Folk & Luce, 1987).

In theories on the processing chain in mental-rotation tasks (e.g., Corballis, 1988; Jolicoeur, 1990; Just & Carpenter, 1976), much effort goes into the identification of the correct rotational angle. Most authors assume that in a first step the angular disparity between original and comparison stimulus must be identified. As the problem of how participants identify the correct rotational angle occupies so much space in theories on mental rotation, relatively little is said about the process of mental rotation itself. Employing rotation cues can drastically reduce the complexity of mental-rotation tasks and help to focus on the process of mental rotation proper. Furthermore, in successive-presentation mental-rotation tasks with rotation cues like those displayed in Figure 1.2E and Figure 1.2F many of the necessary processing steps can be isolated from mental rotation proper. This is because the processing steps are separated into three time intervals:

1. Encoding of the original stimulus starts from onset of the original stimulus.
2. Encoding of the rotation cue starts from onset of the rotation cue. Mental rotation starts when both original stimulus and rotation cue are encoded (see Cooper & Shepard, 1973).
3. Encoding of the comparison stimulus and comparison starts from onset of the comparison stimulus. In addition, response selection cannot start earlier than comparison stimulus presentation.

Assumedly, encoding of the rotation cue does not become more difficult with increasing rotational angle. At least the rotational angle should influence the encoding of the rotation cue less than it would influence the determination of the rotational angle without the aid of a cue. Encoding of original and comparison stimulus as well as the comparison process itself and response selection are temporally separated from mental rotation proper. Consequently, a successive-presentation with rotation cue is the best choice for isolating the process of mental rotation proper from all other cognitive processes operating in mental-rotation tasks.

From an experimental perspective the successive-presentation mental-rotation task with rotation cue has the advantage that in comparison to other mental-rotation tasks less cognitive processes take place (determination of the rotational angle is at least much less complex) and that the processes that take place are better separable. A drawback of this type of task ironically is its complexity from the viewpoint of participants. Correct use of a rotation cue usually takes a while to learn. Task instructions like “Rotate one stimulus into the orientation of the other!" are more intuitive than "Rotate one stimulus according to the rotation cue!" In addition, in successive-presentation mental-rotation tasks working memory demands are high as characteristics of the original stimulus must be maintained during rotation and, if lost, cannot be encoded anew. For certain populations this type of mental-rotation task might even be unsolvable. Indeed, pre-testing our mental-rotation task (as employed in all main experiments reported here) with children did lead to accuracy rates close to or below chance level.

1.4 Disoriented Object Recognition

A rotation, but not a translation increases the difficulty of visually encoding objects. However, as a matter of fact, humans are able to recognize disoriented objects. This problem of object constancy across orientations might in part be solved by mental rotation (e.g., Jolicoeur, 1990; Tarr & Pinker, 1989). The fact that humans are capable of recognizing objects from different perspectives is truly remarkable if one considers how difficult such tasks are for computers (see, e.g., Hyder, Islam, Akhand, & Murase, 2009; Tarr, 2003). In typical experiments on disoriented object recognition, participants name or categorize objects shown disoriented from upright (for reviews, see Jolicoeur, 1990; Leek & Johnston, 2006). On early trials of such experiments, the time to identify objects increases with their angular displacement from upright. The slope of the function relating identification time to angular displacement is of similar magnitude as the slope found in mental rotation studies (e.g., Corballis, Zbrodoff, Shetzer, & Butler, 1978; Jolicoeur, 1985; Jolicoeur & Milliken, 1989; Jolicoeur, et al., 1987). However, in contrast to mental rotation studies, the displacement from upright almost completely loses its impact on identification times over the course of the experiment (e.g., Corballis & Nagourney, 1978; Corballis, et al., 1978). Apparently, participants perform mental rotation on earlier but not on later trials of an experiment (e.g., Jolicoeur, 1985). In addition, even on early trials, the identification of objects disoriented by 180° is faster than would be predicted by a strictly linear relationship (e.g., Jolicoeur, 1985; Jolicoeur & Milliken, 1989; Murray, 1995a, 1995b). Based on the findings from the experiments presented in the following, we will provide an explanation for these differences in data patterns observed in experiments on mental rotation and disoriented object recognition (Chapter 8.7.7).

1.5 Mental Rotation as a Working Memory Function

Working memory is defined as a system that actively maintains (stores/represents) information. Most researchers assume that information is usually maintained for further processing (manipulation) and not for the sole purpose to retrieve it after a retention period (e.g., Baddeley, 2000; Baddeley, 2002; see also the contributions in Miyake & Shah, 1999a and especially the summary by Miyake & Shah, 1999b, p. 445). Only a collaboration of maintenance and processing functions of working memory allows such diverse activities as language comprehension, reasoning, problem solving, decision making and, of course, mental rotation. Typical tasks employed to examine working memory are for example change detection, *N*-back, simple span, and complex span (storage and processing) tasks. As detailed in the following, these tasks focus (exclusively) on maintenance and largely ignore the processing function of working memory. As a consequence and in spite of its prominent theoretical role, processing is strongly underrepresented in empirical research on working memory.

1.5.1 Working-memory tasks

In change detection tasks (for a review, see Luck, 2008), stimulus information has to be encoded and maintained for a short period of time (the retention interval) and subsequently be compared to a second stimulus or stimulus array. From each participant's performance-accuracy an estimate can be derived that reflects how many items the respective participant is able to hold in working memory (Cowan, 2001). Obviously, change detection tasks charge only the maintenance and not the processing component of working memory.

In *N*-back tasks (for a review, see Jaeggi, Buschkuehl, Perrig, & Meier, 2010), a stream of items (e.g., words) is shown and the current stimulus always has to be compared to the item presented *N* positions earlier in time. Processing load increases along with *N* as reflected by decreasing accuracy rates and increasing response times for the comparison. The cognitive affordance in *N*-back tasks is to maintain the last *N* items. As these items constantly have to be updated, *N*-back tasks might charge the executive function (see, e.g., Baddeley, 2000; Baddeley, 2002) of working memory, a manipulation of the stored material, however, is not necessary.

In simple span tasks, on each trial a list of several sequentially presented items (e.g., words) has to be remembered. After presentation of items has ended, participants try to recall all items from the list. Simple span tasks consequently also charge only the storage function of working memory. Complex span tasks (for a review, see Conway, et al., 2005) in contrast also involve the processing function of working memory. In alternation with remembering items, a task like reading a sentence (reading span, Daneman & Carpenter, 1980), solving a math problem (operation span, Turner & Engle, 1989) or counting dots (counting span, Case, Kurland, & Goldberg, 1982) has to be performed. In both simple and complex span tasks the dependent variable of main interest is the number of correctly recalled items. As the processing component interferes to a certain degree with the storage component, fewer items are usually recalled in complex compared with simple span tasks.

Although complex span tasks charge both storage and processing components of working memory, the processing material usually differs from the storage material (e.g., Turner & Engle, 1989). Even in a complex span task like counting span in which the connection between storage and processing material seems rather close (Case, et al., 1982), the result of the processing of each item (the total from counting) must be stored passively. The representation of the result does not need to be manipulated further. However, the capability to manipulate represented information is exactly the reason for which the construct *working memory* was introduced and which differentiates it from its precursor *short-term memory* (e.g., Baddeley, 2002). Of course, during the processing component of complex span tasks information has to be maintained (e.g., digits) and processed (e.g., multiplied). However, the focus in complex span tasks traditionally lies on recall performance and therefore on the storage component. As a consequence, the influence of processing affordances on processing performance is hardly ever examined.

During mental rotation a representation of the original stimulus must be maintained and manipulated, namely rotated. Only if both maintenance and processing are successful, that is, only if the relevant information is represented in working memory and is correctly transformed, participants can successfully compare original and comparison stimulus. The dependent variable of main interest in behavioral mental-rotation tasks is processing (rotation) time. Processing times presumably increase with increasing affordances on the processing of represented information. The main independent variable of interest in mental-rotation tasks is rotational angle, which directly influences processing affordances as evident by the classical mental rotation effect (see Chapter 1.1). Mental-rotation tasks consequently are far better suited to examine working memory as a system for processing maintained information than most purpose-built working-memory tasks.

1.5.2 Parcellation of working memory

It is largely agreed upon that several working memory systems can be differentiated according to the type of information that is stored and/or processed. The differentiation between verbal and visuo-spatial working memory is well-established (for reviews, see Baddeley & Logie, 1999; Logie, 1995). Brain damage can lead to a disruption of visuo-spatial working memory while verbal working memory remains intact and vice versa (e.g., de Renzi & Nichelli, 1975). In addition, visuo-spatial working memory main tasks are more strongly disrupted by visuo-spatial secondary tasks than by verbal secondary tasks. The opposite pattern emerges for verbal working memory main tasks (e.g., Meiser & Klauer, 1999).

Based on these double-dissociations, visuo-spatial working memory is considered largely independent from verbal working memory. Visuo-spatial working-memory can, however, be further subdivided into visual/object and spatial/motor components[1] (for reviews, see, e.g., Logie, 1995; Repovš & Baddeley, 2006; Zimmer, 2008). Also between these components double dissociations in the form of case studies on neuropsychological patients and interference studies have been reported (e.g., Della Sala, Gray, Baddeley, Allamano, & Wilson, 1999; Klauer & Zhao, 2004). Further evidence for this dissociation comes from single-cell recordings in monkeys (Wilson, Ó Scalaidhe, & Goldman-Rakic, 1993), positron emission tomography (PET; e.g., Smith, Jonides, Koeppe, & Awh, 1995), functional magnetic resonance imaging (fMRI; e.g., Belger, et al., 1998), and electroencephalography (EEG; e.g., Mecklinger & Pfeifer, 1996) studies. Indeed, different cortical pathways have been identified that process perceptually relevant (ventral stream; e.g., features of objects) and action relevant (dorsal stream; e.g., orientations and locations) aspects of visually encoded information (e.g., Goodale & Milner, 1992; for a recent review, see Milner & Goodale, 2008). These pathways also serve as working memory stores (for a meta-analysis on PET and fMRI data, see Wager & Smith, 2003).

The differentiation between visual/object and spatial/motor working memory raises the question of which of the two systems is employed in mental-rotation tasks. As the usual assumption goes that mental rotation is performed on visual representations (see Chapter 3.1), several researchers postulated visual working memory as the cognitive system underlying mental-rotation tasks (Hyun & Luck, 2007; Prime & Jolicoeur, 2010). The input modality in mental-rotation tasks indeed usually is visual (as in Figure 1.1 and Figure 1.2). However, the process of rotation is by definition spatial in nature and therefore would rather be considered as belonging to the domain of spatial working memory. Although in principle it appears possible that a spatial process works on a visual representation it appears more efficient that information is represented and processed within one working memory system (see Experiment 3, Chapter 7). This would imply that visual information is recoded into a spatial representation before mental rotation takes place (see Experiment 2, Chapter 6).

Information indeed can reach spatial working memory from different input modalities. For example, auditory-spatial tasks interfere with visuo-spatial tasks

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[1] Note that also interference between verbal and spatial tasks has been reported, which might indicate special affordances for the processing of seriated material (Jones, Farrand, Stuart, & Morris, 1995; see also, Smyth & Scholey, 1994).

(Baddeley & Lieberman, 1980; Lehnert & Zimmer, 2006) and elicit memory-related electrophysiological activity over the same cortical areas (Lehnert & Zimmer, 2008). In addition, mental rotation can be performed on hapticly presented stimuli (Carpenter & Eisenberg, 1978). Independent of the input modality being visual or haptic, mental rotation is apparently performed by the same brain structures. Topographically similar slow potentials emerge during mental rotation for hapticly (Röder, Rösler, & Hennighausen, 1997) and visually (Rösler, Heil, Bajric, & Pauls, 1995) presented stimuli, indicating that at least in one case (haptic or visual presentation) and perhaps in both cases information was recoded in order to be rotated.

1.6 Brain Regions Involved in Mental-Rotation Tasks

Which brain areas are responsible for mental rotation? Knowledge about the cortical circuit that enables humans to perform mental rotation is interesting in its own right. However, such knowledge can also lead to a deeper understanding of the cognitive processes underlying mental-rotation tasks. The very same brain regions that are active during mental rotation are also active during other cognitive, perceptual and motor tasks. By considering this pattern of results from the literature and thereby approaching an understanding of the function of the respective brain region, it is possible to derive well-informed guesses about the respective brain region’s role during mental rotation. This in turn can lead to new hypotheses about the cognitive processes taking place during mental rotation.

For this endeavor, it is helpful to differentiate between mental-rotation tasks and the process of mental rotation proper. As already detailed above (Chapter 1.3), many different cognitive processes take place during mental-rotation tasks. Some of these processes might occur in parallel with and consequently render it difficult to disentangle mental rotation proper. The usually bad temporal resolution of positron emission tomography (PET) and functional magnetic resonance imaging (fMRI) data further aggravates this problem, because even processes that happen sequentially but within a short time-interval are difficult or impossible to differentiate based on their timing alone. Consequently, a comparison of activity during a mental-rotation task with baseline activity (e.g., looking at a fixation cross) will highlight many areas that are not related to mental rotation proper, but to processes as, for example, encoding, maintaining and comparing information and even to processes related to the behavioral response (e.g., button press), general attention allocation or the visual perception of the stimulus. However, as mentioned above (Chapter 1.3.2) the mental rotation effect can be employed to disentangle mental rotation proper from many of these additional processes. Activation in brain areas that are related to the process of mental rotation proper must (linearly) depend on the rotational angle, because more mental rotation must be performed with an increasing rotational angle. In the following we focus on those areas that a recent meta analysis (Zacks, 2008) found consistently activated in such a rotation-specific manner and that are displayed in Figure 1.3.

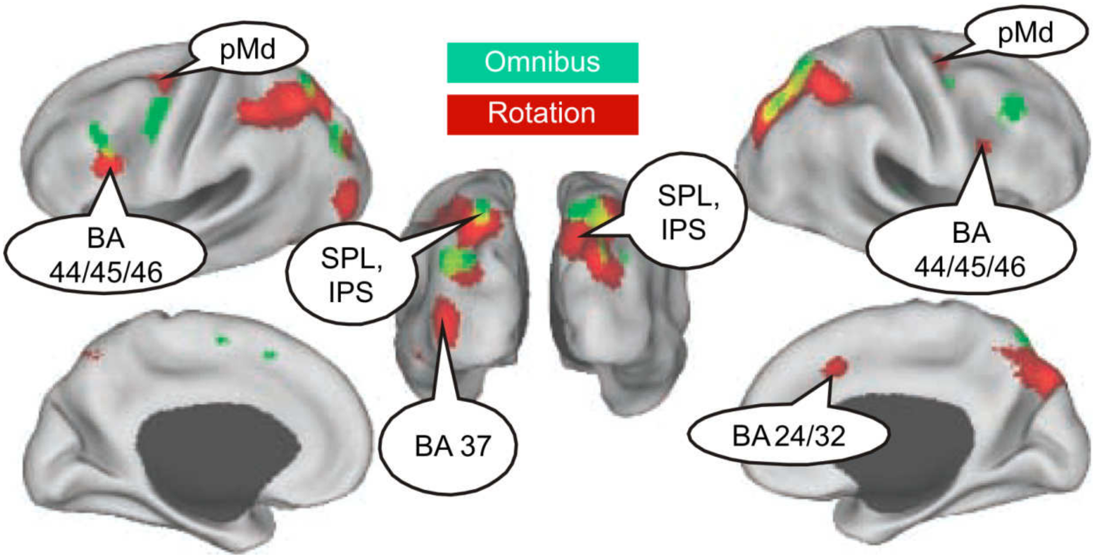

Figure 1.3. *Brain areas activated in mental-rotation tasks as found in a meta-analysis by Zacks (2008). Areas more strongly activated in mental-rotation tasks compared with loose baselines (omnibus) are marked in green. Areas more strongly activated for large rotational angles compared with small angles (rotation) are marked in red. Overlapping areas are marked in yellow. BA = Brodmann's area; pMd = dorsolateral premotor cortex; SPL = superior parietal lobule; IPS = intraparietal sulcus. Adapted from "Neuroimaging Studies of Mental Rotation: A Meta-Analysis and Review," by J. M. Zacks, 2008, Journal of Cognitive Neuroscience, 20, p. 4. © 2007 by the Massachusetts Institute of Technology. Reprinted with permission.*

1.6.1 Parietal cortex

Rotation-specific activation is usually found centered in the superior-parietal lobule (SPL; e.g., M. S. Cohen, Kosslyn, Breiter, & DiGirolamo, 1996; Richter, et al., 2000; Tagaris, Kim, Strupp, & Andersen, 1996, 1997) or (potentially in part due to the spatial proximity of these areas) within the intraparietal sulcus (IPS; e.g., Carpenter, Just, Keller, Eddy, & Thulborn, 1999; Ecker, Brammer, David, & Williams, 2006; Harris, et al., 2000; Jordan, Heinze, Lutz, Kanowski, & Jäncke, 2001; Milivojevic, Hamm, & Corballis, 2009). Only few studies found rotation-specific activation centered in inferior parietal regions (e.g., Alivisatos & Petrides, 1997). There are single reports of left (e.g., Alivisatos & Petrides, 1997; Ecker, et al., 2006) or right (e.g., Harris, et al., 2000) lateralization, whereas usually activation is bilateral (e.g., Carpenter, et al., 1999; M. S. Cohen, et al., 1996; Jordan, et al., 2001; Milivojevic, et al., 2009; Richter, et al., 2000; Tagaris, et al., 1996, 1997). Accordingly, in Zacks' (2008) meta-analysis rotation-specific activation emerges bilaterally and centered within the intraparietal sulcus. From there, the activation extends into the several adjacent areas, including Brodmann's areas (BAs) 7, 19, 39, and 40.

The parietal cortex contains most of the dorsal pathway (see Chapter 1.5.2). This pathway is crucial for processing the spatial, action-relevant aspects of visually encoded information (e.g., Goodale & Milner, 1992; for a recent review, see Milner & Goodale, 2008). Parietal cortex is assumed to code location in motor coordinates (for a review, see Colby & Goldberg, 1999). With such a space representation the (posterior) parietal cortex might provide sensory-motor integration, including the formation of high-level movement intentions (for a review, see Andersen & Buneo, 2002).

The sulcus lying in between the inferior and superior parietal cortex can be subdivided into the anterior and posterior intraparietal sulcus. The anterior part is involved in grasping, manual modeling and tactile exploration of three-dimensional objects (Binkofski, et al., 1998; Jäncke, Kleinschmidt, Mirzazade, Shah, & Freund, 2001). Temporarily inactivating this area in monkeys impedes the shaping of the contralateral hand in preparation for grasping an object. This indicates a role of the anterior intraparietal sulcus in the guidance of goal-directed hand movements (Gallese, Murata, Kaseda, & Niki, 1994). In line with this finding Jäncke et al. (2001) collected evidence that the anterior intraparietal sulcus in humans is involved in complex object-oriented hand movements, like modeling and exploring an object. The specific function of the anterior intraparietal sulcus purportedly is to coordinate object-related hand movements (Jäncke, et al., 2001). Several lines of evidence (for a review, see Jäncke, et al., 2001) indicate that the posterior intraparietal sulcus is a supra-modal integration center, holding an action-oriented object representation which provides input to the anterior intraparietal sulcus.

Activation in the superior parietal lobule depends on the location of a preceding stimulus, but not on subsequent eye or arm movements. Consequently, this activity might constitute a (transient) working memory trace of the preceding stimulus' location (Steinmetz, 1998; see also Chapter 6.1.4.). Apparently, the left superior parietal lobule processes mainly categorical spatial relations whereas the right superior parietal lobule processes mainly coordinate (continual) spatial relations (Trojano, et al., 2002). In another study, the left inferior and the right superior parietal lobule were preferentially active during processing of coordinate (continual) spatial relations whereas parietal involvement in the processing of categorical spatial relations was less conclusive (Kosslyn, Thompson, Gitelman, & Alpert, 1998).

In sum, the parietal cortex is obviously involved in the processing and maintenance of spatial information and also plays a role in object recognition and action planning. Among other functions, the parietal cortex might hold a spatial representation of objects and their locations which is employed to plan and execute manipulations of the respective objects (cf., e.g., Milner & Goodale, 2008). Indeed, the parietal cortex is active only when participants observe object-related actions and not when they observe object unrelated actions (Buccino, et al., 2001, see also Chapter 6.1.3.). As detailed below (Chapter 3.3), the present work aims to demonstrate that mental rotation works on a representation of purely spatial, relational information. The superior parietal cortex and intraparietal sulcus appear likely candidates for holding such a representation.

1.6.2 Motor system

In most mental rotation studies, rotation-specific activation is found in the bilateral dorsolateral premotor cortex (pMd; e.g., Ecker, et al., 2006; Milivojevic, et al., 2009; Richter, et al., 2000; Seurinck, de Lange, Achten, & Vingerhoets, 2011; Windischberger, Lamm, Bauer, & Moser, 2003) resulting in a clear activation of these areas in Zacks' (2008) meta-analysis. Importantly, Carpenter et al. (1999) have shown that this premotor activation is not due to the planning or performance of saccades, as it persists even when the control task induces much more saccades than the mental-rotation task itself (see also, e.g., Vanrie, Béatse, Wagemans, Sunaert, & Van Hecke, 2002). Premotor cortex is related to motor planning and execution (for a review, see Picard & Strick, 2001). During motor imagination premotor cortex is even more active than during motor performance (Gerardin, et al., 2000). Consequently, premotor activity in mental-rotation tasks might reflect motor imagination of performing the rotation (Zacks, 2008). Mental rotation is indeed at least in part guided by motor processes, as indicated by strong influences of concurrently performed manual rotations on mental rotation performance (Wexler, Kosslyn, & Berthoz, 1998; Wohlschläger & Wohlschläger, 1998). Already planning a manual rotation into a direction opposite to a mental rotation that is performed before the motor plan is executed impedes mental rotation (Wohlschläger, 2001). Participants purportedly employ cortical regions for mental rotation that are usually responsible for planning movements and two concurrently planned but incompatible rotations interfere even if one is manual and the other mental.

Some authors went one step further and reasoned that mental rotation might actually be performed in the primary motor cortex which directly controls the performance of voluntary movements. This speculation was unleashed by single-cell recordings in monkey primary motor cortex. While monkeys performed a task which presumably involves mental rotation, the firing pattern of orientation-specific neurons in primary motor cortex behaved as if the rotation was performed manually (but see Cisek & Scott, 1999; Georgopoulos, Lurito, Petrides, & Schwartz, 1989; Lurito, Georgakopoulos, & Georgopoulos, 1991). In humans, the left primary cortex is activated more strongly during the rotation of hand stimuli (see Figure 1.2D) compared with the rotation of objects (Kosslyn, Digirolamo, Thompson, & Alpert, 1998; but see Parsons, Fox, Downs, & Glass, 1995; Vingerhoets, de Lange, Vandemaele, Deblaere, & Achten, 2002). This activation, however, might simply reflect the fact that participants see hands or compare hand-stimuli to their own hands and not necessarily that their primary motor cortex is involved in mental rotation proper.

It consequently is of interest that participants, at times, apparently employ a strategy of imagining the use of their dominant hand for the rotation of objects. Activation in right-handed subjects' left primary motor cortex should be higher when they employ this 'motor' strategy compared with a 'nonmotor' strategy. Kosslyn and colleagues claim to have found such evidence in two experiments in which they manipulated the strategy of their participants. This was achieved by instructions (Kosslyn, Thompson, Wraga, & Alpert, 2001) and by preliminary blocks of trials in which participants mentally rotated drawings of hands and which apparently primed a 'motor' strategy for the subsequent block of object rotation trials (Wraga, Thompson, Alpert, & Kosslyn, 2003). However, as already mentioned by Zacks (2008) the stereotactic coordinates of activation which according to Kosslyn et al. (2001) lie within the primary cortex actually lie within the premotor cortex. Wraga et al. themselves mention that the focus of activation they found lies at the border of premotor and primary motor cortex (the stereotactic coordinates given by Wraga et al. also more probably lie within premotor cortex, although admittedly, rather close to primary motor cortex). Only the activity elicited by the rotation of hand stimuli as reported by Kosslyn et al. (1998) reliably lies within primary motor cortex. However, other studies did neither find activation in primary motor cortex for the rotation of hand stimuli (Parsons, et al., 1995) nor higher activation in this area for rotation of hand stimuli compared with rotation of alphanumeric characters (de Lange, Hagoort, & Toni, 2005) or tools (Vingerhoets, et al., 2002). Consequently, there is no evidence so far that the rotation of objects activates human primary motor cortex and the evidence for such an effect by drawings of body parts is at best inconsistent. Primary motor cortex activation as found in many other studies is apparently due to the motor affordances of the button press which is given at the end of each mental rotation trial (see de Lange, et al., 2005; Ecker, et al., 2006; Richter, et al., 2000; Windischberger, et al., 2003).

The clear left lateralization found in the studies by Kosslyn and colleagues (Kosslyn, Digirolamo, et al., 1998; Kosslyn, et al., 2001; Wraga, et al., 2003) remains interesting, however, because it still indicates that under certain conditions participants might employ an alternative motor imagery strategy biased to their dominant hand. In contrast, as reported above (beginning of this chapter), the consistently observed premotor activation during the mental rotation of objects, usually emerges bilaterally, indicating a strategy not biased to either side (e.g., Ecker, et al., 2006; Richter, et al., 2000; Seurinck, et al., 2011; Windischberger, et al., 2003; but see, e.g., Vingerhoets, et al., 2002).

1.6.3 Mirror-neuron areas

Although bilateral inferior-frontal cortex, mainly BA 44/45/46, is consistently activated in a rotation-specific manner (Zacks, 2008), this activation is seldom discussed (for an exception, see Hugdahl, Thomsen, & Ersland, 2006). Left BA 44/45 (Broca's area) is widely considered to be related to speech motor processes (Poldrack, et al., 1999). Left BA 44 was also found active in an object working-memory task that required mirror-image discrimination, but no mental rotation (Mecklinger, Gruenewald, Besson, Magnié, & Von Cramon, 2002). Hughdahl et al. (2006) as well as Mecklinger et al. (2002) interpret the activation in BA 44/45 as subvocal rehearsal or 'inner speech' in the absence of verbal material. This use of verbal working memory purportedly assists the primary working-memory system involved in these tasks. Indeed, bilateral, slightly left-lateralized BA 44/45 activity is usually observed during verbal working-memory tasks as well (e.g., Paulesu, Frith, & Frackowiak, 1993; Wager & Smith, 2003; see also J. D. Cohen, Perlstein, Braver, & Nystrom, 1997).

An alternative interpretation derives from the fact that also premotor and parietal areas are active during mental-rotation tasks. Bilateral BA 44/45 and the inferior parietal lobule including the intraparietal sulcus are considered the two major regions of the human mirror-neuron system. In addition, dorsolateral premotor cortex and superior parietal lobule were also found active during action observation (for reviews, see, e.g., Rizzolatti & Craighero, 2004; Rizzolatti & Sinigaglia, 2010). As reported above (Chapter 1.6.1), the parietal cortex seems to hold the representation of an object that is manipulated, whereas premotor regions represent the action on the object (Buccino, et al., 2001). Buccino et al. (2001) showed object-related or object-unrelated hand, mouth and foot actions to their participants and measured the neuronal response via fMRI. A comparison of activation in Buccino et al.'s study and Zacks' (2008) meta-analysis indicates that similar regions are active during mental rotation and the observation of object-related hand actions. Bilateral activation of BA 44/45 as well as dorsolateral premotor and parietal cortex might consequently be due to an involvement of the mirror-neuron system for object-related hand actions in mental rotation (cf. Milivojevic, et al., 2009).

1.6.4 Spatial working memory areas

Interestingly, a very similar cortical activation pattern is well-established for working memory (for a meta-analysis, see Wager & Smith, 2003), especially for spatial working-memory tasks (for a review, see Ikkai & Curtis, 2011). Similar to mental rotation, areas consistently found activated in spatial working-memory tasks include the dorsolateral premotor cortex, the inferior precentral sulcus (identical or close to BA 44/45), the intraparietal sulcus, and the transverse parietal sulcus (within the superior parietal lobule; see also, Srimal & Curtis, 2008). The same regions are also found active during tests of spatial attention and motor intention (Ikkai & Curtis, 2011). Dorsolateral premotor cortex and BA 44 contain the superior and inferior frontal eye field which, besides the control of saccadic eye movement, apparently are involved in allocation of spatial attention and in spatial working memory (Kastner, et al., 2007). These findings are consequently in line with the assumptions of allocation of spatial attention as a rehearsal mechanism in spatial working memory (Awh, et al., 1999) and the finding that saccade execution is influenced by spatial working-memory load (Theeuwes, Olivers, & Chizk, 2005). Superior and inferior frontal eye fields as well as many parietal areas, especially the intraparietal sulcus are topographically organized (Silver & Kastner, 2009) and thereby ideally suited for the representation of spatial information.

As already reasoned based on a theoretical comparison (Chapter 1.4), mental rotation might be a spatial working memory function and work on purely spatial information. This speculation is further strengthened by the large overlap in cortical areas active during spatial working memory and mental-rotation tasks (cf. Jordan, et al., 2001). However, mental rotation obviously is more complex than simple working-memory tasks which require only the passive storage of information (see Chapter 1.5). This might explain why brain injury can lead to specific problems in mental rotation and other imagery tasks while performance in passive visuo-spatial working-memory tasks remains intact (Morton & Morris, 1995).

1.6.5 Visual system

Some mental rotation studies found rotation-specific activation in BA 19 (e.g., Barnes, et al., 2000; M. S. Cohen, et al., 1996; Kosslyn, Digirolamo, et al., 1998). One highly plausible candidate for the mental rotation network that lies within BA 19 is the visual motion area (V5/MT; Barnes, et al., 2000; M. S. Cohen, et al., 1996; Vanrie, et al., 2002). This area is functionally relevant for the perception of motion (for reviews, see Silverman, Grossman, Galetta, & Liu, 1995; van Wezel & Britten, 2002) and also responds to apparent motion (Goebel, Khorram-Sefat, Muckli, Hacker, & Singer, 1998; Liu, Slotnick, & Yantis, 2004; Muckli, et al., 2002). As mental rotation actually is the imagery of one special type of motion, Cooper & Shepard (1982) reasoned that mental rotation and apparent motion might be driven by the same (perceptual) processes (see also Shepard & Judd, 1976). In line with this assumption, mental rotation is influenced by a concurrent motion aftereffect. Watching a disc rotating induces a subsequent illusion of a rotation into the opposite direction. This aftereffect accelerates mental rotation into the same and decelerates mental rotation into the opposite direction (Corballis & McLaren, 1982; Heil, Bajrič, Rösler, & Hennighausen, 1997). V5/MT indeed shows rotation-specific increases in activation in some studies (M. S. Cohen, et al., 1996; de Lange, et al., 2005; Seurinck, et al., 2011), although not in others (Ecker, et al., 2006; Jordan, et al., 2001). In a direct test of this hypothesis, Barnes et al. (2000), however, found no rotation-specific activation in V5/MT. Instead they found such activation in a satellite region of V5/MT within the inferior temporal sulcus. The inferior temporal lobe, including the fusiform gyrus (BA 37) also showed rotation-specific activation in other studies (e.g., Carpenter, et al., 1999). The increase in V5/MT activation with rotational angle might however stem from attempts to recognize disoriented stimuli (Gauthier, et al., 2002) and not from mental rotation proper.

Under certain conditions, retinotopic areas in early visual cortex can be activated via feedback from higher visual areas, as for example, during visual imagery (Slotnick, Thompson, & Kosslyn, 2005) and during apparent motion perception (but see Liu, et al., 2004; Sterzer, Haynes, & Rees, 2006). Comparing mental rotation to a loose fixation baseline Ecker et al. (2006) found activation in several visual areas, including early visual (BA 17/18/19), and inferotemporal areas (BA 37, including fusiform gyrus). However, the time-courses of the haemodynamic response functions (HRFs) in these areas depended on the duration of stimulus presentation and not on rotation time, indicating that activation in these areas was not related-to mental rotation proper. Similarly, Jordan et al. (2001) reason that the activation they observed in striate and extrastriate areas, including the fusiform gyrus, reflects the visual processing of stimuli in mental-rotation tasks. Apparently, mental rotation proper does not involve early visual areas. This lack of early visual involvement in mental rotation speaks against the common assumption of visual mental representations in mental rotation (see Chapter 3.1).

1.7 Examining the Process of Mental Rotation via EEG

A close relationship has been established between the process of mental rotation and an event-related potential (ERP) component peaking over the parietal cortex at electrode site Pz. This component has been observed in two different shapes. In one comprehensive review of ERPs in single-stimulus mental-rotation tasks with alphanumeric characters (*character-rotation tasks*, cf. Figure 1.1 and Figure 1.2C), Heil (2002) describes this component as short-lasting (phasic) and with a positive peak around 350-700 ms after stimulus onset (see also, e.g., Bajrič, Rösler, Heil, & Hennighausen, 1999; Gootjes, Bruggeling, Magnée, & Van Strien, 2008; Heil, Rauch, & Hennighausen, 1998; Heil & Rolke, 2002; Núñez-Peña & Aznar-Casanova, 2009; Peronnet & Farah, 1989; Riečanský & Jagla, 2008; Rösler, Schumacher, & Sojka, 1990; Wijers, Otten, Feenstra, & Mulder, 1989). The topography and timing of this component are in the range of another component known as P3b (cf., e.g., Chapter 3.7.4). The P3b is usually elicited by task-relevant stimuli (for recent reviews, see Nieuwenhuis, Aston-Jones, & Cohen, 2005; Polich, 2007; Verleger, 1997, see also Experiment 2). The less expected a stimulus is, the larger the P3b amplitude it elicits (e.g., R. Johnson & Donchin, 1980; Mars, et al., 2008). However, in character-rotation tasks the amplitude of this positive component becomes smaller as the character's tilt increases. As this decrease in amplitude is not explainable by factors that typically influence the P3b in other tasks, it is often assumed that a negative slow potential temporarily overlaps with the P3b. This component and not the P3b itself becomes more negative as more rotation is required.

Another shape of this component has been reported by Rösler, Heil, Bajric and Pauls (for similar ERPs see Röder, et al., 1997; 1995; Rösler, Röder, Heil, & Hennighausen, 1993; Ruchkin, Johnson, Canoune, & Ritter, 1991; Wegesin, 1998). In this study, a star with distinguishable points had to be rotated into an orientation indicated by an acoustic rotation cue. The resulting mental representation had then to be compared to a subsequently presented comparison stimulus. Rösler et al. found a negative slow potential that lasted from 1 s until 9 s after the acoustic cue (the time point after which rotation could start). This component, too, increased in amplitude along with the rotational angle. There is accumulating evidence that slow potentials of this kind reflect the topography and intensity of cortical activation (Khader, Schicke, Röder, & Rösler, 2008; Rösler, Heil, & Röder, 1997), which is why they are frequently interpreted as a correlate of the mental effort allocated to a particular task. In comparison to the short-lasting component (Heil, 2002), this slow potential has a later onset and a longer duration.

The circumstances under which this rotation-related component takes the one or the other shape remain unknown. According to our classification of mental-rotation tasks (Chapter 1.3), the tasks reviewed by Heil (2002) are single-stimulus mental-rotation tasks whereas those like the one employed by Rösler et al. (1995) are successive-presentation tasks with a rotation cue. Furthermore, the former tasks usually employ alphanumeric characters whereas the latter tasks usually employ pre-experimentally unknown stimuli. If the different shapes of the component are due to differences between the tasks (and not due to the stimuli), angle-dependent late-onset and long-lasting slow potentials (Rösler, et al., 1995) should be observed in a successive-presentation task with rotation cues even when alphanumeric characters are employed as stimuli. If the different shapes are due to the different stimuli, an angle-dependent short-lasting component (Heil, 2002) should be observed whenever alphanumeric characters are employed even in a successive-presentation task with rotation cues.

In an experiment with blind-folded sighted and blind participants and a haptic presentation mode, Rösler et al. (1993) indeed found an angle-dependent slow potential similar to the one observed by Rösler et al. (1995) in a successive-presentation task with alphanumeric stimuli but without rotation cue (see Chapter 1.3.3). The component with maximum effect size at Pz and P4 was not embedded into a P3b but clearly inside the negative voltage range, did not start until 1 s after onset of the rotation probe and lasted much longer than the component in the studies reviewed by Heil (2002). It therefore appears possible that the critical aspect of the task that determines the shape of the mental rotation component is whether comparisons must be made between two representations held in working memory or between a tilted stimulus and its long-term memory entry. For example, the former of these two possibilities may be based on a more detailed representation. However, in an EEG study that employed visually presented alphanumeric characters in a successive-presentation mental-rotation task without rotation cue (Rösler, et al., 1990) the observed angle-dependent component was very similar in shape to that found when a single character is shown (Heil, 2002).

Possibly, concerning mental rotation, the critical stimulus characteristic of alphanumeric characters is that they are two-dimensional and relatively simple. This simplicity might be lost in a haptic presentation mode. Critically, also the stimuli employed in the main experiments of the present work, as reported below (see Figure 3.4), are two-dimensional and relatively simple. In order to find out whether the task or stimulus characteristics determine the shape of the rotation-related component, and consequently which shape we would expect in the successive-presentation mental-rotation task employed in Experiments 1a, 1b, 2 and 3, we conducted a preliminary mental-rotation EEG study. Along with doing so, we aimed to add to the knowledge about the process of mental rotation as detailed in the following.

2. Preliminary Experiment—An Effect of Rotational Direction[2]

In character-rotation tasks (i.e., single-stimulus mental-rotation tasks with alphanumeric characters, see Chapter 1.3.2) participants decide whether a disoriented character is presented in its normal or mirrored version—they judge its handedness. Similar to all other mental-rotation tasks, the typical result observed in character-rotation tasks is a monotonic increase in response times with the character's angular deviation from upright (the typical mental-rotation effect). Response times increase up to a character tilt of 180° and decrease for larger angles. The peak of response times at 180° is thought to indicate that participants usually rotate the character along the shortest path into its upright position. Participants are therefore obviously able to rotate in a clockwise (CW) as well as in a counterclockwise (CCW) direction. In the follow-

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[2] This chapter is an adapted version of Liesefeld and Zimmer (2011).

ing, we will indicate tilts to the left with negative numbers, e.g., -120° and tilts to the right with positive numbers, e.g., +120° (see Figure 2.1). If CW and CCW rotations are equally fast, the function relating response times to the character tilt and therefore to the amount of mental rotation should be symmetrical with its peak and axis of reflection at 180°, that means the slope for CW and CCW rotations should be the same. This is the result found in most studies employing the character-rotation task (see, e.g., Cooper & Shepard, 1973; Shepard & Cooper, 1982).

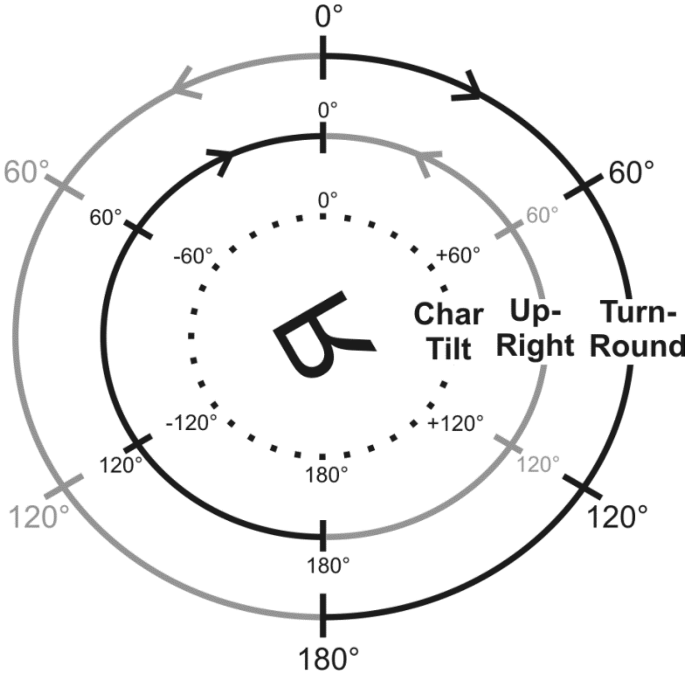

Figure 2.1. *An illustration of the denominations for character (Char) tilts and the two strategies. The dotted circle indicates the character's tilt. Negative angles stand for tilts to the left and positive angles for tilts to the right. The mirrored R is tilted -120° as an example. The solid circles indicate the amount of rotation that has to be performed if a character is "up-righted" from (middle circle) or "turned-round" into (outer circle) a given tilt. The arrows indicate the respective direction of rotation. CW rotations are additionally indicated by black semi-circles and CCW rotations by grey semi-circles.*

However, discrepant results have also been reported. Koriat and Norman (1985a) showed one such asymmetry. In their experiment, participants took considerably longer to judge the handedness of characters tilted +120° than characters tilted -120°. Here, the reader should note that characters tilted to the left (negative angles) have to be mentally rotated CW to reach an upright position. Based on this upright representation a decision about the character's handedness can be made. The reverse applies with characters tilted to the right (see the inner circle of Figure 2.1). Hence, these results indicate that rotations take longer in a CCW than in a CW direction. In a further experiment, Koriat and Norman (1985b) again observed a similar asymmetry, this time for the recognition of tilted Hebrew words. An effect of direction of character tilt was also found by Robertson and Palmer (1983). They investigated the rotation of global and local structure by using large letters made of small ones in a character-rotation task. On each trial participants had to determine whether the letters at either one of the two levels were normal (rather than mirrored) versions. Although the distinction between global and local structure is not important for the present experiment, an ancillary result of this study is interesting: When the global letters were presented in their normal version, response times were markedly longer for stimuli tilted +120° (apparently causing CCW rotation) compared to stimuli tilted -120° (CW rotation). However, additional findings (including those from within the same studies) challenge the assumption of the superiority of CW rotation. When Robertson and Palmer (1983) showed mirror-reversed global letters, response times were shorter for tilts of +120° (CCW rotation) compared to -120° (CW rotation). In addition, in two further experiments by Koriat and Norman (1985a) no asymmetry was observed, and where the effect was observed it appeared only for normal versions of characters. The inconsistency of these results as well as the outcomes from the many studies with similar designs that do not observe any asymmetry (e.g., the seminal work of Cooper & Shepard, 1973), prompts the question as to whether such an effect of the direction of rotation really exists and how it could be demonstrated more clearly. As we assume that variations in participants' strategies in character-rotation tasks cause these inconsistencies across experiments, we now turn to an examination of these strategies.

In character-rotation tasks, there are two potential strategies for determining the handedness of a character. On the one hand, participants may build a mental representation of the presented character and then mentally rotate this representation into an upright orientation—participants “right the character” (see the middle circle of Figure 2.1 and Figure 2.2A). This upright representation can then be compared directly to the respective long-term memory entry. This is the common account for the results of character-rotation tasks. If participants use this strategy, characters tilted to the right are rotated CCW and characters tilted to the left are rotated CW. On the other hand, participants may identify the tilted character and build a mental representation of this character in its canonical upright orientation (by accessing the respective long-term memory entry). They then rotate this representation to bring it into congruence with the presented character (they “turn it round”; see outer circle of Figure 2.1 and Figure 2.2B). Diametrically opposed to the first strategy, characters tilted to the right would elicit CW and those tilted to the left would elicit CCW rotations. In the following, we call these two strategies *up-right* and *turn-round*, respectively. Strategy turn-round is possible only if one can identify the stimulus and its orientation without the need for rotation. Participants are usually able to identify stimuli without rotation after a number of trials (see, e.g., Jolicoeur, et al., 1987) and once this is achieved, identification of orientation should be unproblematic. Furthermore, most researchers (implicitly) assume a turn-round-strategy for paradigms involving the mental rotation of human hands (e.g., Cooper & Shepard, 1975; Ionta & Blanke, 2009; Ionta, Fourkas, Fiorio, & Aglioti, 2007; Parsons, 1994; Sekiyama, 1982). If, as we will show, rotation in a CW direction is easier than in a CCW direction, using a mixture of both strategies would be advantageous in solving mental-rotation tasks. Strategy up-right would be easier whenever the character is tilted to the left, because for negative tilts the representation of the character has to be rotated in CW direction to make it up-right. Strategy turn-round, in contrast, should be more efficient for characters tilted to the right—the representation generated from long-term memory needs rotation in CW direction to align it with the presented stimulus. The relationship between these strategies (up-right vs. turn-round), the directions of character tilt (to the left/negative vs. to the right/positive) and the direction of rotation (CW vs. CCW) are depicted in Figure 2.1. The two strategies are illustrated in Figure 2.2.

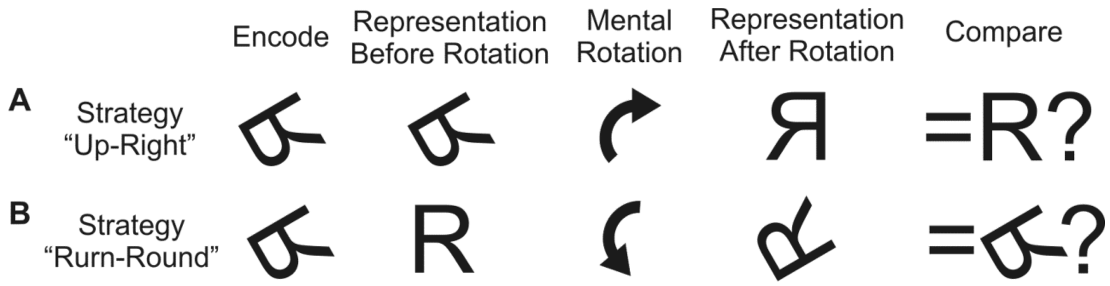

Figure 2.2. *Illustration of the two possible strategies in character-rotation tasks. Both (A) rotating the perceived character into the canonical orientation (to make it "up-right") and (B) rotating a canonical version into the orientation of the presented character (to "turn it round") can lead to the correct decision.*

If participants in character-rotation tasks systematically use both strategies, that is, if they use strategy up-right for characters tilted to the left and strategy turn-round for characters tilted to the right, they can avoid performing any CCW rotation at all. In this case, the function relating response times to the angle of tilt would be the same for characters tilted to the right and those tilted to the left—the result observed by (among many others) Cooper and Shepard (1973). The likelihood of such an efficient strategy might increase with the amount of practice. The eventual ratio of strategies may also depend on the participants' personal preferences, on details of the instructions or on some other arbitrary cues of the experimental context. For example, asking participants explicitly to rotate the tilted character into its canonical orientation should increase the frequency of up-right rotations. In short, the problem is that in the common character-rotation task participants are free to select their strategy and to change it from one trial to the next. The resulting variance in strategy use across experiments could explain why the effect of rotational direction is observed so unreliably.

The most clear-cut way to overcome this problem and to examine effects of rotational direction is to develop a task in which the experimenter can control the rotation strategies participants might use. In such a task, the direction of tilt would directly determine the direction of rotation. This has been inadvertently achieved by one version of Cooper and Shepard (1973)'s character-rotation tasks. Participants initially saw a cue that indicated the identity of the upcoming character (an outline drawing of the normal, upright version of the character;

the original stimulus in terms of the present work). Following this stimulus, an arrow (a rotation cue) indicated the tilt of the upcoming character. After a variable amount of time, the character on which the handedness decision had to be given was shown. Whenever participants had sufficient time (1 s) to prepare for the upcoming critical character, the mental rotation effect on response times to this character was abolished. In contrast, the less time was given for preparation, the greater the effect of character tilt, that is, a mental rotation effect, evolved. It is assumed that during the 1 s of preparation, participants had mentally rotated a representation of the original stimulus into the indicated orientation. When the second character was presented they simply had to compare it to the mental representation they had created in advance. For shorter preparation times, however, participants were unable to finish the rotation and therefore had to continue or even restart the rotation after the appearance of the second character. That means by shortening preparation times the task was effectively transformed from a successive-presentation task with rotation cue into a single-stimulus task (see Chapter 1.3). Importantly, whilst preparing, participants could not choose between strategies up-right and turn-round. Only strategy turn-round was possible, because during the preparation period, only an upright oriented character was available and participants prepared for a comparison with a tilted character (the comparison character).

We employed this task with two major changes in order to circumvent two additional problems. Firstly, whenever CW rotations are to be performed, comparison characters are tilted to the right. Correspondingly, CCW rotations always occur with comparison characters that are tilted to the left (see Figure 2.3b). To avoid this possible confound we operationalized not only strategy turn-round, but also strategy up-right (see Figure 2.3a). Strategy up-right is induced here by presenting the original character tilted and the comparison character upright. Consequentially, in the latter strategy condition, a CW rotation is necessary for original characters that are tilted to the left and vice versa a CCW rotation for original characters that are tilted to the right. According to the strategy that is induced, in the following, we call the two strategy conditions *turn-round* and *up-right*, respectively. Only if we find the same effect of rotational direction in both strategy conditions, can we be assured that effects of rotational direction do not stem from the direction of the tilt of either the original or the comparison character. If, on the other hand, an effect of rotational direction emerges only in one of the two strategy conditions, it must be due to the tilt of the original character or the tilt of the comparison character. We expect to find similar effects of rotational direction in both strategy conditions, because we assume that the direction of rotation is critical.

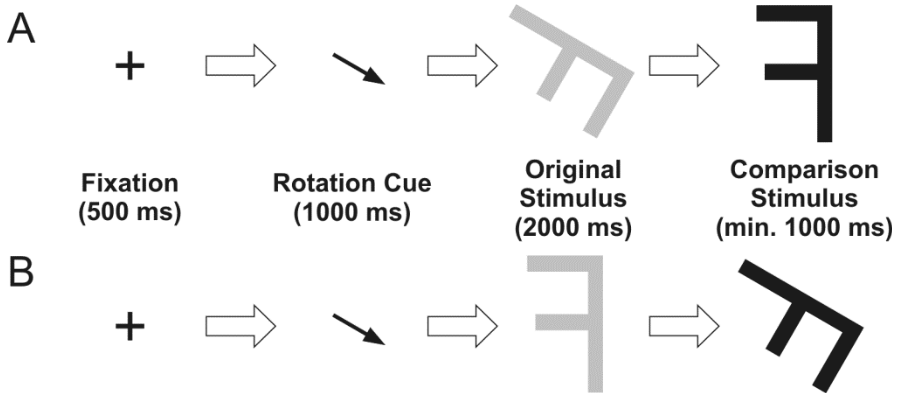

Figure 2.3. *The trial sequence of the two strategy conditions (A) up-right and (B) turn-round, trials with 120° tilts. Both examples show mismatches. There were blank intervals of 750 ms duration between adjacent displays.*

The second change of the task procedure came about as a consequence of the up-right strategy condition. Cooper and Shepard (1973) instructed their participants to determine the second character's handedness. In the strategy condition up-right, it is possible to judge the handedness of the comparison character simply by comparing it to the representation of its prototype in long-term memory. To prevent the use of this strategy, we asked participants to decide if the original character's handedness matches the handedness of the comparison character. In this new version of the task, a mirror-reversed character could also be a matching comparison stimulus. A mismatch trial would be one in which the comparison character has the specified orientation but a different handedness than the original character. It is therefore always necessary to mentally rotate the original character in order to be prepared for its comparison with the comparison character. Participants' task was always to match the result of the mental rotation with the comparison character. Note that, compared to a usual character-rotation task, the mental rotation time window has moved to the point in time when both information about the rotational angle and the original character is available, that is, to the preparation period. When the comparison character appears (and response times are recorded), mental rotation is assumed to be already completed. That means, the time from onset of the comparison character to the participants' key press does not reflect mental rotation, but only the comparison process. The latency of this key press therefore does not reflect *rotation time*, but merely *comparison time*.

In summary, the logic is as follows. On the basis of Koriat and Norman's results (1985a) we conclude that mental rotation of characters in a CW direction is easier than in a CCW direction. We assume that the reason for the irregular emergence of this effect is that two different strategies can be employed to solve the usual character-rotation task and that studies vary in the extent to which these strategies are used. If participants' strategies can be brought under experimental control, it should be possible to observe consistent effects of rotational direction. For that purpose we developed a new character-rotation task. Participants were required to mentally rotate one character (the original character) into a specific orientation and to compare the result of this rotation process to a subsequently presented comparison character. We conducted this experiment under two strategy conditions—the to-be-rotated original character was shown either upright or tilted, and correspondingly the comparison character was shown tilted or upright. By running both strategy conditions, we were able to test for the alternative hypotheses that any effect of direction is due to the tilt of either the original or the comparison character. As the dependent variable of interest, we measured ERPs at parietal electrode sites during the period in which we assumed rotation would take place. The amplitude of the component taken to reflect mental rotation should depend on the amount of rotation in a given trial. This component should be most prominent at Pz and take one of two alternative shapes as described in detail above (Chapter 1.7). It should either manifest itself as a short-lasting amplitude modulation of a P3b or as a long-lasting negative slow potential. Additionally and critically, we expected the amplitude of this component to be more negative for CCW than for CW rotations in both strategy conditions, because the relative negativity should indicate increases in effort.

2.1 Methods

2.1.1 Participants

Sixteen paid volunteers recruited from Saarland University received €8 per hour for participation. They gave written informed consent after the nature of the study had been explained to them. Participants were unaware of the hypothesis being tested and had no prior experience with the task. Data from two participants had to be discarded. One participant constantly gave the wrong answer for rotational angles of 180° (we return to this issue in the general discussion, Chapter 8.7.4). The second participant had excessively long comparison times (more than 1 ½ times the interquartile difference above the group mean). The final sample comprised 14 participants, seven men and seven women. They were between 20 and 31 years of age (mean: 23.8). According to their self-report, all had normal or corrected-to-normal vision and, with the exception of one, all participants were right-handed.

2.1.2 Stimuli

The stimuli presented were alphanumeric characters printed in Arial Narrow font, approximately 2.5° of visual angle in height (viewing distance of about 75 cm). As stimulus-specific learning effects in mental rotation experiments have been reported previously (D. Cohen & Kubovy, 1993), we tried to minimize this influence on our experimental within-factor *strategy condition*. To achieve this, three separate stimulus sets were used, one for the training phase and one for each of the two strategy conditions (up-right vs. turn-round). The sets for the strategy conditions were: G, J, R, k, 2, 5 and F, P, Q, h, 4, 7. For practice trials L, f, t and 1 were employed. The assignment of stimulus sets to the strategy conditions was counterbalanced across participants. The original character in each trial was displayed in gray whereas the comparison character was black. Stimulus timing and collection of behavioral data was controlled by E-Prime 2.0 (Psychology Software Tools, 2005).

2.1.3 Design

We ran two strategy conditions: In strategy condition *up-right* participants initially saw a tilted original character, which they mentally rotated into its upright form (they "made it upright") to prepare for a comparison with the upcoming comparison character. Accordingly, the comparison character in strategy condition up-right was always presented upright. The orientation of the original character was indicated by an arrow preceding the presentation of the character. In strategy condition *turn-round* the original character was always presented upright. It was also preceded by an arrow which indicated the orientation the character had to be rotated into. The original character had to be "turned-round", because the comparison character in strategy condition turn-round was presented in the orientation indicated by the arrow. When no rotation was necessary (because both characters were presented upright), the arrow preceding the original character pointed upwards. Figure 2.3 schematically illustrates the two strategy conditions. In both strategy conditions, participants' task was to indicate, whether the two characters were the same or mirror versions of each other. Participants were instructed that only the match between the result of the mental rotation of the original and the comparison character was relevant, making a decision based solely on the comparison character impossible. Half of the participants pressed a key on the right side of an external response box for *match* with their right index finger and one on the left side for *mismatch* with their left index finger. The remaining participants had the reversed assignment of response buttons. The strategy conditions (up-right vs. turn-round) were blocked and the order of the two blocks was counterbalanced across subjects.

We implemented five character tilts: +60°, +120°, 180°, -120° and -60° (cf. Figure 2.1). Trials in which both characters were presented upright and which therefore required no rotation are subsequently referred to as 0°. The experiment was run with all possible within-subject factor combinations by drawing randomly without replacement at runtime from a 6 (character tilt) × 6 (character identity) × 2 (original character version) × 2 (match) list. Each participant was presented with the counterbalanced list twice per strategy condition (up-right vs. turn-round). As we expected character identity, original character version and match not to influence the rotation itself, this amounts to 48 trials per relevant cell in a 6 (character tilt) × 2 (strategy condition)-design. Direction of rotation (CW vs. CCW) can, of course, only be defined for absolute rotational angles of 60° and 120°, namely, -60° and -120° tilts demand CW rotations in strategy condition up-right and CCW rotations in condition turn-round; +60° and +120° tilts demand CCW rotations in up-right- and CW rotations in turn-round trials (see Figure 2.1). It is unclear why participants failed on trials with erroneous answers, so only correct trials were included into the analysis. As error rates tend to increase with rotational angle in mental-rotation tasks, this would lead to (nonrandomly) less observations per cell for higher rotational angles. Therefore, erroneous trials were rescheduled (with their order determined randomly) at the end of each block without any apparent break between regular and rescheduled trials. As a result, for each cell the number of trials included into the analysis was independent of the cell's difficulty.

2.1.4 Procedure

Each trial started with a fixation-cross that appeared in the center of the screen for 500 ms. 750 ms after its offset, an arrow indicating either the orientation of the upcoming original character (up-right) or the orientation the character had to be rotated into (turn-round) was presented for 1000 ms. Another 750 ms after the offset of the arrow the original character was presented for 2000 ms. The original character was switched off and 750 ms later the comparison character appeared. The trial was terminated by the participant's answer, but the comparison character remained on the screen for at least 1000 ms to ensure that the stimulus offset did not confound the EEG (see Figure 2.3). All stimuli were presented centrally. Trials were separated by intervals jittered between 1 s and 3 s in 100 ms steps.

Participants were encouraged to focus on a high accuracy rate, while the speed of responses was secondary. After every 12th trial there was a break, during which participants were informed about their cumulative percent correct and their mean comparison times on correct trials. The participants themselves terminated the break, which lasted for at least 5 s. Before the regular trials of each block started, participants practiced the task. The practice phase ended and the regular trials started as soon as the participant had given 12 correct answers in a row (irrespective of any breaks in between).

2.1.5 EEG recording, artifacts handling and signal extraction

The EEG was collected by Ag/AgCl-electrodes at frontal (F3, Fz, F4), central (C3, Cz, C4), parietal (P3, Pz, P4) and occipital (O1, Oz, O2) sites according to the extended 10/20 system, amplified with BrainAmp DCs (Brain Products), recorded with BrainVision Recorder 1.03 (Brain Products, 2007) and analyzed with BrainVision Analyzer 2.01 (Brain Products, 2008). An electrode between Fz and Cz served as the ground. Electrodes were referenced to an electrode at the left mastoid and re-referenced offline to an average of the original reference and an electrode at the right mastoid. Electrodes at the outer canthi of both eyes provided the horizontal and two electrodes above and below the right eye the vertical EOG. The impedance was kept below at least 10 kΩ for EOG-electrodes and below 5 kΩ for the other electrodes. Data was analog low-pass filtered at 250 Hz and sampled at 1000 Hz. No high-pass filter was set because we were interested in slow cortical potentials. Whenever one electrode was close to saturation, the experiment was paused during the next break and all channels were reset.

Trials contaminated with severe artifacts other than eye blinks were rejected (4.3% of all trials). Drift artifacts were corrected using the method of Hennighausen, Heil, and Rösler (1993). Eye blinks were detected automatically and corrected according to the method of Gratton, Coles and Donchin (1983). No offline-filter was employed. To extract ERPs, the EEG was segmented into epochs from 200 ms before onset of the fixation cross to 1 s after presentation of the comparison character, drawn to a 200 ms baseline starting at the beginning of the epoch (and therefore ending at the onset of the fixation cross) and averaged for each Strategy Condition × Character Tilt × Original Character Version × Match cell. Only trials answered correctly were used for the averages. As all trials answered incorrectly were rescheduled, we obtained 48 measurements per 2 (strategy condition) × 6 (character tilt) cell of interest minus the 4.3% of trials contaminated with severe artifacts; that is, on average, about 4 measurements per relevant cell.

2.2 Results

2.2.1 Behavioral data

Unless otherwise noted, all data were analyzed by analysis of variance (ANOVA). Effects and interactions were further deconstructed by testing for polynomial trends and other contrasts. Reported *p* values are based on Greenhouse-Geisser corrected degrees of freedom (*df*s) where appropriate (Greenhouse & Geisser, 1959). The original *F* values and *df*s are reported throughout, alongside Greenhouse-Geisser epsilons (ε) and corrected *p* values (p_{corr}) when the correction was adopted. In all graphs the construction of 95%-confidence intervals follows the procedure described by Jarmasz and Hollands (2009). We corrected the critical *t* values' dfs appropriately if εs were too low, as suggested by Loftus and Masson (1994). The effects on which the confidence intervals are based can be found below each figure. We would like to stress that there were no behavioral responses collected during the interval in which mental rotation is thought to have taken place (following the appearance of the original character). Participants responded to the comparison character, making it likely that all or most of the rotation had been finished by the time comparison times were measured. Comparison times are therefore only reported for the sake of completeness and to show that participants complied with the instructions.

Percentage of correct answers was calculated upon regular trials only, that is, we did not include the rescheduled trials into this analysis. Accuracy was very high (98% for strategy condition up-right and 94% for turn-round, see Figure 2.4). Consequently, some cells yielded zero variance (no errors were committed) when original character version and match were included into the analysis. Accuracies were therefore analyzed by a nested 2 (strategy condition) × 6 (character tilt) ANOVA. Main effects of character tilt, $F(5,65) = 9.47$, $\varepsilon = .40$, $p_{\text{corr}} < .01$, $\eta_p^2 = .42$ and strategy condition, $F(1,13) = 10.19$, $p < .01$, $\eta_p^2 = .44$ as well as their interaction, $F(5,65) = 4.04$ $\varepsilon = .46$, $p_{\text{corr}} < .05$, $\eta_p^2 = .24$ were significant. Note that the high overall level of accuracy may have obscured the results. In particular, performance for strategy condition up-right was close to perfect and therefore could not show any effect of character tilt. This might have resulted in a spurious interaction.

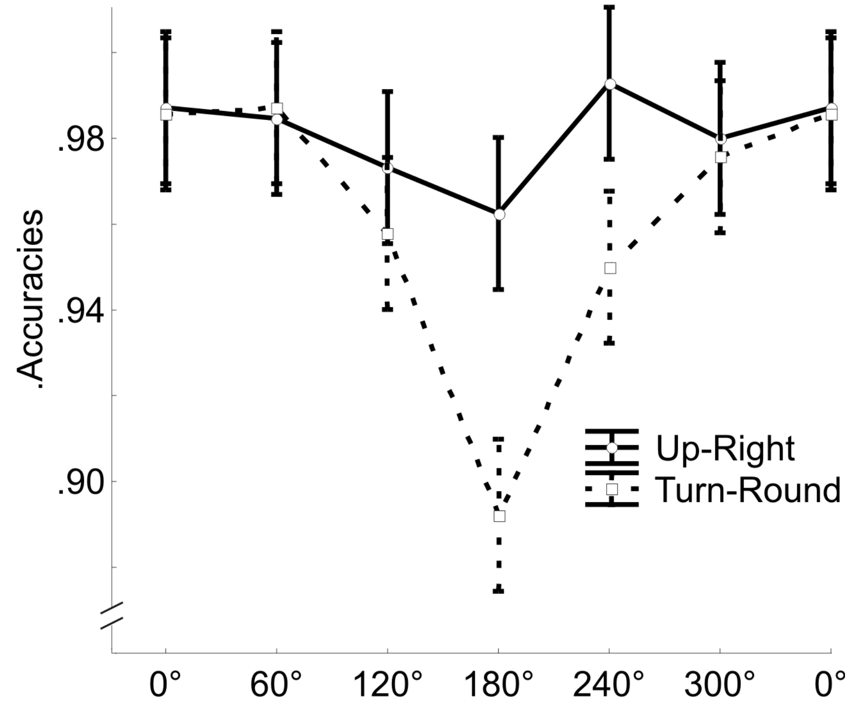

Figure 2.4. *Accuracy as a function of tilt and strategy. 95%-confidence intervals are based on an error estimate pooled over the effects of angle and strategy condition and their interaction.*

As participants were supposed to rotate the character during the 2750 ms before onset of the comparison character and as even the slowest participants of Cooper and Shepard (1973) did not show a mental rotation effect after 1 s preparation time, we did not expect any effect of the amount of rotation on comparison times. Nevertheless, we analyzed the median comparison times per participant associated with correct answers for each 2 (strategy condition) × 6 (character tilt) × 2 (original character version) × 2 (match) cell. Contrary to our expectation the comparison times showed strong main effects of tilt, $F(5,65) = 12.29$, $\varepsilon = .25$, $p_{\mathrm{corr}} < .01$, $\eta_p^2 = .49$, strategy condition, $F(1,13) = 6.82$, $p < .05$, $\eta_p^2 = .34$ and an interaction between the two, $F(5,65) = 9.22$, $\varepsilon = .36$, $p_{\mathrm{corr}} < .01$, $\eta_p^2 = .41$ (see Figure 2.5). Interestingly, there was also a strong interaction between original character version and match, $F(1,13) = 9.40$, $p < .01$, $\eta_p^2 = .42$: Participants' match-responses were faster than their mismatch-responses when the original character was presented in its normal version, *F*(1,13) = 7.78, *p* < .05. In contrast, the latency of mismatch- and match-responses did not differ when the original character was presented in its mirrored version, *F*(1,13) < 1, *p* > .2.

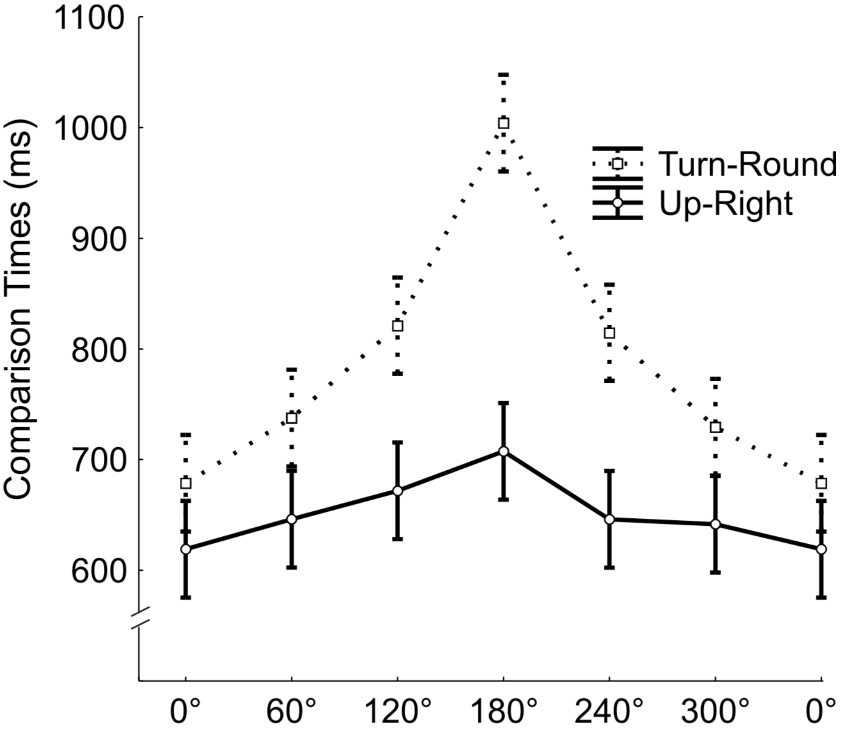

Figure 2.5. *Median comparison times as a function of tilt and strategy condition. Because the more interesting comparisons are within the two strategy conditions, 95%-confidence intervals are based on the effect of tilt.*

Mental rotation is generally assumed to have taken place if response times are linearly related to the absolute rotational angle. To test whether this was the case for our comparison-time data, we further decomposed the reported effect of character tilt. In a first step we collapsed tilts of +60° and -60° as well as tilts of +120° and -120° creating a new factor *absolute character tilt* with four levels (0°, $60°_{abs}$, $120°_{abs}$ and 180°). For each strategy condition, we tested the median comparison times for a linear trend across absolute character tilt—the typical criterion for assuming mental rotation. Indeed, a significant linear trend in strategy condition turn-round, *F*(1,13) = 13.54, *p* < .01 as well as in strategy condition up-right, *F*(1,13) = 8.65, *p* < .05 was found. Turn-round also showed a significant quadratic trend, *F*(1,13) = 9.20, *p* < .01, while up-right did not, *F*(1,13) < 1, *p* > .2. In addition the linear trend was significantly steeper in strategy condition turn-round compared to up-right, as reflected by an interaction between the linear trend of character tilt and strategy condition, $F(1,13) = 10.38$, $p < .01$.

One might argue that some participants may not have rotated during the interval before presentation of the comparison character as instructed, but instead waited for the appearance of the comparison character to start the rotation. This is unlikely to be the case for two reasons. Firstly, as is reported below, ERPs were sensitive to the degree of rotation long before the comparison character appeared. Secondly, an additional analysis indicated that the observed effect of rotational angle at the time of comparison character presentation was only present for women. A 2 (sex) × 2 (strategy condition) × 4 (absolute character tilt) ANOVA showed a significant three-way Sex × Strategy Condition × Character Tilt interaction, $F(3,36) = 5.80$, $\varepsilon = .46$, $p_{\mathrm{corr}} < .05$, $\eta_p^2 = .33$. An analysis of comparison times separately for the two sexes revealed that men (who were—as is frequently the case in mental-rotation tasks—faster, $F(1,12) = 11.44$, $p < .01$, $\eta_p^2 = .49$) showed no significant linear trends for character tilt in any strategy condition, both $ps > .2$. All effects of strategy condition and character tilt on the comparison times of men were due to slower responses in 180°, turn-round trials compared with all other trial-types. Women in contrast showed significant linear trends, $F(1,12) = 15.54$, $p < .01$ and $F(1,12) = 34.45$, $p < .01$ in strategy conditions up-right and turn-round respectively and an additional quadratic trend in strategy condition turn-round, $F(1,12) = 9.43$, $p < .01$. In sum, the harder the task and the slower the participants, the stronger the mental rotation effect on comparison times. This is the pattern one would expect if some participants were not able to finish rotation during the allotted time. We therefore suppose that the effects on comparison times reflect that some participants had to perform some rotation after appearance of the comparison stimulus. Nonetheless, it is likely that most rotation would have been completed during the preparation interval.

2.2.2 ERPs

Prior to any analysis of the effect of rotational direction on ERPs, we have to identify the ERP component which reflects the process of mental rotation in the present study. As expected on the basis of previous mental rotation studies in which ERPs have been employed, the effect of rotational angle was clearest at parietal electrodes, especially at Pz (see e.g. Heil, 2002). Figure 2.6 shows the grand average time-locked to trial onset at Pz. Four prominent positive and one negative component are evident. Of interest for our purposes are (a) the positivity peaking at about 3450 ms (i.e., 450 ms after onset of the original character) which we interpret as a P3b elicited by the original character and (b) the long lasting negativity directly following this P3b.

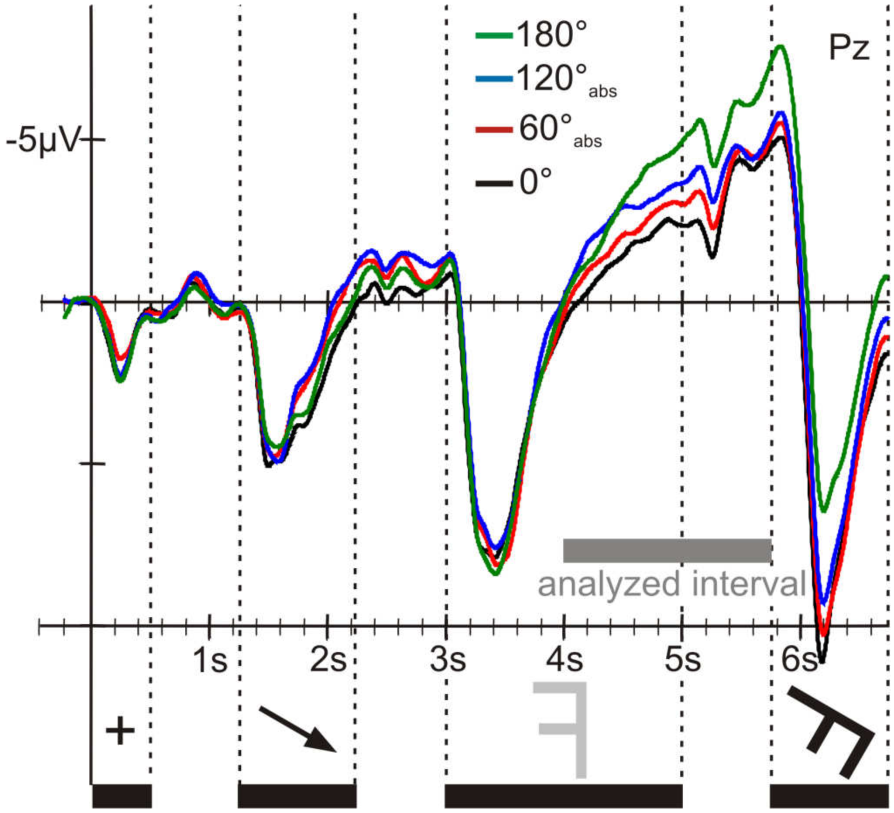

Figure 2.6. *Grand average for the four absolute character tilts (0°, 60°$_{abs}$, 120°$_{abs}$, 180°). Here and in the following graphs negative polarity is plotted upwards. For clarity a 2 Hz low-pass filter has been applied to all ERP-graphs, the analyses in contrast are carried out on the unfiltered waveforms. The data at P3 and P4 show the same pattern.*

The component reviewed by Heil (2002) usually lies in the interval between 300 and 1000 ms after onset of the rotation probe, that is, in the present data it should emerge inside the P3b evoked by the original character. From the fact that the amplitude of this P3b was not influenced by character tilt, it follows that this rotation-related component was not present, in either strategy condition up-right or turn-round. The slow potential starting around 1000 ms after onset of the original character, in contrast, was strongly influenced by character tilt. This slow potential is comparable to the component reported by Rösler et al. (1995). The effect of tilt lasts until the end of the episode in both strategy conditions; that means the component may have persisted even after the comparison character had appeared. This is in line with our interpretation of the comparison time pattern—maybe at least some participants were unable to finish rotation during the preparation interval and therefore had to execute at least some rotation after the comparison character had appeared. However, we did not want to confound our dependent measure with other components or processes starting after the presentation of the comparison character. Therefore, we focused our analysis on the mean amplitude of the component inside the preparation interval, that is, from 4000 ms (i.e., from the beginning of the rotation-related slow potential) until 5750 ms, when the comparison character appeared (eliciting another P3b).

The component appeared at the expected location, inside the expected time-window and has one of the two alternatively expected shapes. Taken together, this indicates that the component reflects the process of mental rotation, as has been previously observed (e.g., Rösler, et al., 1995). The final criterion that a component reflecting mental rotation should meet is that its negativity should increase with rotational angle. To confirm that this is the case for the component observed here, we again combined positive and negative tilts with the same absolute value, resulting in a factor of absolute character tilt with four levels (0°, $60°_{abs}$, $120°_{abs}$ and 180°) and tested for linear trends directly (ANOVA results on the data pooled over electrodes are reported below). All electrodes at parietal locations (P3, Pz and P4) showed linear trends for absolute character tilt (P3: $F(1,13) = 4.90$, $p < .05$; Pz: $F(1,13) = 4.97$, $p < .05$; P4: $F(1,13) = 7.10$, $p < .05$; see Figure 2.7). No electrode showed quadratic or cubic trends, all *ps* > .2. For the parietal locations, there was no Site × Linear Trend interaction, *F*(2,26) < 1, *p* > .2. As the effect measured at the three electrodes was obviously the same, we pooled over these electrodes in the following analyses, obtaining a significant linear trend over all three electrodes from the P-row, *F*(1,13) = 5.88, *p* < .05. It is appropriate to include all three electrodes in the analyses because fMRI studies have shown bilateral parietal increases in blood flow with increasing rotational demand in mental-rotation tasks (for a review see Zacks, 2008; see also Chapter 1.6).

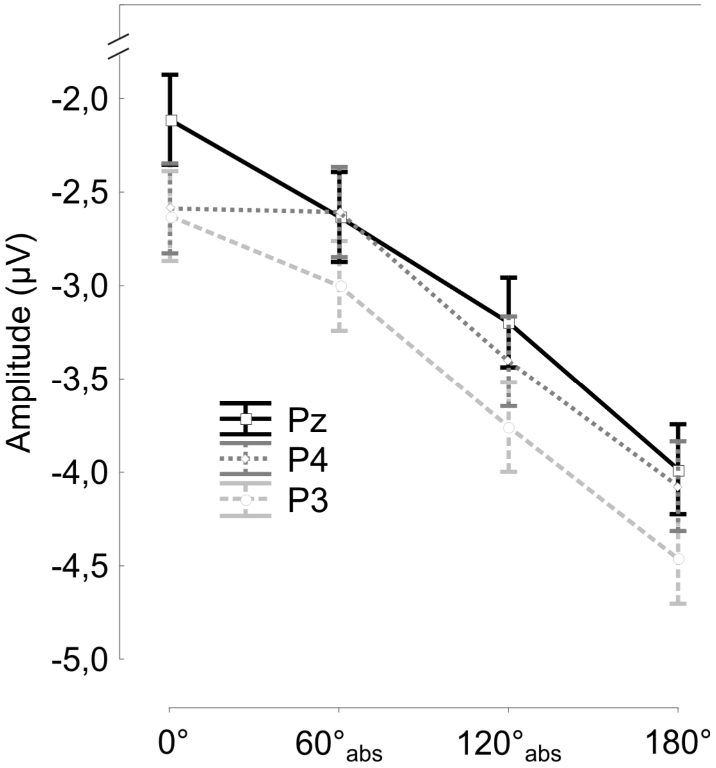

Figure 2.7. *Linear trend of rotational angle at parietal electrode sites averaged over the 4000-5750 ms time window. The displayed 95%-confidence intervals are based on the Electrode Site × Character Tilt interaction.*

After demonstrating the validity of our task as well as our dependent measure (the angle-dependent slow potential), we now turn to the critical test of our main hypothesis. An ANOVA with factors of laterality (P3, Pz, P4), strategy condition (up-right, turn-round), character tilt (0°, 60°, 120°, 180°, -120°, -60°) and original character version (normal vs. mirrored), showed a significant effect of character tilt, *F*(5,65) = 2.52, ε = .60, *p* < .05, η_p^2 = .16 only. The effect of strategy condition was marginally significant, *F*(1,13) = 3.41, *p* = .09.

Our hypothesis concerned the ERPs in trials with -120° and +120° tilts in strategy conditions up-right and turn-round. We focused our analyses on 120° instead of 60° tilts or a combination of both, because the expected effect should be strongest for the larger rotational angle (and Koriat & Norman, 1985a, observed the asymmetry only for tilts of 120°). This allowed us to maximize the power of our statistical tests. The outcomes of these contrasts fully supported our hypotheses. Average amplitudes were more negative for +120° than for -120° tilts in strategy condition up-right, $F(1,13) = 5.43$, $p < .05$, $\eta_p^2 = .29$, and more negative for -120° than for +120° tilts in strategy condition turn-round, $F(1,13) = 5.32$, $p < .05$, $\eta_p^2 = .29$, leading to a significant interaction, $F(1,13) = 10.35$, $p < .01$, $\eta_p^2 = .44$ (see Figure 2.8 and Figure 2.9).

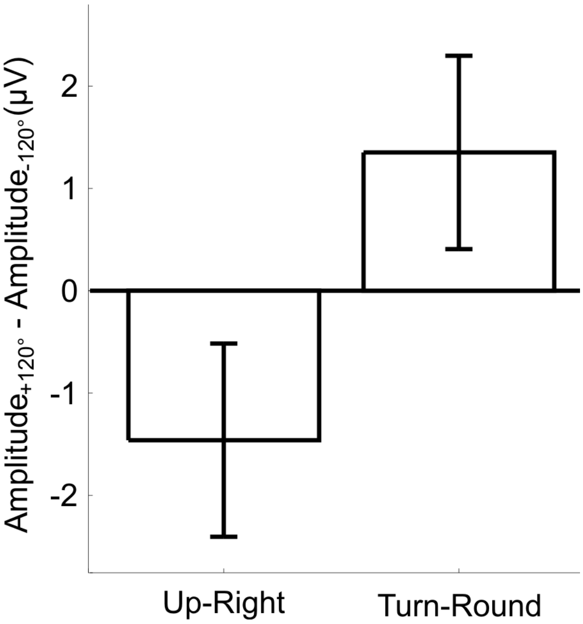

Figure 2.8. *Interaction between direction of tilt and strategy condition. Bars indicate the difference in amplitude between +120° and -120° tilts separately for the two strategy conditions. Amplitude of the rotation-related slow potential is averaged over the time period 1000 -2750 ms after onset of the original character and pooled over P3, Pz and P4. In strategy condition up-right +120° tilts demand a CCW rotation and -120° tilts demand a CW rotation. In strategy condition turn-round -120° tilts demand a CCW rotation and +120° tilts demand a CW rotation. Error bars represent the 95%-confidence interval of these differences.*

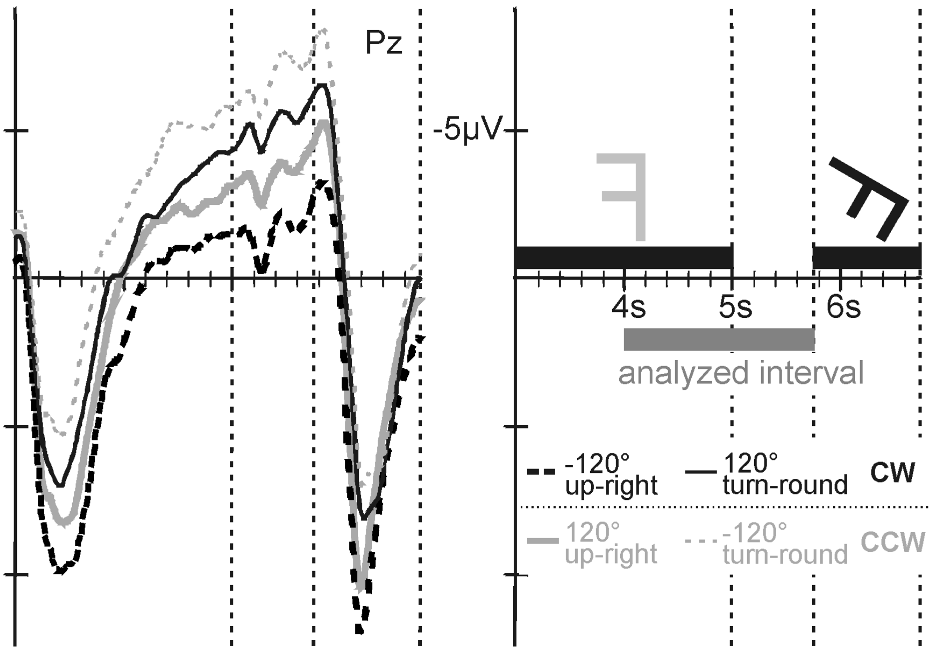

Figure 2.9. *Effect of rotational direction on the ERPs at Pz. Amplitudes are higher for CCW (gray) than CW (black) tilts in strategy condition up-right (thick lines) as well as in strategy condition turn-round (thin lines). +120° tilts are displayed as continuous and -120° tilts as broken lines. P3 and P4 showed the same pattern. Negative polarity is plotted upwards. For clarity, a 2 Hz low-pass filter has been applied.*

2.3 Discussion

An effect of rotational direction has emerged only very inconsistently in previous studies (e.g. Koriat & Norman, 1985a). We assume the reason for this inconsistency is that participants in usual character-rotation tasks can choose between two strategies, both of which cause different rotational directions for a given character tilt. Consequentially, analyses are usually carried out on mixtures of rotations in CW and CCW directions, as the researcher has no means for reliably differentiating between these two rotational directions. Only if a given study induces a strong bias towards one of the two strategies, can an effect of rotational direction emerge. In the study presented here we developed a task that brings the direction of rotation under the control of the experimenter.

2.3.1 Effect of rotational direction

During the rotation interval of our task, we observed a slow potential that became more negative with an increasing rotational angle. This slow potential is comparable to the one reported by Rösler et al. (1995) and is generally interpreted as reflecting the process of mental rotation. As hypothesized, this slow potential was found to be more negative for conditions designed to elicit CCW rather than for CW rotations. The amplitudes of negative going slow potentials are thought to reflect the amount of activation in the underlying cortex or, cognitively speaking, the amount of effort allocated to a task (Khader, et al., 2008; Rösler, et al., 1997). We therefore conclude that mental rotation (at least of alphanumeric characters) is more effortful in a CCW than in a CW direction. The effect was observed whether the original character (strategy condition up-right) or the comparison character (strategy condition turn-round) was presented tilted from upright. This allows us to exclude the alternative hypotheses that the effect stems from the tilt of either the original or the comparison character. In addition, both strategy conditions include trials with rotations in CW and trials with rotations in CCW direction. Obtaining the effect of rotational direction in both strategy conditions corresponds to a replication of the effect, providing further support for our hypothesis.

2.3.2 Possible causes of the effect of rotational direction

We were able to prove an advantage of CW rotations over CCW rotations, but with the data at hand, we can only speculate about the reason for this effect. One possible explanation comes from divided visual field studies. Corballis and Sergent (1989; see also Burton, Wagner, Lim, & Levy, 1992) found a strong interaction between the visual field a tilted stimulus was shown in and the direction in which it was tilted. Specifically, the right hemisphere appears to be superior at rotating stimuli in CW, while the left hemisphere rotates more efficiently in a CCW direction. As the right hemisphere's mental rotation performance is generally superior to that of the left hemisphere (for an overview see Corballis, 1997), a net advantage for CW rotations—which the right hemisphere appears to perform better than CCW rotations—might be expected. The hemispheric asymmetry and the right-hemisphere advantage in turn could be explained in the context of Kosslyn's (1994) theory of visual imagery: He assumes (Kosslyn, 1994; Kosslyn, et al., 2001) that mental rotation can be guided by the motor system. As is the case in most mental rotation experiments, our participants' reactions were recorded by button presses with the participants' palms pointing downwards and their digits pointing towards the screen. From this position one rotational direction was physically easier than the other for each hand—CW for the left and CCW for the right hand. In this situation, therefore, a CW rotation would be rather "unnatural" for the left hemisphere, which controls the right hand, and vice versa for the right hemisphere (see, e.g., Ionta & Blanke, 2009; Ionta, et al., 2007; Parsons, 1994; Sekiyama, 1982). Concerning the right-hemisphere advantage, there is some evidence that the spatial representation of the right hemisphere is continuous whereas the representation of the left hemisphere is categorical (see Kosslyn, 1994). If the representation that is mentally rotated continually goes through intermediate positions, the right hemisphere representation should be better suited for this.

Another explanation for the effect could simply be that people are better able to rotate CW because they are familiar with this direction following exposure to the CW rotation of clocks. Additional evidence for a general preference for CW rotations comes from visual illusions. For example, the *Enigma* figure, devised by Leviant (see Leviant, 1996) induces a perception of rotation. The perceived direction of rotation changes on average every 4.7 s. Interestingly, the overall duration of CW motion is longer than that of CCW motion and there is a strong bias of the perceived movement to start in a CW direction (Gori, Hamburger, & Spillmann, 2006).This bias is also reported for other illusions of rotation (Mackay, 1957).

An alternative reason for the effect of rotational direction might relate to the stimuli that were employed. As more alphanumeric characters are oriented to the right, the perception even of a tilted and mirrored character primes a representation of objects with their mass center to the right which, if they were real objects, would tend to fall to the right (CW).

In contrast to the effect of rotational angle on the ERPs, the effect of strategy condition and the effect of direction of rotation emerged directly following the presentation of the original character (see Figure 2.9). Nevertheless, this does not necessarily mean that all three independent variables (strategy condition, rotational angle, direction of rotation) cannot influence the same process (and therefore the same component). In the beginning the effect of rotational angle may be lacking, because rotations around different angles in the same direction do not yet differ—that means for rotations around a larger angle the smaller angles have to be passed. If this is the case, not only the amplitude, but even more so the duration of the rotation-related slow potential reported here should be sensitive to mental rotation—the more rotation has to be done the longer the underlying cortex should be active above a proper baseline[3] (cf. Pegna, et al., 1997). This would also explain why Rösler et al. (1995), using unknown stimuli—for which rotation takes longer than for familiar stimuli (see Bethell-Fox & Shepard, 1988)—observe a slow potential of much longer duration than we did. They measured angle dependent slow potentials that lasted for up to 8 s, while ours lasted only about 2 s. Alternatively, the earlier onset of the effects of strategy condition and direction of rotation could indicate differences in the initialization phase of mental rotation, for example, a tendency to rotate CW has to be surmounted before rotation in CCW direction can possibly start. However, because the effect of rotational direction emerged in both strategy conditions, it cannot be explained by encoding differences (cf. the reasoning in the introduction to this study).

2.3.3 Two shapes of the rotation-related slow potential

The data presented here, can help determine the conditions under which the rotation-related slow potential shows a late rotational-angle-effect onset and a long duration, as was the case for the rotation-related component observed in the present study (see also Rösler, et al., 1995), instead of the relatively short-lasting shape as reported by Heil (2002). The earlier studies in which these different shapes of the slow potential are observed do not only differ in the stimuli they use, but also in the paradigm. We used the same material as Heil (2002) but

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[3] In 0° trials no rotation is necessary and rotations around 180° seem to differ in another (qualitative) way (see below). Therefore with the data at hand (only two rotational angles that were directly comparable, namely 60° and 120°) we could not further test this hypothesis.

a paradigm more similar to Rösler et al. (1995). The shape of the angle-dependent component we found is comparable to the one Rösler et al. observed, namely a slow potential at parietal electrodes that started about 1 s after rotation could possibly start, whose negativity increased with increasing rotational angle and that lasted for several seconds. In contrast, we did not observe the short-lasting shape of the component described in the review by Heil (2002). Therefore, we suppose that it is the paradigm and not the stimulus set that influences the shape of the component. As the main studies as reported below also employ a successive-presentation mental-rotation task, the mental rotation-related component in Experiment 2 should be similar to that in the present study and that reported by Rösler et al. (1995). The mental rotation effect should emerge in a negative slow potential centered at Pz, show a late onset and should persist until or even slightly beyond the end of the rotation interval.

3. Mental Representations[4]

Humans are able to internally represent visual aspects of the external world. Information initially detected by the photoreceptors of the eyes is eventually transformed into a mental representation which allows us to separate objects, compare them to memory entries, to reason about them and to interact with them. Even after an object has vanished from the scope of view mental representations of the object can continue to exist in mind. Such representations in fact do not even need the object to exist at all. Humans can keep representations of objects active, retrieve them from long-term memory, or construct them at will (cf. Hume, 1748), a faculty called imagery (for a review see Kosslyn, 1994). Everyone virtually always actively represents and processes visual and spatial

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[4] Part of this chapter is adapted from Liesefeld and Zimmer (2012), Copyright © 2012 by the American Psychological Association. Adapted with permission. The official citation that should be used in referencing this material is Liesefeld, H.R., & Zimmer, H.D. (2012). Think Spatial: The Representation in Mental Rotation Is Nonvisual. *Journal of Experimental Psychology: Learning, Memory, and Cognition*. doi: 10.1037/a0028904. No further reproduction or distribution is permitted without written permission from the American Psychological Association.

information. Depending on ancillary factors, these activities are called seeing, reasoning, dreaming etc. Active mental representations of visual and spatial information are among the most important experiences in our daily life and are the building blocks many different mental processes work on. Zimmer and Liesefeld (2011) have claimed earlier that the human cognitive system can adaptively recode a given type of mental representation into another type rendering different types of information explicit. Which information is selected and how it is represented depends on tasks affordances, available and necessary resources, and the cognitive processes that transform the mental representation.

For the present work we assume that mental representations exist and that they can be subject to empirical testing (for a discussion of some diverging standpoints see Chapter 3.4). Mental representations are then purportedly transformed by mental processes. In principle, it should be possible to examine the properties of mental representations and mental processes separately. However, the nature of a mental representation obviously restricts the nature of the process by which it is transformed. As an example, if in mental rotation picture-like representations are rotated, the process of mental rotation must specify how the picture looks like after each rotational step. If on the other hand only certain spatial characteristics of an object are rotated, only these need to be updated. Therefore, a theory of mental rotation must take into account the nature of both the employed mental representation and the employed mental process, and a deeper understanding of the one informs a deeper understanding of the other. Shepard and Cooper (1982, p. 12) even note that it might be impossible to determine the nature of the process of mental rotation without knowledge about the representation in mental rotation. However, although much is already known about the process of mental rotation, the representation in mental rotation has so far received only little empirical testing.

3.1 Holistic vs. Piece-Meal Representations

“[I] experienced a spontaneous kinetic image of three-dimensional structures majestically turning in space” (Shepard & Cooper, 1982, p. 7) is how Shepard described the vital spark that had led to his seminal study on mental rotation

(Shepard & Metzler, 1971); in fact, this description is close to the subjective experience of most participants performing mental-rotation tasks and purportedly close to the experience you had if you tried to answer the question posed in the first sentence of this work. Accordingly, it is generally assumed that mental rotation is performed on some kind of visual mental image, that is, a depictive representation of the visual characteristics of the stimulus which is in many ways similar to a picture of the stimulus (cf., e.g., Kosslyn, Thompson, & Ganis, 2006). However, sometimes introspection is misleading, as we argue is the case for mental rotation.

Early theories of mental rotation assumed that a single visual mental image is rotated that represents visual characteristics of the to-be-rotated stimulus in an integrated, holistic fashion (e.g., Cooper & Shepard, 1978). The main line of support for the *holistic hypothesis* came from studies observing that stimuli which clearly differed in visual complexity were rotated at an identical pace (D. Cohen & Kubovy, 1993; Cooper, 1975; Cooper & Podgorny, 1976). In these studies, the slope of the function which relates rotation time to rotational angle and which is generally interpreted as a reflection of rotational speed, did not differ between visually simple and visually complex stimuli. Consequently, the strongest challenges to the holistic hypothesis come from reports of modulations of rotational speed by the stimuli's visual complexity (M. D. Folk & Luce, 1987; Heil & Jansen-Osmann, 2008), by the stimuli's dimensionality (Bauer & Jolicoeur, 1996; Jolicoeur, Regehr, Smith, & Smith, 1985), and by the difficulty of the comparison task, which might also influence characteristics of the rotated mental representation (M. D. Folk & Luce, 1987; Förster, et al., 1996; Pylyshyn, 1979). The alternative *piece-meal hypothesis* states that under conditions of high complexity not the whole stimulus is rotated at once, but its parts in sequence, necessitating at least two iterations of encoding, rotation and matching (Just & Carpenter, 1976; Just & Varma, 2007; Pylyshyn, 1979; Yuille & Steiger, 1982); the more stimulus parts have to be rotated, the lower the apparent rotational speed. However, most proponents of both competing hypotheses explicitly or implicitly assume that mental rotation works on visual mental images. Instead of one holistic image of the stimulus, several images of the stimulus' parts might be rotated in a piece-meal fashion (see Bauer & Jolicoeur, 1996; Bethell-Fox &

Shepard, 1988; Folk & Luce, 1987; Heil & Jansen-Osmann, 2008; Yuille & Steiger, 1982).

3.2 Visual Mental Images as One Type of Visual (Depictive) Representations

Both the holistic and piece-meal hypothesis are in line with the assumption of visual mental images in mental rotation. In order to empirically examine whether mental images indeed play a role in mental rotation, a careful theoretical consideration of the properties of visual mental images is necessary. Most characteristics that apply to physical representations (pictures, stick figures, written or spoken words) also apply to mental representations, including visual mental images. The information a representation represents is its *representational content*. The same content can in principle be represented by several types of representations differing in their *representational format*. Depending on the representation's format different subsets of its content are encoded *explicitly* or *implicitly*. Explicitly encoded information is directly accessible from the representation, whereas implicitly encoded information has to be derived from the explicitly encoded information in order to be accessed[5]. Visual information (the content) can, for example, be represented as a written description (verbal format, Figure 3.1A) or as a picture (visual format, Figure 3.1B; cf. the dual-coding theory by Paivio, 1971). Note that even with the extensive verbal description in Figure 3.1A, it is still impossible to accurately redraw the rather simple stimulus in Figure 3.1B. For example, the size and the color of the stimulus are unspecified and it is still unclear how and where exactly the square touches the smaller line and whether the two lines intersect. On the other hand, while reading the verbal representation you might became aware of stimulus

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[5] Our definition of "explicit" obviously deviates from Kosslyn et al.'s (2006) definition. According to their example, the representation of the three points (3,2), (3,5), and (3,7) in Cartesian format makes "explicit" that the points lie along the same vertical line. However, for deriving this fact, at least two comparisons of the points' x-coordinate values have to be performed. As this spatial-relational information ("lying on the same line") has to be derived, it is not explicit in our use of the word. An explicit representation of this fact might, for example, be the sentence "The three points lie along the same vertical line". The human cognitive system obviously is very fast in deriving this fact from the Cartesian coordinates given. If in Kosslyn et al.'s writing "explicit" is replaced by "very fast derivable/detectable/accessible by the human cognitive system", we perfectly agree with their comments on it.

properties which are implicitly present in the visual representation, but which had to be made explicit in order to be processed by your cognitive system, as, for example, the size ratios between the stimulus parts[6]. In all visual representations, including visual mental images, besides the explicitly represented information (e.g., the color of each pixel) a near infinite number of spatial relations between the stimulus' parts are represented implicitly; all these spatial relations between stimulus parts are available from the visual representation but must be made explicit in order to be directly accessible for subsequent mental processes.

A The stimulus consists of two lines and a square. One line is 1/3rd the size of the other line and the square is 1/8th the size of the larger line. The smaller line touches the larger line and the square. All angles between the two lines have a value of 90°. The larger line is horizontal with respect to the page. With respect to the page, the smaller line is on top of the larger line and the square is to the right of the smaller line.

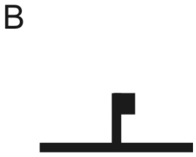

Figure 3.1. *A visual representation is worth more than 87 words. Much less information is derivable from the verbal representation (A) than from the visual representation (B) of the stimulus. Furthermore, the two representations make different subsets of information explicit.*

One characteristic of visual representations is crucial for the present article. Any visual representation that implicitly encodes the spatial relation between two stimulus parts is a representation of at least the two stimulus parts themselves. By representing two stimulus parts visually, not only the intended spatial relation but many other spatial relations between the two stimulus parts are represented. Consequently, certain spatial relations cannot be erased from a visual representation without also erasing other spatial relations[7], because they are represented implicitly by the same explicit sets of pixel values. In Figure 3.1B, the spatial relation "the square is to the right of the smaller line" can be erased by erasing the pixels that form the square in the visual repre-

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[6] The verbal description can also implicitly represent information. For example, the size ratio between the smaller line and the square (3/8th) can be derived from the two given ratios.

[7] Note that even in visual representations the presence or absence of many other types of stimulus properties can be varied fully independently. Consider, for example, stick figures that represent objects without specifying color, texture or detail about shape (Fodor, 1975).

sentation. Having erased these pixels, not only the spatial relation that was intended to be erased is lost, but also, for example, the spatial relation “the square is affixed to the top of the smaller line”. These two spatial relations cannot be represented separately and representing them both does not cost more “resources” (pixels) than representing just one of them—the visual representation implicitly specifies these pieces of spatial-relational information (and many others) either way. Some storage capacity might of course be saved by, for example, representing the square with fewer pixels. But even if the square shrinks to one pixel in the extreme, both spatial relations are still implicitly represented. That certain pieces of spatial-relational information (like those that were erased with the square) cannot be represented separately is the minimal prediction which can be derived from the assumption of visual mental images and which we will use to falsify the hypothesis that mental rotation works on visual mental images. In the following, we develop the alternative hypothesis that in mental rotation only a specific type of spatial information is represented in a nonvisual form.

3.3 A New Hypothesis: Rotation of Orientation-Dependent Information

That mirror images have to be discriminated appears to be critical for mental rotation to occur (for reviews, see Corballis, 1988; Shepard & Cooper, 1982). Takano (1989) pointed out the specific type of information in which mirror images differ and which reliably induces mental rotation. To-be-compared stimuli must differ in at least one piece of information that changes whenever the orientation of the stimulus varies (but see Förster, et al., 1996). For example, whether the arc of the letter *R* is located to the right or left of the larger stroke depends on the *R*’s absolute orientation with respect to the viewer. When the *R* is rotated 180° in the picture-plane for example, the arc has moved from the right to the left side of the larger stroke. Whether the smaller stroke of the *R* is connected to the arc or not, on the other hand, is not influenced by the *R*’s orientation; that means that this piece of information does not change its value when the stimulus orientation varies. Note that these two types of information are quite similar as both describe spatial relations between stimulus parts. Their differing characteristic that is important for our purposes is that the first type is *orientation-dependent*, whereas the second type is *orientation-independent.* All orientation-dependent information can be reduced to "to the left/right of", "above/below" or in "front of/behind". Takano (1989) found that mental rotation occurred only if orientation-dependent information has to be compared between stimuli. In contrast, when mismatching stimuli always differ in orientation-independent information, comparison time is short and independent of the stimuli's angular disparity, indicating that in these cases mental rotation was not performed, because it was unnecessary.

This finding allows for a fundamentally new hypothesis about the representational content during mental rotation. Mental-rotation tasks could be solved by rotating only pure, explicit orientation-dependent information instead of visual mental images[8]. In contrast, in any visual mental image, orientation-dependent information would be represented implicitly by an image of two stimulus parts, namely those stimulus parts whose relation is described by the respective piece of orientation-dependent information. These images would additionally implicitly specify much other information about the spatial relation between the represented stimulus parts (including orientation-independent information). These additional pieces of spatial-relational information would therefore be inextricably interwoven with the original piece of orientation-dependent information (cf. Figure 3.1 and the example for this general point in Chapter 3.2).

In visual mental images a piece of orientation-dependent information that describes a spatial relation between stimulus part A and stimulus part B (e.g., "A is to the right of B") cannot be represented separated from certain other pieces of information about the spatial relation between A and B, for example, from the piece of orientation-independent information "A is in the middle of B". If we, however, can show that two such pieces of information are indeed represented

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[8] Note that Takano (1989) explicitly does not take up a position concerning the mentally rotated representation. He states that the presence of orientation-dependent information is necessary for mental rotation to occur and that orientation-dependent information probably is represented explicitly during the comparison process. The process of mental rotation itself, in contrast, might as well work on a holistic representation, that is, on something like a visual mental image.

separately during mental rotation, we can conclude that the representation underlying mental rotation is not visual in any sense, not even structural pictorial in the sense of Fodor (1975). The bottom line is that participants might not rotate visual mental images of a stimulus' parts nor any other type of visual representation, but explicit and abstract spatial-relational information (for a similar speculation on the representation employed for mechanical reasoning, see Hegarty, 2004), or more specifically, orientation-dependent spatial-relational information.

How can this claim be reconciled with the strong introspection that visual mental images are indeed employed in mental rotation (see above, Chapter 3.1)? Analogous to Shepard and Cooper's (1982, p. 10) observation that "on introspection […] the mind's most efficient and automatic operations appear to the mind itself to be virtually instantaneous as well as effortless", we argue that on introspection, the mind's most complete representations appear to the mind itself to be virtually identical to the perception of the represented object. None of these introspections, however, needs to reflect reality. Mental rotation becomes more difficult with increasing rotational angle and the rotated representation might not be a full-blown mental image of the stimulus[9].

3.4 Are Statements About Mental Representations Possible?

Although it certainly is of utmost importance to cognitive psychology, there is some reserve among cognitive psychologist to tackle the question of the format of mental representations and there are good reasons for this reserve.

Already the basic distinction between representations and processes might be called into question. In "neural network" models (e.g., McClelland, Rumelhart, & Hinton, 2002), both representations and processes are instantiated by the pattern of weights given to the links between the elements of the network (processing units). Processing units influence each other by means of excitation or inhibition. These models consequently blur the distinction between representations and processes and might thereby be more parsimonious than those

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[9] Note how nicely this speculation fits to the assumption that representations in the dorsal stream (which apparently plays an important role in mental rotation) cannot be accessed consciously (Milner & Goodale, 2008).

employing a strict distinction. However, we consider this distinction as being at least of explanatory value. Consequently, for the present work we simply assume that a distinction between mental representations and mental processes is possible. Furthermore, one critical implication of the assumption that mental processes and mental representations are only two sides of the same coin is that they cannot appear separated (cf. Kosslyn, et al., 2006, pp. 22-23). The existence of "mental flipping" as reported below (Chapter 8.7.4, see Figure 8.2), however is at least suggestive evidence that the representation employed in mental rotation can also be manipulated by other processes than mental rotation.

A further problem arises from Anderson (1978)'s logical proof of the fundamental inability of behavioral data to support strong claims on the format of mental representations. His central claim is that a mental representation of any format can mimic the behavior of the mental representation of any other format if appropriate encoding and recoding processes are applied. According to Anderson, also physiological data would only be informative on the issue, if it was possible to directly observe the physiological instantiation of a mental representation (e.g., observing images that are laid out in real physical space on the brain)[10]. This might, however, be meant ironically and not as a real possibility. Either way, Anderson's argumentation concerns only the representational format and not the representational content. If one representation mimics another, independent of their format, their informational content actually is identical. In the following, we will demonstrate some new or underestimated techniques to identify the nature of representational contents.

We agree with Anderson (1978) that any type of representation can in principle represent any type of informational content. That means, we cannot differentiate representational formats by testing under which conditions they work. We will however show that we can differentiate representational formats by testing under which conditions they fail. Anderson did not fully appreciate the power of the fact that certain pieces of informational content cannot be erased from certain types of representations without also erasing other pieces of infor-

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[10] Anderson (1978) explicitly left open two additional possibilities to derive knowledge about the format of mental representations of which we will make use: Model plausibility/parsimony and computational efficiency.

mation as discussed above (Chapter 3.2). A similar idea might, however, have inspired his statement that “it may be possible to decide that there are different representations without deciding how they are different”. By carefully manipulating the to-be-represented information and then examining the resulting representational content, we consequently might be able to draw conclusions even about representational format (see Chapter 8.3).

3.5 Other Features of Mental Representations

The question of whether analog representations (mental images) are part of human thoughts has generated a great deal of scientific dispute and research (for reviews on this so-called imagery debate see, e.g., Block, 1981; Kosslyn, 1994; Pylyshyn, 2003; Tye, 1991). The relational structure of objects is considered to be essentially preserved in analog but not in non-analog (e.g., propositional) mental representations. Indeed, one reason for the strong interest in the mental rotation effect is that it is apparently more naturally explained in terms of analog thinking than in terms of propositional thinking (see Kosslyn, 1994 for an analog; and Pylyshyn, 1979 for a propositional explanation of the mental rotation effect). The subject matter of the imagery debate is the format of mental representations. The primary subject matter of the present work, however, is the content of the mental representation in mental rotation. As detailed in Chapter 3.4, positive statements on the format of mental representations might even be impossible (cf. Anderson, 1978; but see Chapter 8.3 for a negative statement on the format of the mental representation in mental rotation). Consequently, the imagery debate is of only marginal interest here and will not be considered in detail.

Shepard and Cooper (e.g., 1982, p. 14) assume that while performing mental rotation, “the brain is passing through an ordered series of states that (whatever their neurophysiological nature) have much in common with the perceptual states that would occur if the appropriate physical object were presented in successively more rotated orientation in the external world.” Such a second-order isomorphism allows for several types of representational format and content in mental rotation as long as the same representations also play a role in perception. The assumption of a second-order isomorphism in mental rotation appears plausible to us but direct testing is beyond the scope of the present work.

3.6 How to Manipulate Representational Content

To explore *how* information is represented during mental rotation, the experimenter must first gain some control over *which* information is represented. Generally speaking, in mental-rotation tasks participants compare information from one stimulus to information from a comparison stimulus (see Chapter 1.3) and indicate whether the two stimuli match in all pieces of information they carry or not; according to Farell's (1985) classification, mental-rotation tasks are "same"-"different" judgment tasks with a conjunctive criterion. In order to successfully solve such tasks (see Farell, 1985), participants only need to encode and maintain information that potentially differs between to-be-compared stimuli and is nonredundant. These pieces of information are *comparison-relevant*, whereas all remaining information about the stimuli is comparison-irrelevant. As soon as participants recognize that a piece of information is comparison-irrelevant it becomes advantageous not to waste any resources on its representation or processing[11]. For example, in mental-rotation tasks to-be-compared stimuli usually do not differ in size. Participants consequently do not need to check the stimuli for potentially subtle differences in size in order to determine whether the stimuli match or not, even though a difference in size would in fact constitute a mismatch.

We deliberately differentiate between the terms 'comparison-relevant' and 'task-relevant'. For example, the absolute orientation of an alphanumeric character in a mental-rotation task as displayed in Figure 1.2C is of course task-relevant, because it determines the amount of to-be-performed rotation. For the comparison itself (which takes place after rotation) the absolute orientation however is by definition not relevant. Furthermore, it has been observed that

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[11] Note that we explicitly state only that it is unnecessary to represent other than comparison-relevant or task-relevant (see the following paragraph) information. This is meant in a purely theoretic-analytical but not empirical sense. We do not claim that it is under no circumstances beneficial to represent such irrelevant information. Possibly, in certain situations certain types of information are processed automatically and the costs of actively suppressing these types of information would be higher than simply representing them. Ironically, in these cases, suppressing irrelevant information would waste resources.

comparison-irrelevant information influences performance in change detection tasks. When the spatial-relational arrangement of objects on a screen is changed from the original to the comparison display performance accuracies drop and comparison times increase even when these spatial relations are not comparison-relevant (Jiang, Olson, & Chun, 2000; Santa, 1977; Zimmer, 1998; Zimmer & Lehnert, 2006). This might be the case, because the spatial relations were helpful in establishing a correspondence between individual objects during S1 and S2 which might have worked as an additional retrieval cue and were therefore in some sense task-relevant. Task-relevance apparently is also an empirical question whereas comparison-relevance fully depends on the experimental design.

If, in a comparison task, a participant has reached a high accuracy rate, the researcher can deduce that this participant has at least represented all comparison-relevant information (for a statistical procedure to determine, which information was ignored by participants achieving a low accuracy rate, see Chapter 4.2.1). Comparison-relevant information is an experimentally well-defined subset of all available stimulus information (see Figure 3.2). As working memory capacity is highly limited (e.g., Luck & Vogel, 1997), participants can actively represent only a certain amount of stimulus information. They consequently have to select a subset from the near-infinitely large and rather ill-defined set of available information. It would be advantageous to represent comparison-relevant and to filter out comparison-irrelevant information (for limitations, see footnote 11). However, comparison-relevance might be difficult to determine for participants who are new to a task (cf. M. D. Folk & Luce, 1987; Yuille & Steiger, 1982). In order to reassure that they will be able to detect all possible mismatches, participants might in addition to comparison-relevant information represent much information that is not comparison-relevant. In praxis, it consequently happens that participants unnecessarily represent some of the comparison-irrelevant information and fail to represent some of the comparison-relevant information; the sub-samples of represented and comparison-relevant information are only partially overlapping (as depicted in Figure 3.2), although in the ideal, most efficient case they would be identical. This complicates the experimenter’s task of accurately manipulating representtational content—perfect control can be exerted over which information is comparison-relevant, but this translates to only partial control over which information is eventually represented.

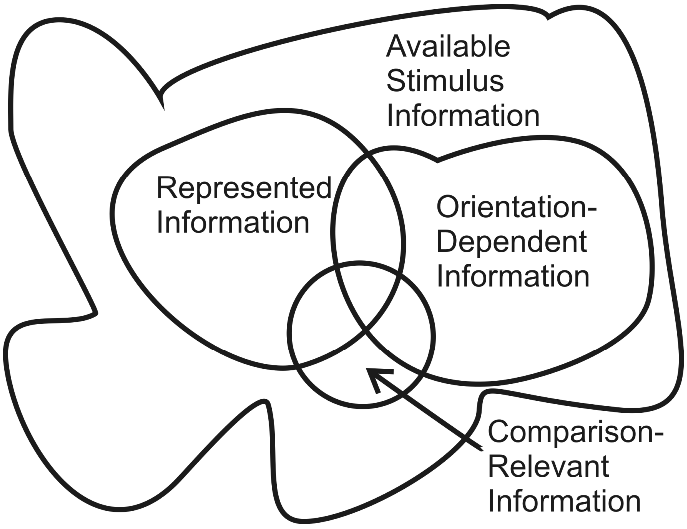

Figure 3.2. *A schematic illustration of the relations between available, represented, comparison-relevant and orientation-dependent stimulus information. Only the subsample of comparison-relevant information can be brought under full experimental control, because it is defined by the task-design. In contrast to the other subsamples of information, it is therefore displayed as a perfect circle. Which information participants actually represent also depends on the participants' experience with the employed task and stimuli. How effective the task is performed depends on how large the overlap between the sets of represented and comparison-relevant information is. How efficient the representation is depends additionally on how small the overlap between represented information and other than comparison-relevant information is. As participants purportedly strive to increase effectiveness and efficiency, experimental control over represented information should increase with appropriate instructions and training on the task and/or stimuli.*

One way to increase the overlap between the subsamples of comparison-relevant and represented stimulus information is to employ stimuli that provide as little comparison-irrelevant information as possible. Further, participants can be informed about the comparison-relevant informational content of the stimuli by revealing how stimuli potentially differ, that is, which mismatches are possible. Even then, the cognitive system might still need some time to be tuned for the specific encoding and processing of comparison-relevant information. As familiarity with a task and with the employed stimuli increases, mental representations should approach the most efficient state. The overlap between represented and comparison-relevant information should increase, the amount of represented comparison-irrelevant information should decrease and the proportion of actually represented comparison-relevant information should approach 100% (within the limits of individual working memory capacity, of course). This amounts to an increase in the quality of experimental control over the represented information over the course of the experiment. In sum, experimental control over participants' representational content is always imperfect but should increase by using simple, information-poor stimuli, making participants aware of comparison-relevant information and allowing them to practice the task and become accustomed to the employed stimuli and mismatches.

The general approach to manipulate participants' mental representations followed here is to employ stimuli with different amounts of comparison-relevant information (please refer to Chapter 3.8 for the specific implementation). Participants have to represent more information for a stimulus that includes more comparison-relevant information. It consequently is possible to examine the effect of a certain type of information by comparing two stimuli that differ in the number of comparison-relevant pieces of this type of information.

As detailed above (Chapter 3.2) the type of content of a representation is defined as the type of information that it explicitly represents. Only the amount of this type of information determines the complexity of the representation. A difference in other than the type of explicitly represented information, in contrast, does not influence this representation's complexity. However, it appears quite plausible that participants hold several mental representations at the same time. A type of information that is not explicitly represented in the mental representation of interest might be explicitly represented in an alternative mental representation.

In order to collect evidence that a representation of interest explicitly represents a certain type of information, the effect of two stimuli must be compared that differ in the amount of exactly this and no other type of comparison-relevant information. The stimulus that contains more pieces of this type of information should induce a higher representational complexity. Further, it is of importance to prove that the mental representation of interest is specific for this first type of information, that is, that it does not explicitly represent other types of information. This can be achieved by employing a second pair of stimuli. This pair would contain the identical amount of the first type of information (that is purportedly represented), but differ in the amount of other types of comparison-relevant information that are hypothesized not to be represented in the mental representation of interest[12]. If the representation is indeed specific to the first type of information participants must store these latter types of information somewhere outside the examined representation. The complexity of the representation of interest would consequently not differ for this second pair of stimuli.

3.7 How to Measure Representational Content

The theory detailed above (Chapter 3.6) allows (to a certain degree) controlling which information is mentally represented and manipulating how much of this information is represented. The next step in an empirical endeavor is to measure, how this information is represented; especially, to prove that it is, as hypothesized, represented in the representation of interest. The two stimuli that differ in the amount of purportedly explicitly represented information should influence appropriately chosen dependent variables differently (as, e.g., processing speed, see below). The two stimuli that do not differ in the amount of explicitly represented information should not exert such a differential influence, even if they differ in many other features. In order to measure how these stimuli are eventually mentally represented, several techniques are possible. In the present work we employ five such techniques as detailed in the following.

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[12] To exhaustively test for all types of information and features that are purportedly *not* represented is, of course, impossible. It is possible, however, to test for plausible candidates as derived from the literature and for those types of information or features that are similar to the purportedly represented type.

3.7.1 Technique 1: Processing speed

Processing slows down when the amount of processed and therefore explicitly represented information is increased. This should be the case, because the represented information must be updated at each processing step. Processing speed is, however, uninfluenced by the amount of information represented in an alternative representation or implicitly in the representation of interest. The measure of processing speed employed in Experiment 1a, 1b and 3 is the slope of the function relating rotation time to rotational angle.

3.7.2 Technique 2: Comparison time

A mismatch in a type of information that is not explicit in the active mental representation should be detected later than a mismatch in a type of information that is explicitly represented. Different types of representations might be mutually exclusive, that is, perhaps only one representation can be active at a given point in time. This would mean that only a certain type of information can be active at the onset of the comparison stimulus. We employ this strategy in each of the four following experiments.

3.7.3 Technique 3: Slow potentials

From the electroencephalogram (EEG) recorded during the retention interval of working-memory tasks slow potentials can be extracted. These components have two characteristics that are of interest for our purposes. Firstly, the topography of slow potentials apparently depends on the type of information maintained in working memory (e.g., Mecklinger & Pfeifer, 1996; Ruchkin, Johnson, Grafman, & Canoune, 1997). Secondly, the amplitude of slow potentials increases with increasing working-memory load (Arend & Zimmer, 2011; Lehnert & Zimmer, 2008; Mecklinger & Pfeifer, 1996; Rämä, et al., 1997; Ruchkin, Canoune, Johnson, & Ritter, 1995; Ruchkin, et al., 1997), that is, with the amount of explicitly represented information. In Experiment 2, we employ this online-measure in order to observe how the mental representation in mental rotation is recoded over the course of an experimental trial.

3.7.4 Technique 4: P3bs

The P3b, is a component peaking usually between 250-650 ms after onset of a task-relevant stimulus at parietal electrode sites (for recent reviews, see Nieuwenhuis, et al., 2005; Polich, 2007; Verleger, 1997).The amplitude of the P3b following stimulus onset is interpreted as reflecting the subjective probability of the class of events the eliciting stimulus is subjectively perceived to belong to (e.g., R. Johnson & Donchin, 1980; Mars, et al., 2008). Consequently, this amplitude can be employed to measure which events are subjectively perceived to belong to the same or different classes. In Experiment 2, by considering the single and joint probabilities of mismatches in orientation-dependent and orientation-independent information and the P3b amplitudes these events elicit, we determine which types of mismatches fall into the same or different subjective classes of events. This allows concluding whether different types of comparison-relevant information (even within the same stimulus) belong to the same or different subjective classes of information.

3.7.5 Technique 5: Cortical activation patterns

Slow potentials are assumed to reflect activation of the underlying cortical areas (e.g., Khader, et al., 2008). That the topography of slow potentials depends on the type of maintained information consequently reflects that different cortical areas store the different types of information. By using neuroimaging techniques like functional magnetic resonance imaging (fMRI) these cortical areas can be identified with a higher spatial resolution. Indeed, the maintenance of different types of information in working memory elicits different cortical activation patterns (for a review, see Wager & Smith, 2003). Activation as measured by fMRI is apparently also modulated by the amount of information represented in working memory (e.g., Todd & Marois, 2004). In Experiment 3, we employ this method to localize the brain areas that hold the mental representation employed in mental rotation.

3.8 Theoretical Considerations on the Specific Design of the Present Studies

As Takano (1989) has pointed out (see also Chapter 3.3) only orientation-dependent information is comparison-relevant in typical mental-rotation tasks. The typically employed mirror images differ in many pieces of orientation-dependent information. However, as, for example, all “to the left of” relations are “to the right of” relations in the mirror image, only one piece of orientation-dependent information in this dimension is nonredundant. Note further that in typical mental-rotation tasks a stimulus’ absolute orientation (e.g., the angular disparity from upright) is not comparison-relevant (cf. Takano, 1989). For two-dimensional stimuli this effectively means that only one from the initially two fully nonredundant pieces of orientation-dependent information (“above/below”, “to the left/right of”) can potentially vary between to-be-compared stimuli and therefore has to be represented during rotation. In order to relax this constraint for the studies described below, we employ a rotational cue that indicates the target orientation into which the stimulus on each trial has to be rotated (see Figure 3.3). Due to this rotation cue, also the second piece of nonredundant orientation-dependent information (which usually determines the target orientation) can be rendered comparison-relevant. Besides, as discussed above (Chapter 1.3.4), this rotational cue allows an improved separation of mental processes taking place during the task.

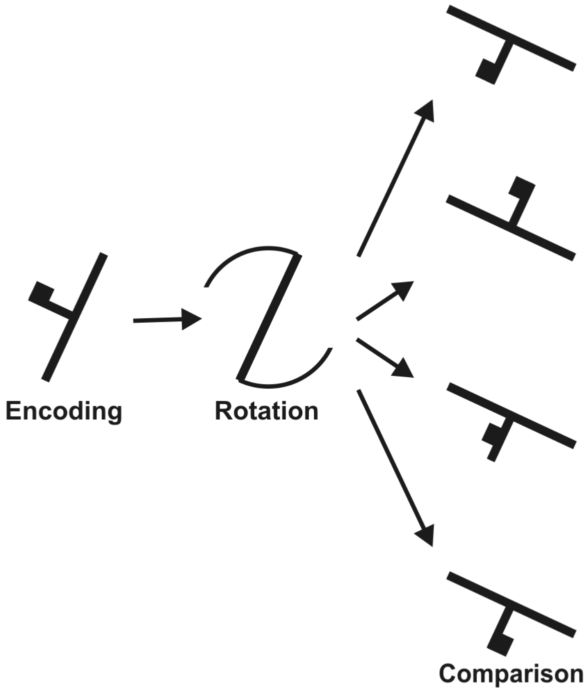

Figure 3.3. *Illustration of the general trial structure with a complex stimulus. The original stimulus is followed by rotation cues (the arcs). After rotation is finished, the comparison stimulus appears. The rotation cues shown during the rotation interval indicate the direction (here: counterclockwise) and the amount (here: 90°) of to-be-performed rotation on each trial. The stimulus has to be mentally rotated from the one to the other end of these arcs as if the arcs were rails along which the stimulus moves. In 50% of trials one piece of information differed between to-be-imagined and comparison stimulus. Participants' task was to indicate whether the two stimuli matched or not. The uppermost comparison stimulus is a match, whereas the remaining comparison stimuli are the mismatches that were possible in this example (given the original stimulus and the rotation cues displayed, for further details on stimulus types and their mismatches see Figure 3.4).*

We constructed three types of stimuli with controlled amounts of comparison-relevant spatial-relational information and as little distracting detail as possible (see Figure 3.4). For *simple stimuli* only one piece of information was comparison-relevant, namely to which side of the larger line the smaller line is attached. *Visually complex stimuli* included an additional piece of comparison-relevant information concerning whether the square is in the middle or at the end of the smaller line. *Complex stimuli* additionally included a third piece of comparison-relevant information, namely on which side of the smaller line the square is located. Whether the square is located in the middle or at the end of the smaller line can be encoded orientation-independently. On which side of the larger line the smaller line is attached and on which side of the smaller line the square is located, in contrast, must be encoded orientation-dependently.

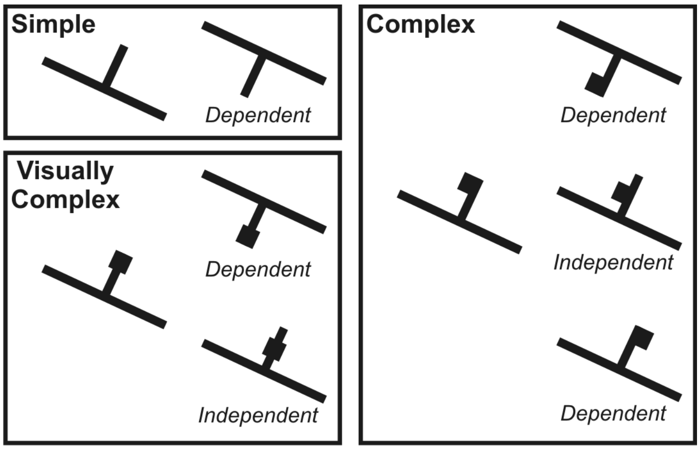

Figure 3.4. *Examples of stimulus types and their mismatches. On each trial, the comparison stimulus either matched the to-be-imagined stimulus (left side of each box) or had the expected absolute orientation but mismatched in exactly one piece of information (right side of each box). Whether the mismatching piece of information is orientation-dependent or orientation-independent is indicated below each mismatching stimulus. As rotation cues indicated the final, to-be-imagined stimulus position on each trial (see Figure 3.3), the simple and visually complex stimuli mismatching in orientation-dependent information were indeed mismatches, even though they can be rotated into congruence if the rotation cues are ignored.*

The visually complex stimuli employed here are of greater comparative visual complexity relative to simple stimuli according to all criteria employed in earlier mental rotation studies. They are made up of more (nonredundant) parts (Yuille & Steiger, 1982), have more inflictions on their perimeter (more angles and vertices; e.g., Cooper, 1976) and are less compact (e.g., Bethell-Fox & Shepard, 1988). Visually complex and complex stimuli, in contrast, share a comparable level of visual complexity according to these criteria. As Kosslyn (1994) discusses possible influences of stimulus circumference on rotational speed, we took care that visually complex and complex stimuli have exactly the same circumference.

Critically, complex stimuli differ from simple and visually complex stimuli in the amount of comparison-relevant orientation-dependent information, whereas simple stimuli differ from both other types in the amount of comparison-relevant orientation-independent information, in visual complexity, in circumference and in the number of comparison-relevant stimulus parts (see Table 3.1). In the following, we will for convenience use *orientation-independent information/visual complexity* as an umbrella term for the differences between simple and visually complex stimuli. If holistic visual mental images were rotated, representational complexity might differ between simple and visually complex stimuli, for example, because their circumference differs (cf. Kosslyn, 1994). Visually complex and complex stimuli would however be of equal representational complexity. Notably, even if only comparison-relevant stimulus parts were rotated in a piece-meal fashion, visual mental images of visually complex and complex stimuli would not differ in complexity. Once the spatial relation between the smaller line and the square is encoded in any visual way, all comparison-relevant spatial-relational information that these parts carry is represented implicitly (see Chapter 3.2). A visual mental image of only the smaller line and the square would already implicitly represent the comparison-relevant piece of orientation-independent information in visually complex stimuli and two pieces of comparison-relevant information (one orientation-dependent, one orientation-independent) in complex stimuli (see Figure 3.4 and Table 3.1). We, in contrast, predict that representational complexity is equal for simple and visually complex stimuli and higher for complex stimuli. For simple and visually complex stimuli one piece and for complex stimuli two pieces of orientation-dependent information must be rotated in order to successfully solve the comparison task (see Table 3.1).

Table 3.1

Crucial Characteristics of the Employed Stimuli.

Stimulus Type	Dep	Indep	Parts	Visual complexity
Simple	1	0	2	Low
Visually complex	1	1	3	High
Complex	2	1	3	High

Note. Dep = Number of pieces of orientation-dependent information. Indep = Number of pieces of orientation-independent information. Parts = Number of comparison-relevant stimulus parts (a spatial relation exists between at least two stimulus parts).

As mentioned above (Chapter 3.3), Takano (1989) has shown that whenever two stimuli that differ in orientation-independent information are presented simultaneously, no mental rotation is performed, because a mismatch can be detected without mental rotation. For our stimuli this means that on trials in which the position of the square on the smaller line (the piece of orientation-independent information) differs between stimuli, participants would not perform mental rotation at all. Our critical question however concerns the representation of both orientation-dependent and orientation-independent information during mental rotation. This is why we did not present the two stimuli simultaneously, but presented the comparison stimulus on each trial after the rotation had already been performed (see Figure 3.3). That is, we employ a successive-presentation mental-rotation task with rotation cues (see Chapter 1.3). With this successive presentation, while performing mental rotation, participants do not know whether the upcoming stimulus will match the original stimulus, differ in orientation-dependent information or differ in orientation-independent information. They consequently cannot compare the comparison-relevant orientation-independent relation between the smaller line and the square prior to performing mental rotation. Instead, they have to represent all comparison-relevant information until the rotation process is finished and the comparison stimulus appears[13].

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[13] We will show that only orientation-dependent information is rotated. Critically, our design forces participants to also represent orientation-independent information. Therefore, we will in the following also discuss, how orientation-independent information might be represented outside the rotated representation.

4. Experiment 1a: An Influence on Rotational Speed

As mentioned above (Chapter 3.1), the slope of the function relating rotation time to rotational angle is generally interpreted as reflecting the speed of mental rotation which in turn is assumed to be influenced by characteristics of the rotated representation. The more information is represented and consequently has to be processed, the slower the performed rotation. This allows us to derive specific predictions from the holistic and visual piece-meal hypotheses on the one and our hypothesis that only orientation-dependent information is represented in the rotated representation on the other hand. The visual piece-meal hypothesis would predict that the slopes for visually complex and complex stimuli should be identical and steeper than the slope for simple stimuli, because simple stimuli are visually less complex and contain one comparison-relevant stimulus part less than the other two stimuli. The original holistic hypothesis would not predict any differences in rotational speed. Nevertheless, one explanation for differences in rotational speed is in line with the holistic hypothesis. Stimuli with a larger circumference might be rotated more slowly, because the scanning around the rotated stimulus' circumference becomes necessary after each rotational step in order to keep its shape intact (Kosslyn, 1994). Therefore, if it predicts any difference in slope at all, the holistic hypothesis would predict the same pattern as the visual piece-meal hypothesis, namely a slower rotation of visually complex and complex compared with simple stimuli. In contrast, we predict that the slope for simple and visually complex stimuli is identical and shallower than the slope for complex stimuli, because complex stimuli contain one piece of comparison-relevant orientation-dependent information more than the other two stimuli (Technique 1, see Chapter 3.7).

Our main hypotheses concern the mental representation during mental rotation. We might however also gain some insight into the mental representation after mental rotation. Probably, after rotation is performed, the resulting mental representation is recoded in order to prepare for the comparison process and other or additional information than during the rotation phase is made explicit. If this final representation is a visual mental image of the stimulus parts, all types of mismatches should be detected at an equal speed, because it can be matched directly to the perceptual visual input from the comparison stimulus—comparison times should not differ for the different types of mismatches. If, in contrast, the final representation explicitly represents only orientation-dependent information, mismatches in orientation-dependent information should be detected much faster than mismatches in orientation-independent information (Technique 2, see Chapter 3.7).

4.1 Method

4.1.1 Participants

Twenty-eight members of Saarland University (16 female; age range: 17-36, median age: 22) received €8 per hour for participation. They reported having normal or corrected-to-normal vision and gave informed consent after the nature of the study had been explained to them. Data from one participant was excluded for not following the instructions as evident by an overall accuracy (.53) at chance level (.50).

4.1.2 Design

The original stimulus, which was simple, visually complex or complex (*stimulus type*), was displayed in one of six orientations (±70°, ±110°, ±150°) and had to be rotated around one of three angles (45°, 90°, 135°; *rotational angle*) either clockwise or counterclockwise. Original values for each of the maximally three pieces of information within a stimulus were determined at random. There were two possible values for each of the maximally three pieces of comparison-relevant information (e.g., for complex stimuli, the smaller line was attached either to the one or to the other side of the larger line, the square was either in the middle or at the top of the smaller line and either to the one or to the other side of it). On half of the trials the comparison stimulus exactly matched the to-be-imagined stimulus. On the other half of trials, the comparison stimulus differed from the original stimulus in a single piece of information. The two possible mismatches (see Figure 3.3) for visually complex stimuli were equiprobable. A mismatch in the second piece of orientation-dependent information (on which side of the smaller line the square was located) appeared twice as often as the other two types of mismatches for complex stimuli. This imbalance was introduced in order to avoid the overall probability of a mismatch in the second piece of orientation-dependent information becoming too low. A low probability would make processing this piece of information unimportant for obtaining a high accuracy rate and thereby might encourage participants to simply ignore it. To sum up, depending on the stimulus type there were between two and four possible *match types* (matches, mismatches in the first piece of orientation-dependent information, mismatches in orientation-independent information and mismatches in the second piece of orientation-dependent information). All factors were varied within participants. The experiment consisted of 432 regular trials plus rescheduled trials as detailed below.

4.1.3 Procedure

Stimulus presentation and response recording was controlled by E-Prime 2.0 Software (Psychology Software Tools, 2005). All stimuli were 3° of visual angle in size and presented in black against a gray background at the center of the screen. The trial procedure is displayed in Figure 4.1. On each trial, after a fixation cross of 500 ms duration the original stimulus was shown for 1000 ms. Two arcs whose one end touched the original stimulus' main axis indicated the direction and amount of rotation. They appeared 200 ms before the offset of the original stimulus. Participants were instructed to press the space bar as soon as they had finished rotation along these arcs. The *rotation time* from offset of the original stimulus until pressing of the space bar was our main dependent variable of interest. Immediately after this press, the comparison stimulus appeared for 500 ms. The comparison stimulus was always of the same type as the original stimulus and appeared in the indicated orientation but could differ in one piece of information (see Figure 3.4). From onset of the comparison stimulus, participants had 800 ms to decide whether it was the stimulus they had to imagine or not by pressing a key with their left or right index finger. If this key press was not given within the time limit, the trial counted as a *miss*. Response hand-assignment was counterbalanced across participants. The *comparison time* from onset of the comparison stimulus until participants' second key press was our secondary dependent variable of interest. The time window allotted for the comparison was rather narrow in order to discourage participants from pressing the space bar before having finished the rotation. During the 500 ms inter-trial interval an empty screen was shown. In this first study, participants were not informed about the amount and type of the stimuli's informational content to find out whether they would spontaneously identify all comparison-relevant information.

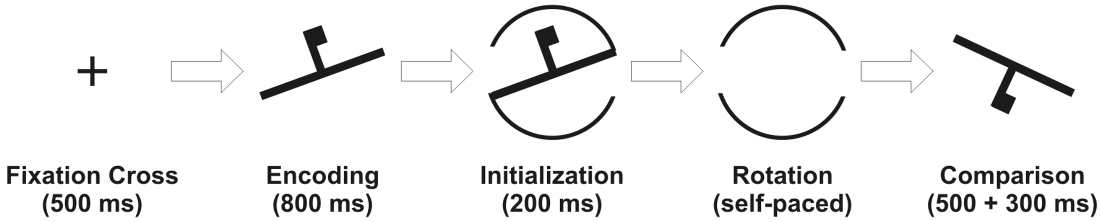

Figure 4.1. *Trial procedure of Experiment 1a. Participants had to rotate a mental representation of the encoded original stimulus around the angle indicated by the rotation cues and to compare the final mental representation to the ensuing comparison stimulus. Rotation times and comparison times were recorded separately. The comparison stimulus was shown for only 500 ms but participants had 800 ms in total to decide whether it matched the rotated original stimulus or not.*

Before data acquisition started, participants practiced the task until they had responded correctly to 10 simple stimuli in a row. As we analyzed rotation times of correct trials only, after the 432 regular trials, we rescheduled all incorrectly answered trials. Rescheduling continued (each time assigning a new random order) until all trials were correctly solved exactly once. In addition, participants were encouraged to achieve an accuracy rate of 90% or more. Feedback on accuracies and rotation times was provided every 20th trial. When participants' accuracy fell below 90% they were reminded of this target value. In total we obtained 48 observations per participant and Stimulus Type × Rotational Angle cell.

4.2 Results

4.2.1 Excluded participants

If information is systematically ignored, it cannot influence rotation times. Therefore the final analysis only included data from participants who processed all comparison-relevant information. As an objective criterion that information *x* of stimulus *y* was not ignored, we conducted a χ^2-test (on data from all except the reentered trials) of whether the relative frequency of mismatch answers in case of a change in information *x* (*x*-hit) was significantly higher ($p < .05$) than the relative frequency of mismatch answers in case of a match (false alarm) for stimulus *y*. Data of 7 participants failed this test for at least one type of information. Among these, 6 participants ignored the piece of orientation-independent information in complex stimuli. Four participants additionally ignored the piece of orientation-independent information in visually complex stimuli and 2 participants additionally ignored the second piece of orientation-dependent information. One participant ignored only the second piece of orientation-dependent information. The final sample included 20 participants (50% female; age range: 20-36, median age: 22).

4.2.2 Rotation times

All following analyses are based on median reaction times as these are less sensitive to outliers than mean reaction times. We employed MANOVAs instead of ANOVAs, because in the employed all-within subjects design the sphericity assumption underlying repeated-measurements ANOVA was often violated. Significant interactions and main effects were further decomposed by testing for polynomial trends and computing pair-wise comparisons. In all graphs, 95%-confidence intervals are shown. If not otherwise noted, for this and for all following experiments, construction followed the procedure described by Jarmasz and Hollands (2009). *Df*s to establish the criterion *t*-value for the confidence intervals were corrected for violation of the sphericity assumption by ε (Greenhouse & Geisser, 1959) as suggested by Loftus and Masson (1994). The effect on which the respective confidence intervals are based is indicated below each figure.

As evident in Figure 4.2, rotational angle had a linear influence on rotation time for complex and visually complex but not for simple stimuli. As predicted, this linear trend was clearly modulated by the amount of orientation-dependent information. The slope for complex stimuli was steeper than that for visually complex stimuli. The difference in slope between simple and visually complex stimuli, however, is more complicated. A within-subject 3 (stimulus type) × 3 (rotational angle) MANOVA on median rotation times showed main effects of stimulus type, $F(2,18) = 9.85$, $p = .001$, $\eta_p^2 = .49$, and rotational angle, $F(2,18) = 22.46$, $p < .001$, $\eta_p^2 = .68$, which were modulated by a Stimulus Type × Rotational Angle interaction, $F(4,16) = 4.45$, $p = .01$, $\eta_p^2 = .31$. Linear trends of rotational angle were present for each stimulus type (*p*s < .001), whereas quadratic trends were absent for complex and visually complex stimuli (*p*s > .47), but clearly present for simple stimuli, $F(1,19) = 16.12$, $p < .001$. The Stimulus Type × Rotational Angle interaction was driven by a modulation of the linear trend by the amount of orientation-dependent information, $F(1,19) = 5.36$, $p = .03$, which had no quadratic component, $F(1,19) = 0.22$, $p = .64$, and by a modulation of the linear trend by orientation-independent information/visual complexity, $F(1,19) = 7.06$, $p = .02$, which, in contrast, had a quadratic component, $F(1,19) = 3.78$, $p = .07$. As predicted, rotational speed was lower for complex than for visually complex stimuli. The difference between simple and visually complex stimuli, in contrast, was not predicted and was apparently more complicated.

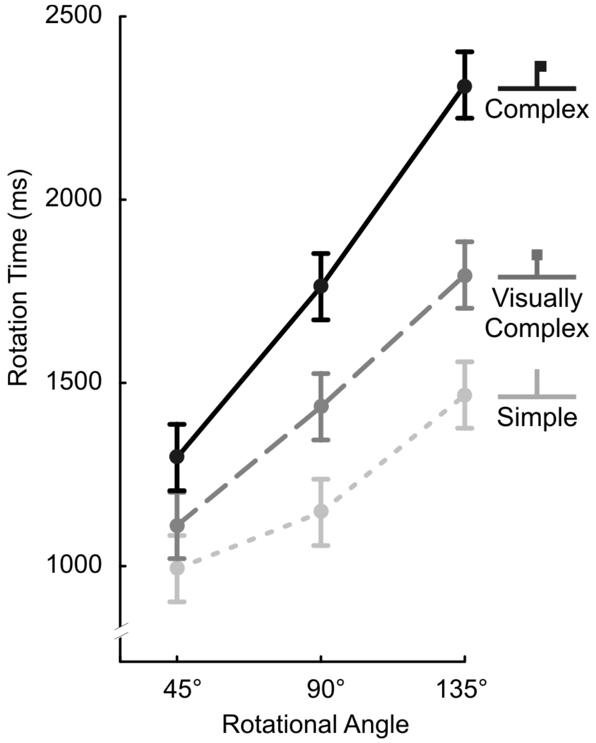

Figure 4.2. *Rotation times as a function of rotational angle and stimulus type in Experiment 1a. The amount of orientation-dependent but not of orientation-independent information influences rotational speed. Confidence intervals are based on the Stimulus Type × Rotational Angle interaction.*

The presence of the nonlinear trend of rotational-angle on rotation times for simple stimuli means that either the increase from 45° to 90° or the increase from 90° to 135° was influenced by additional factors not directly related to mental rotation. As evident in Figure 4.2, the only data point deviating from the exact parallelism of slopes for the lower two lines (simple vs. visually complex stimuli) was the rotation time for 45° rotations of simple stimuli, which was actually the easiest cell of the design. We suspected that the rotation time in this cell of the design was overestimated, because the time needed for rotation might have been shorter than the time needed to perform other cognitive processes working in parallel with mental rotation. Testing for a modulation of the increase in rotation times from 45° to 90° and from 90° to 135° of rotational angle by the amount of orientation independent information (the interaction contrasts) led to, $F(1,18) = 9.24$, $p < .01$ and , $F(1,18) = 0.61$, $p > .2$; that means, the increase from 45° to 90° was significantly modulated, but the increase from 90° to 135° was clearly not. These two modulations were consequently of different magnitude, $F(1,19) = 3.80$, $p = .06$. When only the increase from 90° to 135° is considered, slopes for simple and visually complex stimuli are identical.

4.2.3 Comparison times

As introduced above (Technique 2, Chapter 3.7.2), the pattern of comparison times (the time from onset of the comparison stimulus until participants press a key to indicate the outcome of their comparison) might shed some light on the content of the representation which participants hold active after the process of mental rotation has been finished. Figure 4.3 shows the very orderly pattern of comparison times over the three types of stimuli. As stimulus types differed in the number of mismatch types, the influence of this variable on comparison times had to be analyzed by three separate Match Type MANOVAs for each stimulus type and each match type. A main effect of match type was present for each of the three stimulus types, $F(1,19) = 13.51$, $p = .001$, $\eta_p^2 = .42$, $F(2,18) = 64.12$, $p < .001$, $\eta_p^2 = .77$, and $F(3,17) = 41.19$, $p < .001$, $\eta_p^2 = .79$ for simple, visually complex and complex stimuli, respectively. Responses to matches were fastest (all $ps < .007$) and responses to mismatches in orientation-dependent information were faster than those to mismatches in orientation-independent information (all *ps* $< .001$). In contrast to the following three experiments, responses to mismatches in the second piece of orientation-dependent information were slower than responses to the first piece of orientation-dependent information in complex stimuli, $F(1,19) = 19.06$, $p < .001$. Additionally, as evident in Figure 4.3, comparison time increased over stimulus types with the absolute amount of comparison-relevant information. To statistically confirm this pattern we conducted three additional Stimulus Type MANOVAs for each match type that occurred for more than one stimulus type (i.e., for all but mismatches in the second piece of orientation-dependent information). The main effect of stimulus type was present for matches, $F(2,18) = 31.01$, $p < .001$, $\eta_p^2 = .69$, as well as for mismatches in the first piece of orientation-dependent information, $F(2,18) = 28.96$, $p < .001$, $\eta_p^2 = .61$, and in the piece of orientation-independent information, $F(1,19) = 37.85$, $p < .001$, $\eta_p^2 = .67$. Loosely speaking, the comparison time pattern reflects main effects of stimulus type and match type without an interaction.

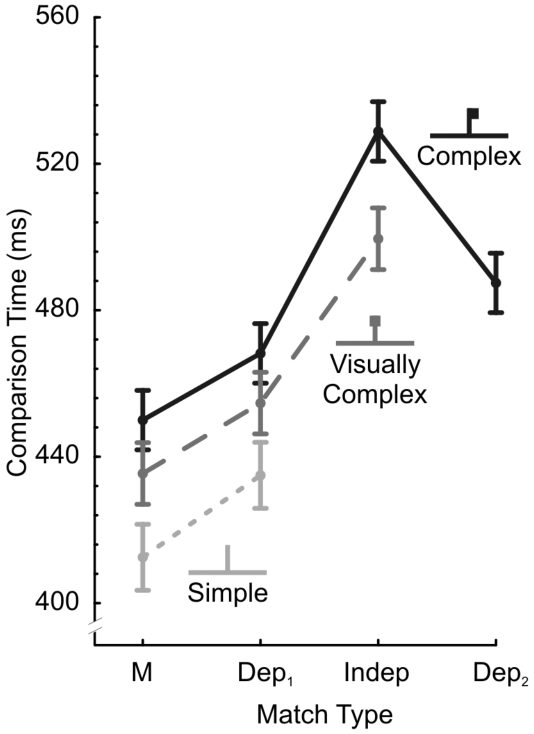

Figure 4.3. *Comparison Times as a function of stimulus and match type in Experiment 1a. Notably, mismatches in orientation-independent information are detected much slower than mismatches in orientation-dependent information. Confidence Intervals are based on the effect of match type separately for each stimulus type. M, match; dep$_1$, orientation-dependent mismatch 1 (side of the larger line, the smaller line is attached to); Indep, orientation-independent mismatch (position of the square on the smaller line); Dep$_2$, orientation-dependent mismatch 2 (side of the smaller line, the square is attached to).*

4.2.4 Accuracies

An examination of the pattern of accuracies showed that none of the reported effects can be explained by a speed-accuracy trade-off. In this and all following experiments accuracies tended to simply mirror the patterns of rotation and comparison times. Speed-accuracy trade-offs would predict short reaction times in cells with low accuracies. As usual in mental rotation studies, we observed the exactly opposite pattern, namely a tendency for high accuracies in cells with short reaction times and low accuracies in cells with long reaction times. Accuracies can principally be influenced by any process occurring before the response is given and are therefore much less conclusive than the measured reaction times. As analyses of accuracies did not further add to the understanding of the data we consequently refrained from unnecessarily crowding the result sections of the present work. Analyses on accuracies are neither reported for the present experiment or for any of the following experiments. Instead, Table A1 in the appendix shows mean accuracies from all four main experiments.

4.3 Interim Discussion

The pattern of rotation times confirmed our hypothesis that the representation in mental rotation includes orientation-dependent information. As predicted, the amount of orientation-dependent information influenced rotational speed. This was apparent in the difference in the linear trend of rotation times for complex and visually complex stimuli. However, the difference in linear trend for simple and visually complex stimuli might indicate that also other than orientation-dependent information is explicitly represented during mental rotation. We assume that this is not the case and that an additional process other than mental rotation influenced rotation times for 45° rotations of simple stimuli. In line with this interpretation the slope for simple stimuli, in contrast to visually complex and complex stimuli, clearly differed from linearity. As 45° rotations for simple stimuli actually are the easiest type of trials in the experimental design, it appears most probable that the estimation of rotation time in this cell was flawed.

Possibly, participants had not finished encoding at the time rotation cues were shown. Part of the encoding process would then have influenced measured rotation times. This should usually prolong all rotation times evenly (a shift of the y-intercept) and not influence the slope of the function. However, if at least part of the subject sample finished encoding only after a 45° rotation of the simple stimulus, encoding time would fully determine our indicator of rotation time in this cell. If 45° rotations of simple stimuli took shorter than the encoding process, the measured rotation times were overestimated. A second reason for such an overestimation might be that participants were able to proceed to the comparison stimulus only after the original stimulus had disappeared. As rotation cues appeared 200 ms before the original stimulus disappeared, very fast participants might already have finished the rotation before they were allowed to proceed. Because of these possible confounds, only the increase from 90° to 135° is a valid indicator of rotational speed for simple stimuli. According to this measure, rotational speed did not differ between simple and visually complex stimuli, indicating that the mental representation of these two stimuli was of equal complexity. It therefore appears that—as hypothesized—only orientation-dependent information is mentally rotated.

5. Experiment 1b: An Even More Controlled Influence on Rotational Speed[14]

The influence of rotational angle on rotation times for simple stimuli in Experiment 1a deviated from linearity. We assumed that other processes than mental rotation proper influenced the measured rotation times for 45° rotations of simple stimuli. We reasoned that sometimes rotation in this cell was finished before the encoding process had ended or before participants were allowed to proceed to the comparison stimulus. In Experiment 1b, consequently participants were given enough time to encode the original stimulus and they were allowed to proceed to the comparison stimulus as soon as the rotation cue was shown. As rotation cannot start sooner than with the onset of the rotation cue, this latter manipulation assured that even very fast participants were allowed to proceed to the comparison stimulus directly after having finished the rotation.

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[14] Experiment 1b and 2 are also reported in Liesefeld and Zimmer (2012). See also the credit line in Footnote 4.

Many participants of Experiment 1a ignored orientation-independent information. One reason might be that participants did not realize that mismatches in orientation-independent information were possible and therefore did not encode or maintain this piece of information. The number of participants ignoring information should therefore be drastically reduced if the instructions make participants aware of all comparison-relevant information. Furthermore, as discussed above (Chapter 3.6), we assume that not only instructions but also training on the task should influence experimental control over participants' representational content and thereby the purity of observed results. In order to test for such training effects we redesigned the task as to allow for a comparison of results in the first and second half of trials.

We deliberately included a slight imbalance into the design of Experiment 1a. In order to assure that the second piece of orientation-dependent information is processed, a mismatch in this type of information happened twice as often as a mismatch in the other two pieces of information in complex stimuli. The observed data pattern however indicates that participants' tendency to ignore this type of information was rather low (see Chapter 4.2.1). In Experiment 1b, we consequently also equated the probability of mismatch types in complex stimuli.

5.1 Methods

5.1.1 Participants

Experiment 1b was conducted while the first author was visiting the Chinese Academy of Sciences, Institute of Psychology in Beijing. Twenty-four students recruited at Beijing universities (12 women; median age: 21, age range: 17-25) received between 20-40 RMB (Chinese Yuan) for participation. The exact amount depended upon the participants' performance as clarified below. Participants reported having normal or corrected-to-normal vision and gave informed consent.

5.1.2 Design

The first stimulus shown on each trial (the *original stimulus*), which was either simple, visually complex or complex (*stimulus type*), was displayed in one of six orientations (-150°, -110°, -70°, 70°, 110°, 150°) and took one of the two possible values for each of the maximally three pieces of comparison-relevant information (e.g., for complex stimuli, the smaller line was attached either to the one or the other side of the larger line, the square was either in the middle or at the top of the smaller line and either to the one or to the other side of the smaller line, see Figure 3.4). Rotation was performed around one of three angles (45°, 90°, 135°; *rotational angle*) either clockwise or counterclockwise. In 50% of trials, the comparison stimulus differed from the to-be-imagined stimulus in exactly one piece of information. The maximally three possible types of mismatches (see Figure 3.4) for each stimulus type were equiprobable. All independent variables were varied within participants. The experiment consisted of two blocks with at least 216 trials each. The exact number of trials depended on the participants' performance as clarified below.

5.1.3 Procedure

Stimulus presentation and response recording was controlled by E-Prime 2.0 (Psychology Software Tools, 2005). All stimuli were about 3° of visual angle in size and presented in black against a gray background at the center of the screen. The trial procedure is displayed in Figure 5.1. Each trial began with a 500 ms forward-mask consisting of an overlay of all possible versions of the upcoming stimulus type. This resulted in different forward masks for each stimulus type and stimulus orientation and participants could consequently prepare for the type of the upcoming original stimulus and the orientation of its main axis. The original stimulus was then shown until participants pressed the space bar (*encoding time*). If this press was made within 1000 ms, the trial continued with a backward-mask consisting of the rapid presentation of seven or eight exemplars of the stimulus type. This mask was applied in order to discourage participants from pressing the space bar before having finished encoding. When the press was not made within the time limit, the trial was truncated and counted as a *miss*. After the backward-mask only the main axis of the stimulus remained on the screen and two arcs that touched this main axis appeared in order to indicate the direction and amount of rotation. Participants were instructed to press the space bar as soon as they finished rotation along these rotation cues. The *rotation time* from onset of the rotation cues until pressing of the space bar was our main dependent variable of interest. Immediately after this press, the comparison stimulus appeared. It was always of the same type (simple, visually complex, complex) as the original stimulus and its main axis always appeared in the orientation as indicated by the arcs. Mismatching stimuli differed in one piece of information only. Participants had 1000 ms to decide whether the comparison stimulus was the stimulus they had imagined or not (*comparison time*). The time-window allotted for this comparison was rather narrow in order to discourage participants from proceeding from the rotation interval to the comparison stimulus before having finished the rotation. Participants indicated the outcome of their comparison by a press with the left or the right index finger. If this key press was not given within the time limit, the trial counted as a *miss*. Response hand-assignment was counterbalanced across participants. During the 2000 ms inter-trial interval the screen was empty.

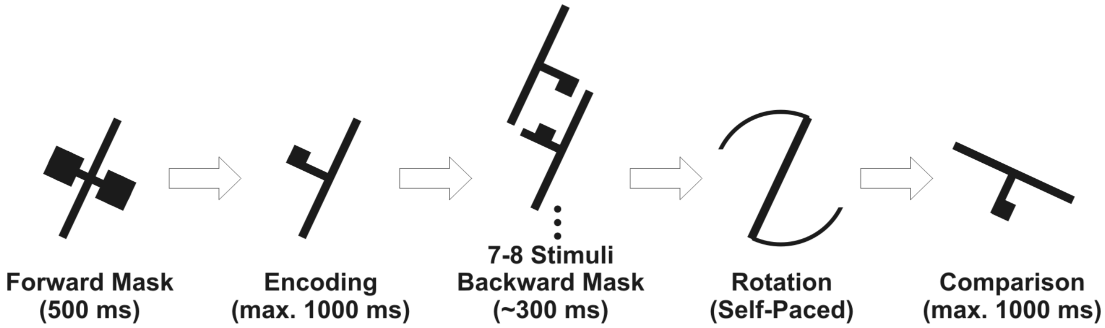

Figure 5.1. *Trial procedure of Experiment 1b. Encoding times, rotation times and comparison times were recorded separately.*

Participants were informed about the comparison-relevant stimulus characteristics in order to ensure that they were aware of all comparison-relevant information. Before data acquisition began, participants performed 30 trials with successively stricter time limits for encoding and comparison intervals. They continued practicing the task with the final 1000 ms-time limits until they either provided 10 correct answers in a row or worked through 50 additional practice trials. Only rotation times from correctly solved trials from the main part of the experiment were analyzed. Trials with incorrect answers or violations of a time limit (*misses*) were reentered into the random trial sequence so that all 216 trials were solved correctly exactly once on each block. After the first block, the second block started without any apparent break so that participants were unaware of the experiments' block structure. In addition to a 30 RMB basic pay participants received a bonus of 10 RMB for an overall accuracy rate of 90% or above and were penalized 0.1 RMB for each miss. Feedback on accuracy, misses and reaction times was provided in a self-terminated break after every 20th trial. Whenever participants' mean accuracy since the last feedback fell below 90% they were reminded of this target value. In total we obtained 48 data points per participant and Stimulus Type × Rotational Angle cell.

5.2 Results

5.2.1 Ignored information

Following the same procedure as described for Experiment 1a, we excluded participants who systematically ignored comparison-relevant information. Three participants ignored at least one type of information in complex stimuli. One participant ignored all information in complex stimuli (with an accuracy rate of .58 for this stimulus type; chance level: .50), one ignored the piece of orientation-independent and one ignored the first piece of orientation-dependent information in complex stimuli. Excluding these data sets resulted in the final sample of 21 participants (11 women; median age: 21, age range: 17-25).

5.2.2 Rotation times

As in Experiment 1a, all following analyses are based on median reaction times employing MANOVAs. Effects of stimulus type were decomposed by separate MANOVAs into effects of orientation-independent information/visual complexity by testing simple against visually complex stimuli, and effects of orientation-dependent information by testing visually complex against complex stimuli, respectively. Significant interactions and main effects were further decomposed by testing for polynomial trends and computing pair-wise comparisons.

As evident in Figure 5.2, rotational speed was modulated by the amount of orientation-dependent information but not by orientation-independent information/visual complexity. The slope for complex stimuli was steeper than that for visually complex stimuli whereas the slopes for simple and visually complex stimuli were of the same magnitude. A within-subject 3 (stimulus type) × 3 (rotational angle) MANOVA on median rotation times showed main effects of stimulus type, $F(2,19) = 12.83$, $p < .001$, $\eta_p^2 = .55$, and rotational angle, $F(2,19) = 15.17$, $p < .001$, $\eta_p^2 = .60$, which were modulated by a Stimulus Type × Rotational Angle interaction, $F(4,17) = 4.65$, $p = .01$, $\eta_p^2 = .33$. Linear trends of rotational angle were present for each stimulus type (ps < .001), whereas quadratic trends were absent (ps > .36). In order to deconstruct the interaction, we separately analyzed the effect of orientation-independent information/visual complexity (simple vs. visually complex stimuli) and the effect of the amount of orientation-dependent information (visually complex vs. complex stimuli) by two 2 (stimulus type) × 3 (rotational angle) MANOVAs. Both main effects were present in both MANOVAs (all ps < .010). In contrast and critically, there was no Stimulus Type × Rotational Angle interaction for orientation-independent information/visual complexity (simple vs. visually complex stimuli), $F(2,19) = 1.32$, $p = .29$, $\eta_p^2 = .05$, but only for the amount of orientation-dependent information (visually complex vs. complex stimuli), $F(2,19) = 8.71$, $p = .002$, $\eta_p^2 = .38$. This latter interaction was driven by a modulation of the linear trend by the amount of orientation-dependent information, $F(1,20) = 14.80$, $p = .001$, which had no quadratic component, $F(1,20) = 0.11$, $p = .74$. As predicted, rotational speed was lower for complex than for visually complex stimuli but did not differ between simple and visually complex stimuli.

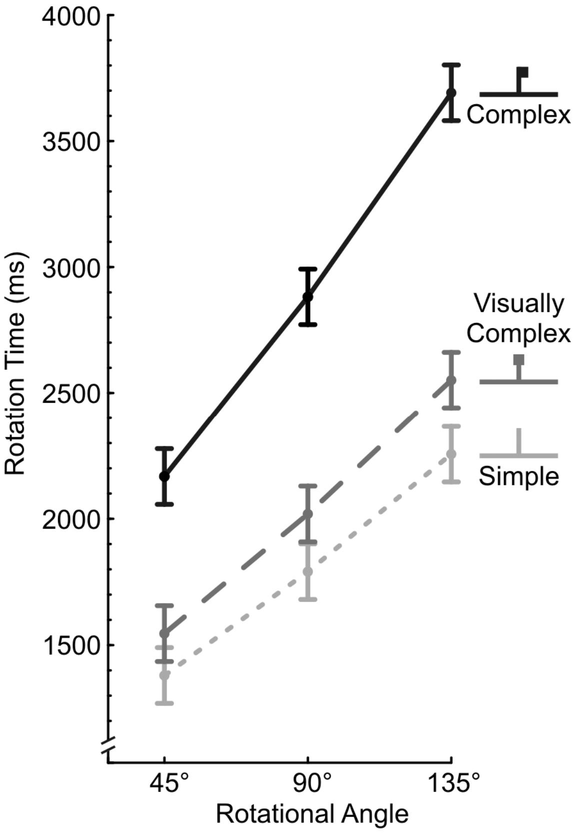

Figure 5.2. *Rotation times as a function of stimulus type and rotational angle in Experiment 1b. Only the amount of comparison-relevant orientation-dependent information influences rotational speed as reflected by the steeper slope for complex stimuli. Confidence intervals are based on the Stimulus Type × Rotational Angle interaction.*

5.2.3 Training effects on rotation times

A strict quantitative interpretation of our hypothesis that only orientation-dependent information is explicitly represented during rotation would predict that complex stimuli are rotated exactly half as fast as visually complex stimuli, because the former stimulus type contains double the amount of comparison-relevant orientation-dependent information compared with the latter stimulus type. We calculated rotational speeds in millisecond per degree of rotational angle (ms/°) for each Participant × Stimulus Type cell as *rotational speed* = (*rotation time*$_{135°}$ − *rotation time*$_{45°}$)/90°. In line with our general hypothesis, rotation was clearly slower for complex (mean: 16.93 ms/°) than for visually complex stimuli (mean: 11.17 ms/°), $t(20) = 3.85$, $p = .001$, $d_z = 0.84$[15]. However, rotation of complex stimuli was still significantly faster than the 22.34 ms/° predicted by a strict quantitative interpretation of our hypothesis, $t(20) = 3.52$, $p = .002$, $d_z = 0.77$. The reason for this divergence from the quantitative prediction might be that in spite of the careful instruction and the training phase, participants still represented comparison-irrelevant orientation-dependent information during a substantial part of the earlier trials (cf. Figure 3.2). Nevertheless, until the second half of the experiment they might have learned to employ a more efficient representation of only comparison-relevant orientation-dependent information.

As mentioned in the method section, the experimental structure allows for a division into a first and a second block of trials. As the second block was a replication of the first block and hence the two blocks are fully comparable, this allows us to directly test for training effects within the experiment. Rotation became faster from the first to the second block for all stimulus types, $t\text{s} > 3.21$, $p\text{s} < .005$, $d_z\text{s} > 0.70$, from an average speed of 16.00 ms/° to 8.71 ms/°. Importantly, in the second block of trials, rotation of complex stimuli (12.61 ms/°) was about half as fast as rotation of visually complex stimuli (7.22 ms/°), $t(20) = 3.67$, $p < .002$, $d_z = 0.80$, and therefore did not differ significantly from the speed predicted by a linear relationship between rotational speed and the amount of orientation-dependent information (14.44 ms/°), $t(20) = 1.09$, $p = .29$, $d_z = 0.24$.

5.2.4 Comparison times

Figure 5.3 shows the pattern of comparison times over the three types of stimuli. As in Experiment 1a, comparison times were analyzed by three separate Match-Type MANOVAs for each stimulus type and three Stimulus-Type MANOVAs for each match type that occurred for more than one stimulus type. A main effect of match type was present for each of the three stimulus types, $F(1,20) = 22.24$, $p < .001$, $\eta_p^2 = .53$, $F(2,19) = 33.30$, $p < .001$, $\eta_p^2 = .60$ and $F(3,18) = 29.76$,

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[15] We report d_z (J. C. Cohen, 1988, p. 44) as a measure of effect size for paired t-tests. Throughout the present work, only one effect size per effect is reported. That means whenever a η_p^2 is given we do not additionally report d_z for nested contrasts.

$p < .001$, $\eta_p^2 = .66$ for simple, visually complex and complex stimuli, respectively. Responses to matches were fastest (all *p*s < .001) and responses to mismatches in orientation-dependent information were faster than those to mismatches in orientation-independent information (all *p*s < .007). Responses to the two types of orientation-dependent mismatches in complex stimuli, in contrast, were equally fast ($p = .86$). In addition, comparison times increased with the absolute amount of comparison-relevant information for matches, $F(2,19) = 55.59$, $p < .001$, $\eta_p^2 = .73$, as well as for mismatches in the first piece of orientation-dependent information, $F(2,19) = 37.94$, $p < .001$, $\eta_p^2 = .64$, and in the piece of orientation-independent information, $F(1,20) = 37.67$, $p < .001$, $\eta_p^2 = .65$. Loosely speaking, the comparison time pattern reflects main effects of stimulus type and match type without an interaction.

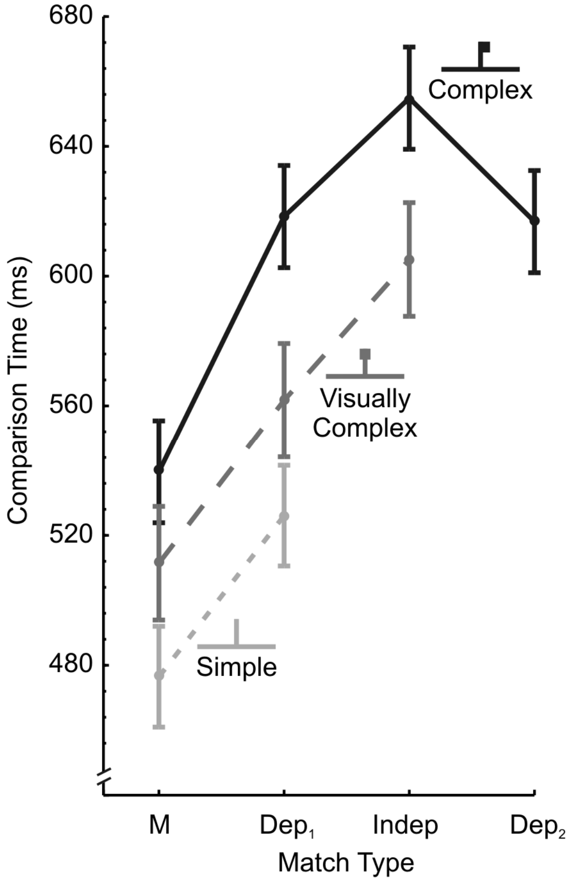

Figure 5.3. *Comparison times as a function of stimulus type and match type in Experiment 1b. Importantly, comparison times for mismatches in orientation-dependent information are shorter than those for mismatches in orientation-independent information. Confidence intervals are based on the match type main effects of each stimulus type. M, match; dep$_1$, orientation-dependent mismatch 1; Indep, orientation-independent mismatch; Dep$_2$, orientation-dependent mismatch 2.*

5.2.5 Encoding times

Encoding times differed between simple (409.26 ms), visually complex (465.10 ms) and complex (484.84 ms) stimuli, $F(2,19) = 26.42$, $p < .001$, $\eta_p^2 = .71$; $p < .001$ for all pair-wise comparisons. A quadratic trend, $F(1,20) = 18.00$, $p < .001$, and a linear trend, $F(1,20) = 55.53$, $p < .001$, reflected a larger increase from simple to visually complex stimuli compared with the increase from visually complex to complex stimuli.

5.3 Discussion

Rotation times for three types of stimuli (see Figure 4.2 and Figure 5.2) were measured in a successive-presentation mental-rotation task. We examined the slopes of the functions relating rotation time to rotational angle as indicators of rotational speed, because rotational speed should decrease with an increasing amount of information explicitly represented during rotation. As predicted, in Experiment 1a and 1b rotational speed was lower for complex than for visually complex stimuli, indicating that rotational speed was influenced by the only characteristic that differed between these two stimulus types, namely the amount of comparison-relevant orientation-dependent spatial-relational information. In contrast and as predicted, even though simple stimuli differed from visually complex stimuli in the amount of comparison-relevant orientation-independent spatial-relational information, in the number of comparison-relevant stimulus parts, and in visual complexity (see Table 3.1), rotational speeds for these two types of stimuli were identical.

In Experiment 1a, median rotation time in the easiest cell of the design differed from the predicted pattern. We reasoned that rotation times for 45° rotations of simple stimuli might be contaminated by influences other than mental rotation proper. As a consequence, in Experiment 1b we employed an improved experimental design. The result pattern from this latter experiment is exactly as predicted. We can consequently conclude that only orientation-dependent information is explicitly represented in the rotated representation.

Furthermore, we observed that mismatches in orientation-dependent information are detected much faster than mismatches in orientation-independent information. As a mismatch in explicitly represented information should be detected more easily than other types of mismatches, this finding indicates that even after mental rotation has finished, only orientation-dependent information is explicitly represented. This constitutes indirect additional evidence for our claim that the representation in mental rotation is nonvisual. If a visual mental image was rotated in order to be compared to a visually presented comparison stimulus, it would be very inefficient to recode this image after the rotation and make a type of nonvisual information explicit that is only implicitly represented in the incoming visual input from the comparison stimulus. It appears more reasonable to assume that the rotated nonvisual representation is simply not recoded before the comparison process starts. However, comparison-relevant orientation-independent information is not lost during rotation. After a short delay, participants are able to detect mismatches in orientation-independent information. We assume that orientation-independent information is stored in an alternative more passive mental representation which is not actively held in working memory. This hypothesis is discussed in detail below, where we can take converging evidence from Experiment 2 into account.

Eye fixation studies indicate that stimulus complexity influences only the encoding stage of mental-rotation tasks (Carpenter & Just, 1978; Just & Carpenter, 1985). These authors assume that for more complex stimuli it takes longer to extract the critical features of the stimulus. There are two potential reasons: Increasing stimulus complexity might render it difficult to determine which the critical, comparison-relevant features are. As we kept the employed stimuli simple and assured that participants would be aware of all comparison-relevant features, this explanation is rather improbable for the pattern of encoding times observed here. Alternatively, complex stimuli might include more critical features to extract. In line with this reasoning, the observed encoding times increase from simple through visually complex to complex stimuli, that is, with the amount of comparison-relevant information. However, the increase in encoding times from simple to visually complex stimuli was much stronger than the increase from visually complex to complex stimuli. This indicates that something additional had happened for orientation-independent information. Orientation-independent information is apparently not retained in the rotated representation. Possibly, storing it in an alternative, more passive representation takes extra encoding time. Indeed, this speculation is in line with fMRI data reported in Experiment 3 as discussed below.

One alternative explanation for the observed pattern of rotation times is in line with the visual piece-meal hypothesis and should be considered here. Maybe participants rotated only those stimulus parts that actually encoded comparison-relevant orientation-dependent information and therefore had to be rotated in order to solve the task (cf. Takano, 1989). Participants would then have rotated the square from our complex stimuli as a visual mental image but not the square from our visually complex stimuli. The visual mental image of visually complex stimuli would then have looked identical to the visual mental image of simple stimuli.

However, this alternative hypothesis predicts different comparison time patterns for complex and visually complex stimuli and therefore stands in contrast to the observed analogous pattern of comparison times for these two stimulus types in Experiment 1a and b (and in all of the following experiments). The alternative hypothesis can admittedly be brought into accordance with the observed comparison times for visually complex stimuli. A mismatch in orientation-independent information (a change of the square's position) is detected more slowly than a mismatch in orientation-dependent information. If for visually complex stimuli the square is not visually represented within the rotated representation, the alternative explanation would, like our hypothesis, implicate some alternative representation of orientation-independent information. Accessing this alternative representation might prolong comparison times relative to a simple template-match between the rotated visual representation and the comparison stimulus (which would be sufficient to detect a mismatch in orientation-dependent information). However, this explanation cannot be brought into accordance with the observed comparison times for complex stimuli. It predicts that all types of mismatches in complex stimuli are detected equally fast, because all comparison-relevant information would be present in the rotated visual representation. The difference in comparison times for mismatches in the piece of orientation-independent information and in the second piece of orientation-dependent information is especially strong evidence against the alternative interpretation, because both types of mismatches are due to a change of the square's position.

In contrast to the prediction from the alternative interpretation and in line with our hypothesis, the comparison time patterns for visually complex and complex stimuli are similar. This indicates that at the onset of the comparison stimulus orientation-independent information is similarly represented and consequently processed equally slow for both types of stimuli. This is in line with our hypothesis, because we assume that the rotated representation of neither stimulus type represents orientation-independent information and therefore detection of mismatches in orientation-independent information for both stimulus types should require a (comparatively slow) comparison with an alternative representation.

We predicted that rotational speed decreases with an increasing amount of represented orientation-dependent information. From our hypothesis, it does not inevitably follow that this relationship is linear. However, in the second block of trials of Experiment 1b, rotational speed for two pieces of comparison-relevant orientation-dependent information (complex stimuli) was indeed half the rotational speed for one piece of comparison-relevant orientation-dependent information (visually complex stimuli). As reasoned above (Chapter 3.6), with practice on a "same"-"different" judgment task participants' ability to differentiate comparison-relevant from comparison-irrelevant information should increase. This means that our participants might have represented more comparison-irrelevant information during trials of the first than of the second block. If part of this represented comparison-irrelevant information was orientation-dependent (e.g., if participants represented "the smaller line is to the right of the larger line" and additionally the then redundant information "the square is to the right of the larger line"), rotational speed unnecessarily slowed down. After the first block of trials our participants had indeed reached at a representation that was very efficient for the purpose of mental rotation, as indicated by the fact that their rotational speed had almost doubled.

This reasoning is in line with stimulus specific training-induced increases in rotational speed (e.g., Bethell-Fox & Shepard, 1988; Heil, Rösler, Link, & Bajrič, 1998)—not the process of mental rotation itself is trained, but participants learn to employ a more efficient mental representation of the trained stimuli. It appears that with training, the amount of represented information approaches the directly controllable amount of comparison-relevant information and consequently experimental control over the amount of represented orientation-dependent information increases. As a consequence, in the second block of the present study, rotational speed for two pieces of comparison-relevant orientation-dependent information did not differ significantly from half the speed for one piece of comparison-relevant orientation-dependent information. This supports a strong quantitative version of our hypothesis that mental rotation works on a representation that explicitly represents orientation-dependent information only.

6. Experiment 2: Tracking the Recoding of a Mental Representation via EEG[16]

In Experiment 1a and 1b we have shown that mental rotation does not work on a visual representation. However, participants perceive presented stimuli in mental-rotation tasks visually and consequently encode stimulus information via their visual system. The encoded information must therefore initially be represented visually. As Experiment 1a and 1b have shown, this early representation is apparently later recoded into a nonvisual representation which is mentally rotated. Might it be possible to observe such a recoding of people's mental representations? More direct evidence for this recoding would not only constitute converging evidence for our claim that the representation during mental rotation is nonvisual but might also inform a more detailed theory about the chain of mental processes taking place in mental-rotation tasks.

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[16] Experiments 1b and 2 are also reported in Liesefeld and Zimmer (2012). See also the credit line in Footnote 4.

6.1 Exploiting Slow Potentials as Online-Measures of Representational Content

One characteristic our mental-rotation task shares with common working-memory tasks is that participants have to maintain information over a short period of time. The change-detection task (for a review, see Luck, 2008) is a prototypical working-memory task that shares even more characteristics with our task. Participants have to decide whether two stimulus arrays that are separated by a short retention interval are the same or not. Like mental-rotation tasks in general, the typical change-detection task is a “same”-“different” judgment task with a conjunctive criterion and, like the mental-rotation task employed here, a stimulus onset asynchrony larger than zero (a retention interval; Farell, 1985; see also, Hyun & Luck, 2007). The change-detection task therefore is in many critical aspects similar to our mental-rotation task. As mentioned above (Technique 3, Chapter 3.7.3), from the electroencephalogram (EEG) recorded during the retention interval of change-detection tasks slow potentials can be extracted which have two characteristics that make them ideally suited as potential online-measures of explicitly represented information. Firstly, the topography of slow potentials depends on the type of comparison-relevant information that has to be maintained (e.g., Mecklinger & Pfeifer, 1996; Ruchkin, et al., 1997). Changes in the type of explicitly represented information (the representational content), might therefore lead to topographical changes in slow potential patterns. Secondly, the amplitude of slow potentials has been shown to increase with increasing working-memory load (Arend & Zimmer, 2011; Lehnert & Zimmer, 2008; Mecklinger & Pfeifer, 1996; Rämä, et al., 1997; Ruchkin, et al., 1995; Ruchkin, et al., 1997), that is, with the amount of explicitly represented information.

In Experiment 1a and 1b, we demonstrated that only orientation-dependent information is mentally represented during mental rotation by comparing the rotational speeds of stimuli that differ in orientation-dependent information only (visually complex vs. complex stimuli as shown in Figure 3.4) on the one hand and stimuli that differ in another type of spatial-relational information and in visual complexity (simple vs. visually complex stimuli as shown in Figure 3.4) on the other hand. In Experiment 2, we apply a similar logic to slow potentials in order to examine how the mental representation in mental rotation evolves over time. During intervals in which visual information is explicitly represented, slow potential amplitude should differ between simple and visually complex stimuli. Amplitudes should differ between visually complex and complex stimuli, in contrast, during those time-intervals during which orientation-dependent information is explicitly represented. Visually encoded information is known to be processed from the occipital cortex on into an anterior direction. The effect of the more abstract (i.e., further processed) orientation-dependent information should consequently emerge over a region more anterior compared with the effect of visual complexity.

Note, however, that slow potentials usually have a rather broad topography, including activation at many adjacent electrode sites. Additionally, if information in our task is indeed processed along the dorsal visual pathway (see Chapter 1.5.2 and 1.6.1), adjacent regions presumably process both types of information. As a consequence, we expect topographical differences only in as far as the center of activation of slow potentials should move into an anterior direction. The spatial resolution of slow potentials as measured by EEG is not sufficient to expect these differences to be significant in the present study. Therefore, we employ an explorative definition of the respective regions of interests (ROIs) as the set of those electrodes at which the respective effect is not significantly weaker than at all surrounding electrodes (see Chapter 6.4.2 for details). ROIs defined by this method might overlap. Nevertheless, the ROI for the effect of orientation-dependent information should be located more anterior compared with the ROI for the effect of orientation-independent information/visual complexity.

The effect of orientation-dependent information should emerge within a time-interval when mental rotation takes place. In the preliminary experiment (Chapter 2) we found that the process of mental rotation in the employed type of mental-rotation task might be reflected by a negative slow potential centered at Pz, starting about 1 s after rotation can potentially start and lasting for the whole rotation interval and slightly beyond. This component will be taken to confirm that mental rotation occurred and to determine when it was performed.

An effect of visual complexity during stimulus presentation would only indicate that our manipulation of visual complexity was successful, because in this phase the stimulus is physically present. Kosslyn et al. (2006, p. 4) consider only those representations mental images that are maintained active beyond perception of a stimulus. Evidence for the maintenance of a visual representation would be an effect of visual complexity that has a topography comparable to the topography of the effect during perception and that persists even beyond stimulus perception. Critically, we have to take into account that the timing of stimulus perception does differ from the timing of stimulus presentation. It takes about 150-200 ms until stimuli are consciously perceived (e.g., Fisch, et al., 2009; Gaillard, et al., 2009; Sergent, Baillet, & Dehaene, 2005) and it takes some time before a visual representation vanishes from iconic memory (e.g., Keysers, Xiao, Földiák, & Perrett, 2005; Loftus, Duncan, & Gehrig, 1992). For the event-related potential analyses, we will consequently define a perception interval that starts and ends slightly later than stimulus presentation.

6.2 Identification of Mismatches and the P3b

In Experiment 1a and 1b, we found that mismatches in orientation-dependent information are detected much faster than mismatches in orientation-independent information. We reasoned that this pattern of results indicates that even after rotation has finished, participants continue to actively represent orientation-dependent information only. Orientation-independent information, in contrast, has to be retrieved from an alternative, passive representation in order to be compared to the comparison stimulus. We might find converging evidence for this interpretation in the event-related potential emerging after onset of the comparison stimulus. The P3b, a component peaking at parietal electrode sites, usually between 250-650 ms after onset of a task-relevant stimulus, is a potential candidate (for recent reviews, see Nieuwenhuis, et al., 2005; Polich, 2007; Verleger, 1997). Although its exact interpretation is rather controversial, most researchers agree that the amplitude of the P3b depends on the subjective probability of the class of events the eliciting stimulus is subjectively perceived to belong to—the less expected the stimulus, the larger the P3b amplitude it elicits (e.g., R. Johnson & Donchin, 1980; Mars, et al., 2008). By comparing P3b amplitudes between different mismatch-types, we can consequently gain evidence about how participants group the different types of mismatches into classes (Technique 4, Chapter 3.7.4). From our interpretation of the comparison time pattern in Experiment 1b it follows that the two types of mismatches in orientation-dependent information are treated similar to each other but different from mismatches in orientation-independent information. Furthermore, we might gain additional insight into the comparison process in our task by measuring the latency of the P3b which under certain conditions is correlated with comparison times (for a review, see Verleger, 1997). Interpretation of P3b latency is even more controversial than its amplitude, but it seems to indicate the timing of a process mediating between stimulus evaluation and response selection (Verleger, Jaśkowski, & Wascher, 2005). A delay of this or a preceding process might be the reason for the delay of comparison times for mismatches in orientation-independent information. If this is the case also P3b latency should be prolonged for this type of mismatch.

To sum up, we expect (a) a long lasting effect of visual complexity on posterior slow potentials during perception and potentially for some time afterwards, and (b) an effect of orientation-dependent information on more anterior distributed slow potentials in a later time window; (c) P3b amplitude and (d) P3b latency should be larger for mismatches in orientation-independent than for mismatches in orientation-dependent information in visually complex as well as complex stimuli but be similar for the two types of mismatches in orientation-dependent information in complex stimuli.

6.3 Methods

6.3.1 Participants

Thirty-nine students recruited at Saarland University (21 women; median age: 22 years, age range: 20-34 years) received €8 per hour of participation. Participants reported having normal or corrected-to-normal vision and gave informed consent. Data from 1 participant were excluded from further analysis because of failure to follow the instructions, as evident by an overall accuracy (.48) at chance level (.50). We further excluded data from 3 participants with outlier overall accuracies below .75 (1½ times the interquartile difference below the group mean).

6.3.2 Design

The original stimulus which was either simple, visually complex or complex (*stimulus type*), was displayed in one of sixteen orientations (±15°, ±35°, ±55°, ±75°, ±105°, ±125°, ±145°, ±165°), and took one of the two possible values for each of the maximally three pieces of comparison-relevant information (e.g., for complex stimuli, the smaller line was attached either to the one or to the other side of the larger line, the square was either in the middle or at the top of the smaller line and either to the one or to the other side of it). Rotation was performed around one of three angles (45°, 90°, 135°; *rotational angle*) either clockwise or counterclockwise. In 50% of trials, the comparison stimulus differed from the to-be-imagined stimulus in a single piece of information. The two possible mismatches (see Figure 3.4) for visually complex stimuli were equiprobable. As in Experiment 1a, a mismatch in the second piece of orientation-dependent information (on which side of the smaller line the square was located) appeared twice as often as the other two types of mismatches for complex stimuli. This imbalance might help to differentiate between the influence of local and global mismatch probabilities on P3b amplitudes. All factors were varied within participants. The experiment consisted of 432 trials.

6.3.3 Procedure

Stimulus presentation and response recording was controlled by E-Prime 2.0 (Psychology Software Tools, 2005). All stimuli were about 3° of visual angle in size and presented in black against a gray background at the center of the screen. The trial procedure is displayed in Figure 6.1. Each trial began with a 500 ms fixation cross. The original stimulus was then shown for 1000 ms. Two arcs indicating the direction and amount of rotation appeared 200 ms before offset of the original stimulus and remained on screen for the whole rotation interval. Participants had to perform a mental rotation along these rotation cues. The comparison stimulus appeared 5500 ms after onset of the rotation cues[17]. It was always of the same type (simple, visually complex, complex) as the original stimulus and always appeared in the orientation indicated by the rotation cues. Mismatching stimuli differed from matching stimuli in one piece of information only. Participants had maximally 800 ms to decide whether the comparison stimulus was the stimulus they had imagined or not (*comparison time*). Participants indicated the outcome of their comparison by a press with the left or the right index finger. If this key press was not given within the time limit, the trial counted as a *miss*. Response hand-assignment was counterbalanced across participants. Between trials an empty screen was shown for an interval jittered between 1500 ms and 3500 ms.

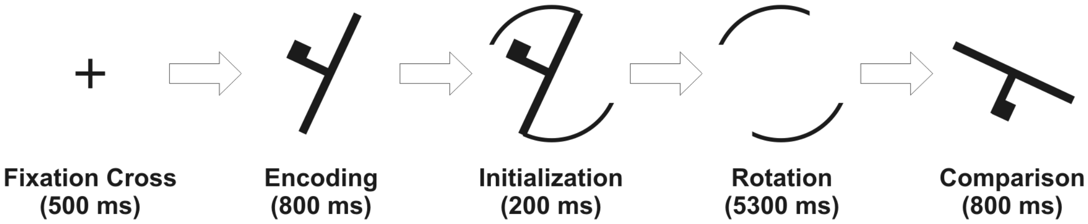

Figure 6.1. *Trial procedure of Experiment 2. Within the allotted 5500 ms, participants had to rotate a mental representation of the encoded stimulus around the angle indicated by the rotation cues in order to compare the final mental representation to the ensuing comparison stimulus.*

As in Experiment 1a, participants were not informed about the comparison-relevant stimulus characteristics. Before data acquisition began, participants trained the task until they gave at least 10 correct answers in a row or the experimenter decided to proceed to the main part of the experiment. Feedback on accuracy and comparison times was provided in a break after every 20th trial. Whenever participants' mean accuracy since the last feedback fell below 90% they were reminded of this target value. During each such break the amplifier was reset by the experimenter in order to avoid saturation.

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[17] As rotation times vary strongly within and between subjects, in order to obtain event-related potentials, we had to employ a fixed rotation interval. As a consequence, no rotation times were measured.

6.3.4 EEG recording

The EEG was collected by Ag/AgCl-electrodes at frontal (F3, Fz, F4), central (C3, Cz, C4), parietal (P3, Pz, P4) and occipital (O1, Oz, O2) positions according to the extended 10/20 system[18], amplified with BrainAmp DCs (Brain Products) and recorded with BrainVision Recorder 1.03 (Brain Products, 2007). An electrode between Fz and Cz served as the ground. Electrodes were referenced to an electrode at the left mastoid and re-referenced offline to an average of the original reference and an electrode at the right mastoid. Electrodes at the outer canthi of both eyes provided the horizontal and two electrodes above and below the right eye the vertical EOG. The impedance was kept below at least 10 kΩ for EOG-electrodes and below 5 kΩ for all data electrodes. Data was analog low-pass filtered at 250 Hz and sampled at 1000 Hz. No high-pass filter was set, because we were interested in slow potentials.

6.3.5 EEG artifacts handling and signal extraction

EEG data were analyzed with BrainVision Analyzer 2.01 (Brain Products, 2008). Drift artifacts were corrected using the method of Hennighausen, Heil, and Rösler (1993). We were interested in the effect of stimulus type on slow potentials emerging prior to comparison stimulus onset and in the effect of mismatch type on P3bs following comparison stimulus onset (see Figure 6.1). In order to extract slow potentials, data were first low-pass filtered at 30 Hz (48 dB/8ve). The EEG was then segmented into epochs from 800 ms before onset of the fixation cross until 1000 ms after onset of the comparison stimulus and drawn to a baseline from 200 ms before until onset of the fixation cross. Epochs whose 200 ms-baseline was contaminated with blink artifacts were rejected. Eye blinks were detected automatically and corrected according to the method of Gratton, Coles and Donchin (1983). Remaining epochs contaminated with severe artifacts were detected and rejected via a semi-automatic procedure. Epochs were drawn to a new baseline from 600 ms before until onset of the fixation cross and then averaged separately for each stimulus type and for each

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[18] We also recorded electrodes at P5 and P6 in order to check for lateralizations of the rotation-related slow potential. As there was none and without P5 and P6 we had a symmetric arrangement of electrodes, we do not further consider data measured at these electrodes.

rotational angle. Data from 4 participants were excluded because of an excessive number of artifacts in their EEG recording. Rejection of artifacts resulted in on average 76.00 (17.59%) retained epochs for each of these excluded participants. For all remaining participants we obtained at least 200 and on average 330.74 (76.56%) artifact-free epochs.

As P3bs were measured after comparison stimulus onset, only correctly solved trials were included into the averages. However, due to the much shorter time interval of interest, the number of retained epochs was increased considerably by preprocessing P3bs separately from slow potentials. Data were low-pass filtered at 40 Hz (48 dB/8ve). The EEG from correctly solved trials was segmented into epochs from 200 ms before until 800 ms after onset of the comparison stimulus and drawn to a baseline from 200 ms before until onset of the comparison stimulus. Epochs with blinks were rejected or, if too many epochs were lost, corrected as described above. Remaining epochs with other severe artifacts were also rejected, resulting in at least 317 and on average 367.13 (84.98%) artifact- and error-free epochs.

6.4 Results

6.4.1 Ignored information

Following the same procedure as described for Experiment 1a, we excluded 7 participants who ignored at least one type of information in at least one stimulus type. All of these participants ignored the piece of orientation-independent information in complex stimuli. Some additionally ignored the piece of orientation-independent information in visually complex stimuli, but none of these participants ignored any orientation-dependent piece of information. The final sample consisted of data from 24 participants (12 women; median age: 22, age range: 20-30). As preliminary analyses indicated no interaction between stimulus type and rotational angle for the regions and time intervals of interest, we separately analyzed slow potentials for each stimulus type averaged over rotational angles and for each rotational angle averaged over stimulus types. For each participant this lead to an average of 109.99 measurements per cell of interest (range: 73.33-134.00).

6.4.2 Slow potentials

Analogous to the analysis of rotation times in Experiment 1a and 1b and as described in detail above (Chapter 3.6), effects of stimulus type were decomposed into effects of orientation-independent information/visual complexity and effects of orientation-dependent information. As evident in Figure 6.2A, the effect of orientation-independent information/visual complexity was centered at electrode position Pz and the effect of the amount of orientation-dependent information at electrode position Cz. According to theoretical considerations as described above (Chapter 6.1) and to visual inspection of the grand averages at these two electrode sites (Figure 6.2B), we defined three time-intervals of interest, namely a *perception phase* from 700 ms until 1700 ms (from 200 ms after stimulus onset until 200 ms after stimulus offset), an *early processing phase* from 1700 ms until 2600 ms and a *late processing phase* from 4100 ms until 6900 ms. Topographical regions of interest (ROIs) were defined separately for the effect of orientation-independent information/visual complexity, the effect of orientation-dependent information and the effect of rotational angle for each time-interval in which the respective effect occurred. ROIs were determined by starting from a full 4 (anterior-to-posterior rows) × 3 (left-to-right columns) × 2 or 3 (respective effect) MANOVA on the mean voltages in the respective time-interval and then stepwise excluding those electrode rows, columns and single electrodes for which the effect was comparatively weak until no significant interaction ($p < .05$) with electrode site remained that included the respective effect.

The effect of orientation-independent information/visual complexity (simple vs. visually complex stimuli) was strongest at rows C (C3, Cz, C4) and P (P3, Pz, P4) for both the perception and early processing phases. The ROI for the effect of the amount of orientation-dependent information (visually complex vs. complex stimuli) during the late processing phase consisted of electrodes Fz, C3 and Cz, that means it was more anteriorly distributed and slightly left lateralized. ROIs for the effect of rotational angle consisted of electrode rows P (P3, Pz and P4) and O (O1, Oz, O2) for the early processing phase. During the late processing phase the effect of rotational angle was significantly stronger at Pz than at all other electrode sites. The ROI for the effect of rotational angle consequently differed between the early (rows P and O) and late processing phase (Pz only).

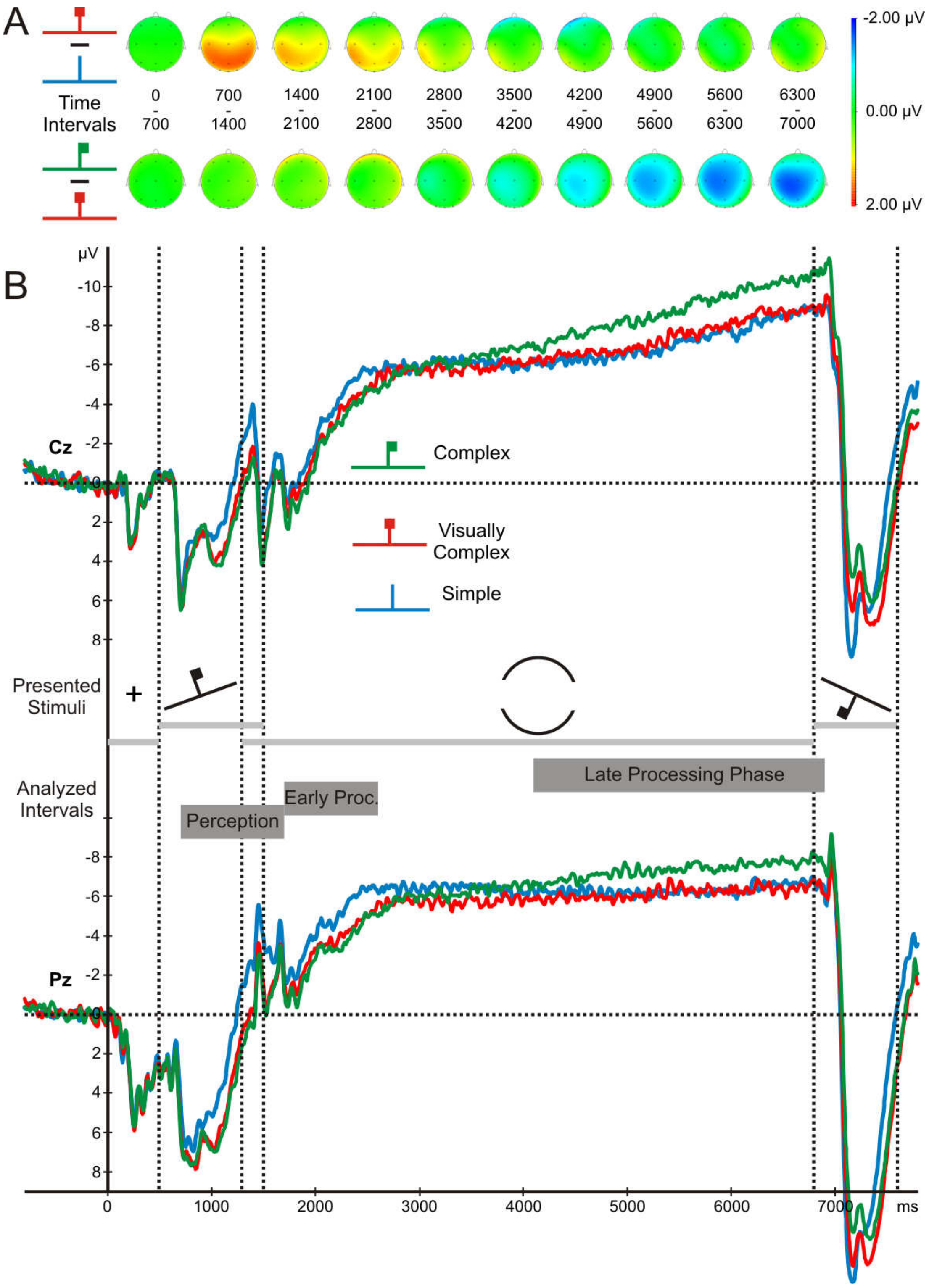


Figure 6.2. *Please refer to the figure caption on the right.*

Figure 6.2. *Effects of the stimulus types on slow potentials. (A) Spline-interpolated topographic maps of the effects of orientation-independent information/visual complexity (difference between visually complex and simple stimuli, upper row) and of the effect of the amount of orientation-dependent information (difference between complex and visually complex stimuli, lower row) displayed over time. During perception and in an early time-window directly following perception a positive effect of orientation-independent information/visual complexity at parieto-central electrode sites is present. In a later time window, this effect has vanished and a more anterior distributed negative effect of the amount of orientation-dependent information has emerged. (B) Grand averages showing the effect of stimulus type averaged over rotational angles at electrode sites Cz (where the effect of the amount of orientation-dependent information was strongest) and at Pz (where the effect of orientation-independent information/visual complexity was strongest).*

Analyzing the effect of orientation-independent information/visual complexity (see also Figure 6.3A), a 3 (time-interval) × 2 (simple vs. visually complex stimuli) MANOVA on mean amplitudes from the orientation-independent information/visual complexity ROI yielded an interaction, $F(2,22) = 8.58$, $p = .001$, $\eta_p^2 = .34$. The effect was present during perception, $t(23) = 6.35$, $p < .001$, $d_z = 0.93$, and during the early processing phase, $t(23) = 3.13$, $p = .004$, $d_z = 0.57$. During the late processing phase, in contrast, the effect of orientation-independent information/visual complexity was absent, $t(23) = .57$, $p = .57$, $d_z = 0.14$. The effect tended to be smaller during the early processing relative to the perception phase, $t(23) = 1.97$, $p = .06$, $d_z = 0.40$, and it clearly ceased from the early to the late processing phase, $t(23) = 3.05$, $p = .006$, $d_z = 0.62$.

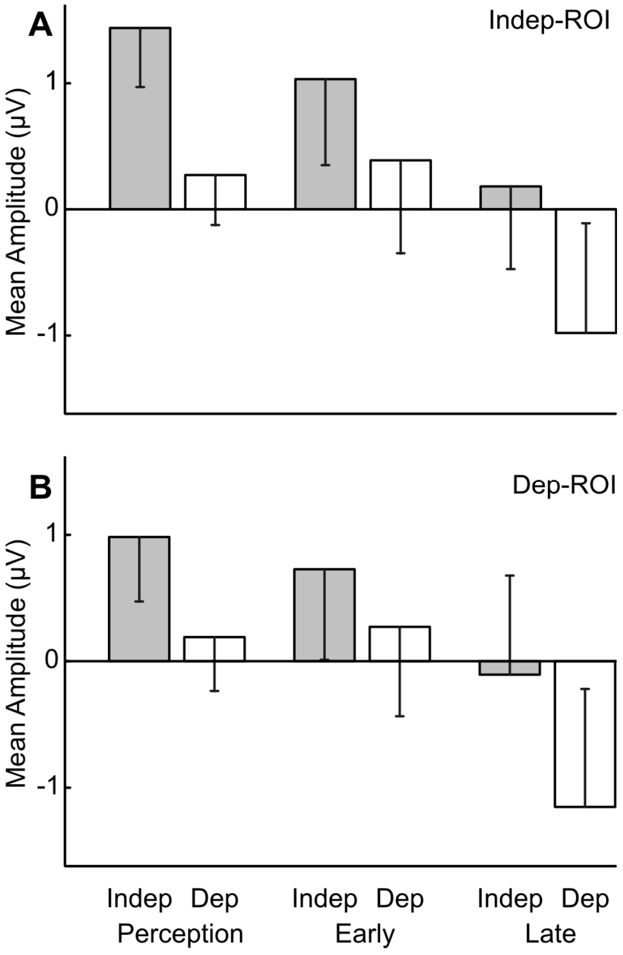


Figure 6.3. *The effect of the amount of orientation-independent information/visual complexity (Indep, gray bars, difference between visually complex and simple stimuli) and the effect of the amount of orientation-dependent information (Dep, white bars, difference between complex and visually complex stimuli) separately for the perception, early processing and late processing phase on amplitudes at (A) the region of interest (ROI) for the effect of orientation-independent information/visual complexity (Indep-ROI) and (B) at the ROI for the effect of orientation-dependent information (Dep-ROI). Error bars indicate the meaningful half of 95%-confidence intervals for the respective difference. Differences for which error bars do not cross the x-axis are significant with $p < .05$, two-tailed.*

Analyzing the effect of the amount of orientation-dependent information (see also Figure 6.3B), a 3 (time-interval) × 2 (simple vs. visually complex stimuli) MANOVA on mean amplitudes from the orientation-dependent information ROI also yielded an interaction, $F(2,22) = 9.82$, $p < .001$, $\eta_p^2 = .39$. This interaction was driven by a pattern exactly opposite to the pattern for the effect of orientation-independent information/visual complexity. An effect of orientation-dependent information was absent during perception, $t(23) = 0.93$, $p = .36$, $d_z = 0.16$, as well as during the early processing phase, $t(23) = 0.80$, $p = .43$, $d_z = 0.16$. During the late processing phase, in contrast, the effect was present, $t(23) = 2.56$, $p = .017$, $d_z = 0.46$. The effect did not differ between early processing and perception phase, $t(23) = 0.38$, $p = .71$, $d_z = -0.10$. That the effect of the amount of orientation-dependent information did not emerge before the late processing phase was further confirmed by significant interaction contrasts between late processing phase and perception phase, $t(23) = 4.03$, $p < .001$, $d_z = 0.82$, as well as between late and early processing phase, $t(23) = 4.45$, $p < .001$, $d_z = 1.03$.

As rotation cues did not appear before 1300 ms, it is not surprising that an effect of rotational angle was absent during the perception phase (from 700 ms until 1700 ms) at the early rotation ROI, $F(2,22) = 0.95$, $p = .40$, $\eta_p^2 = .05$, and at the late rotation ROI (Pz), $F(2,22) = 1.03$, $p = .37$, $\eta_p^2 = .06$ (see Figure 6.4). However, an effect of rotational angle was present during the early processing phase at the early rotation ROI, $F(2,22) = 15.63$, $p < .001$, $\eta_p^2 = .48$. This effect was due to a linear trend, $t(23) = 5.69$, $p < .001$, without quadratic component, $t(23) = 0.63$, $p = .54$. Also during the late processing phase an effect of rotational angle on amplitudes at the late rotation ROI, $F(2,22) = 8.49$, $p = .002$, $\eta_p^2 = .39$, and a linear trend, $t(23) = 4.11$, $p < .001$, were present. In contrast to the early processing phase, the quadratic component, $t(23) = 2.46$, $p = .021$, was significant, reflecting a smaller increase in amplitude from 45° to 90°, $t(23) = 2.05$, $p = .05$, compared with the increase from 90° to 135°, $t(23) = 4.03$, $p < .001$,. That the effect of rotational angle differed between the two processing phases was confirmed by two separate 2 (early vs. late processing phase) × 3 (rotational angle) MANOVAs on amplitudes at the early and late rotation ROI, respectively. For both ROIs, interactions between processing phase and rotational angle were present, $F(2,22) = 9.84$, $p < .001$, $\eta_p^2 = .17$, and $F(2,22) = 8.40$, $p < .002$, $\eta_p^2 = .15$, respectively.

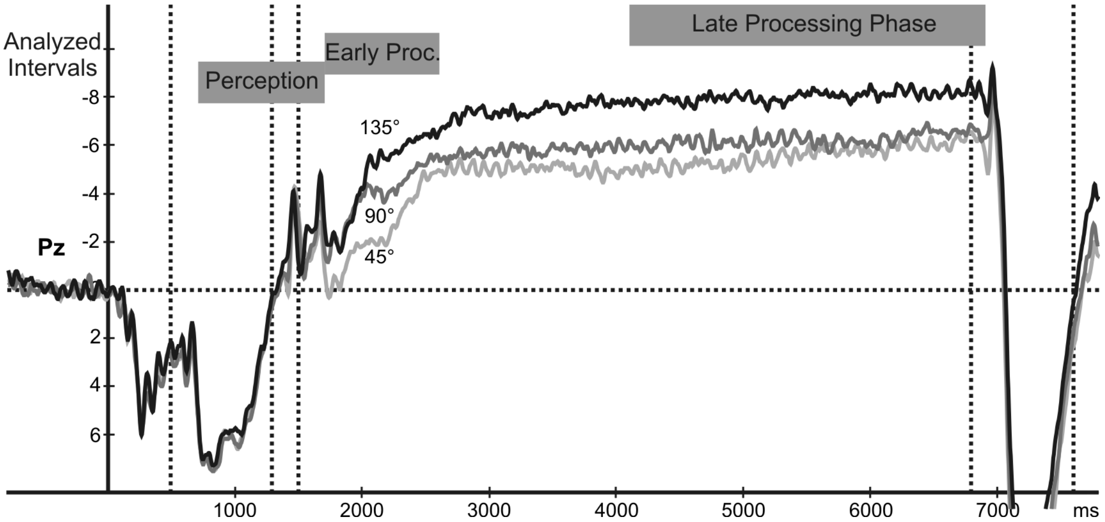
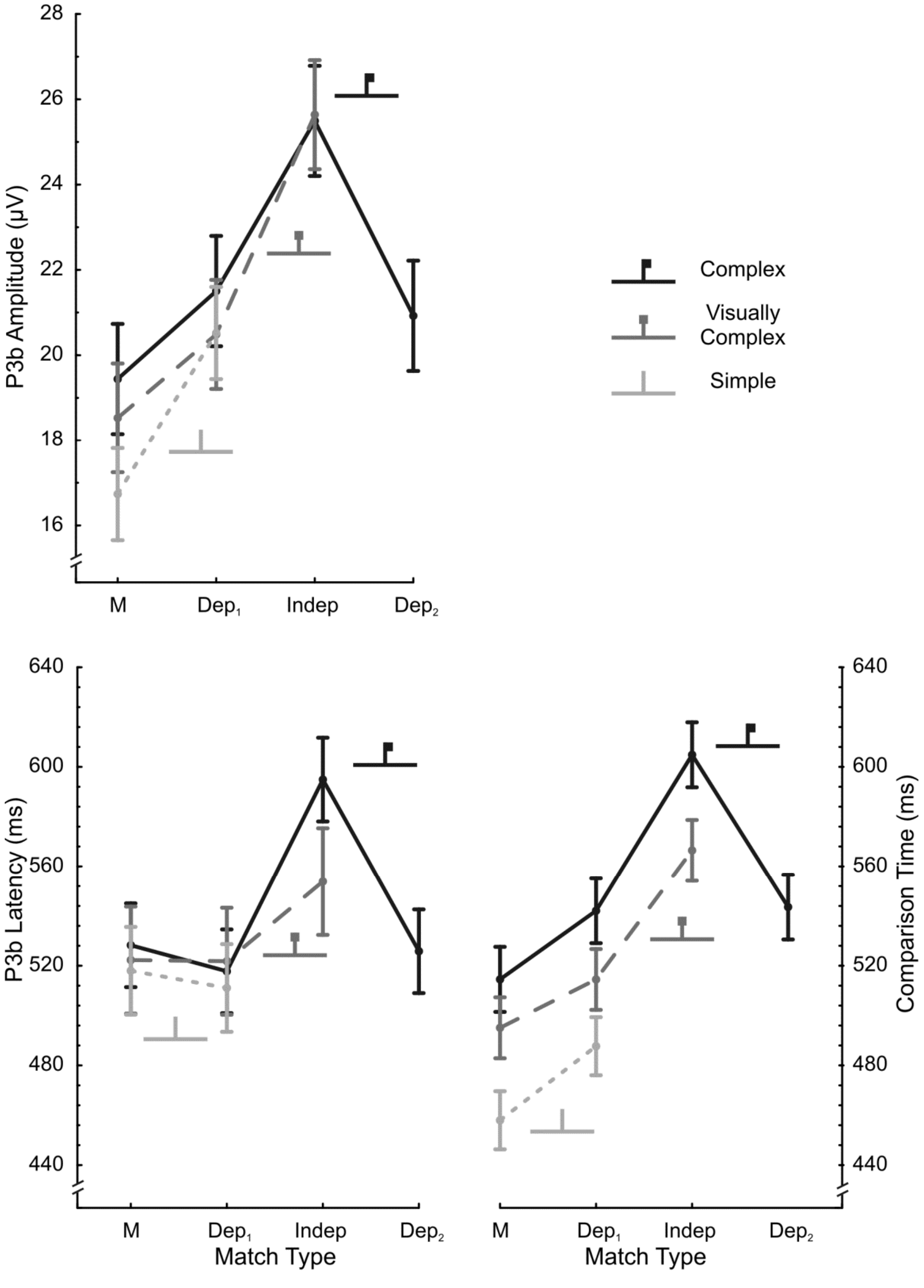


Figure 6.4. *Grand averages for the three rotational angles averaged over stimulus types. The components become more negative with increasing rotational angle from 45° (light gray) to 90° (dark gray) to 135° (black).*

6.4.3 Comparison times

Amplitudes and latencies of P3bs at Pz as well as comparison times for correctly solved trials are displayed in Figure 6.5. Effects of match type on comparison times were present for simple, $F(1,23) = 13.87$, $p = .001$, $\eta_p^2 = .38$, for visually complex, $F(2,22) = 30.62$, $p < .001$, $\eta_p^2 = .62$, and for complex stimuli, $F(3,21) = 51.04$, $p < .001$, $\eta_p^2 = .60$. Replicating the findings from Experiment 1b, responses to matches were fastest, all *p*s < .03, and responses to mismatches in orientation-dependent information were faster than those to mismatches in orientation-independent information, all *p*s < .001, whereas responses to the two types of mismatches in orientation-dependent information in complex stimuli were given at the same speed, $t(23) = 0.15$, $p = .88$. Main effects of stimulus type were present for matching comparison stimuli, $F(2,22) = 59.74$, $p < .001$, $\eta_p^2 = .76$, for mismatches in the first piece of orientation-dependent information, $F(2,22) = 27.00$, $p < .001$, $\eta_p^2 = .62$, and for mismatches in the piece of orientation-independent information, $F(1,23) = 25.40$, $p < .001$. All pairwise-comparisons were significant, *p*s < .001. As in Experiment 1a and 1b, loosely speaking, the comparison time pattern reflects main effects of stimulus type and match type without an interaction.



Electrophysiological

Behavioral

Figure 6.5. *Effects of stimulus and match type on P3b amplitudes, P3b latencies and comparison times in Experiment 2. Changes in orientation-independent information give rise to stronger and later P3bs as well as slower comparison times. Confidence intervals are based on the effects of match type separately for each stimulus type. M, match; Dep*$_1$*, orientation-dependent mismatch 1; Indep, orientation-independent mismatch; Dep*$_2$*, orientation-dependent mismatch 2.*

6.4.4 P3bs

As evident in Figure 6.6, P3bs peaked two times. As the effect of match type was strongest on the second peak, P3b peaks were defined as the local positive amplitude maximum within the time window 450 ms until 650 ms after comparison stimulus onset. Peak latencies and mean amplitude values ±10 ms around the peak were exported for statistical analysis. P3b amplitudes were higher at Pz than at all other electrodes (all *p*s < .006).

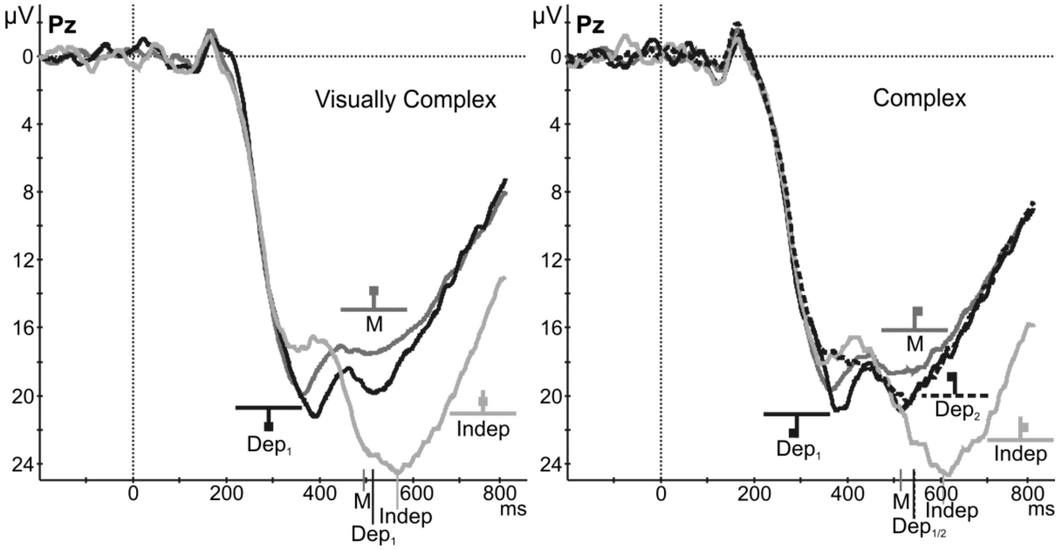


Figure 6.6. *Grand average P3b waveforms locked to comparison stimulus onset for visually complex and complex stimuli, separately for each match type. The P3bs following mismatches in orientation-independent information (Indep, light gray) differ considerably from P3bs following matches (M, dark gray) and mismatches in orientation-dependent information (*Dep_1* and *Dep_2*, black solid and black dotted, respectively). For comparison, mean comparison times for each condition are indicated at the x-axis.*

Effects of match-type on P3b amplitudes were present for simple, $F(1,23) = 26.29$, $p < .001$, $\eta_p^2 = .53$, for visually complex, $F(2,22) = 42.10$, $p < .001$, $\eta_p^2 = .59$, and for complex stimuli, $F(3,21) = 17.66$, $p < .001$, $\eta_p^2 = .41$. There was a tendency for matches to elicit the smallest P3bs, all *p*s < .10. Mismatches in orientation-dependent information elicited smaller P3bs than mismatches in orientation-independent information, all *p*s < .001, whereas P3b amplitude did not differ between complex stimuli mismatching in one of the two pieces of orientation-dependent information, $t(23) = 0.80$, $p = .43$. P3b amplitude did not differ between stimulus types for any type of mismatch, both $ps > .49$, that is, in contrast to the comparison time pattern there was no main effect of stimulus type (see Figure 6.5). Only for matches an effect of stimulus type on P3b amplitude was present, $F(2,22) = 9.93$, $p < .001$, $\eta_p^2 = .38$.

P3b latencies and reaction times were correlated over Participants × Stimulus Types × Match Type cells, $r = .41$, $p < .001$. P3b latency was significantly longer in response to mismatches in orientation-independent information than to matches and to mismatches in orientation-dependent information, all $ps < .05$. In addition, mismatches in orientation-independent information elicited a later P3b-peak in complex than in visually complex stimuli, $t(23) = 3.56$, $p = .002$. No other difference was significant, all $ps > .26$.

6.5 Discussion

We measured event-related potentials during the performance of a successive-presentation mental-rotation task, in order to explore how the mental representation employed in mental-rotation tasks evolves over time. An effect of orientation-independent information/visual complexity was observed at centro-parietal electrodes during stimulus perception. This effect persisted without changing topography for at least 1100 ms after the eliciting stimulus had already vanished from view. This long duration indicates that the original representation of the stimulus was kept active in working memory beyond iconic memory. In contrast and as predicted, an effect of the amount of orientation-dependent information emerged after the effect of orientation-independent information/visual complexity had started vanishing. In line with our hypothesis, this indicates that orientation-dependent information was made explicit and accessible in order to be rotated. Furthermore, the more anterior distribution of this effect indicates that the explicit representation of orientation-dependent information is located later in the processing chain and therefore is purportedly more abstract than the initial visual representation. This conclusion is based on the fact that visually encoded information is from the visual cortex on processed into an anterior direction. In sum, the observed pattern of slow potential activity includes several pieces of converging evidence for our hypothesis that the process of mental rotation works on a nonvisual mental representation that represents orientation-dependent information only. Note, however, that due to the low spatial resolution of the EEG and due to the explorative definition of ROIs in the present study, topographical differences must, for the moment, be interpreted with caution (see Chapter 6.1). In Experiment 3, we make use of the much higher spatial resolution of fMRI to further substantiate the findings reported here.

There is some concern about whether increases in slow potential amplitude reflect increasing working-memory load or other influences, as increasing effort or arousal (e.g., McCollough, Machizawa, & Vogel, 2007). Fortunately, this does not influence the interpretation of slow potential amplitudes as we exploit them. If holding information of type A but not of type B increases effort or arousal this fact just as nicely shows that information type A was explicitly represented and processed.

How are several pieces of orientation-dependent information rotated? Three explanations for the slowing down of rotational speed as a function of the amount of orientation-dependent information as observed in Experiment 1a and 1b (see also Experiment 3) are conceivable. Rotation might be performed on a representation that comprises several pieces of orientation-dependent information and rotation slows down, because more information has to be updated at each rotational step. Alternatively, pieces of information might be represented independently and rotated in parallel but all these rotation processes share a common limited resource. As these two hypotheses both implicate that all orientation-dependent information is made explicit before rotation begins, both predict an effect of the amount of orientation-dependent information starting no later than the mental rotation process itself. The present data therefore point to a third alternative. Pieces of information might be represented and rotated one after the other. Apparent rotational speed decreases simply because two rotations have to be performed for complex stimuli whereas only one rotation is necessary for simple and visually complex stimuli. That the effect of orientation-dependent information emerged only long after rotation had purportedly begun indicates that during the first rotation the amount of orientation-dependent information explicitly represented in working memory was the same for all three stimulus types. The second piece of orientation-dependent information in complex stimuli did apparently enter working memory only after this first rotation had been finished. No earlier than from this time point on did the representation for complex stimuli represent two pieces of orientation-dependent information and did therefore differ in complexity from the representation of visually complex stimuli.

The effect of mental rotation had a slightly different topography in the late compared with the early processing phase. In addition the effect had a quadratic trend in the former but not in the latter time-interval. This might indicate that we actually observed two different components that were sensitive to rotational angle. The later component was a negative slow potential as expected for the employed type of mental-rotation task based on the results from the preliminary experiment (Chapter 2). The earlier component in contrast was rather similar to the component reviewed by Heil (2002). It became manifest as a negative amplitude modulation of a P3b. Although this question cannot be fully solved here, it appears that this earlier component was induced by the processing of the rotation cue or the preparation of mental rotation and not by mental rotation proper.

At the time the second piece of orientation-dependent information was purportedly made explicit, the original stimulus had vanished from the screen, from iconic memory and, as indicated by the observed slow potential pattern, from working memory. We must consequently assume that in addition to the rotated representation, our participants held a passive backup representation. This backup representation was apparently not actively held in working memory.

In Experiment 1a, 1b and 2, participants took much longer to detect a mismatch in orientation-independent information. Apparently, the rotated representation is not recoded before comparison stimulus onset and consequently only orientation-dependent information is actively represented when the comparison process starts. This interpretation receives strong additional support by the finding that slow potentials are sensitive to the amount of orientation-dependent information only even after the onset of the comparison stimulus at 6800 ms (see Figure 6.2B). How were participants then able to detect mismatches in orientation-independent information? Orientation-independent information might be derived from an alternative representation that was not held active in working memory at the time of comparison stimulus onset. This possibly is the very same backup representation which was used to derive the second piece of orientation-dependent information during rotation of complex stimuli.

P3b amplitude is assumed to reflect how strongly the subject expected the stimulus class the eliciting stimulus is subjectively perceived to belong to (e.g., R. Johnson & Donchin, 1980; Mars, et al., 2008). These expectations might be influenced by the stimulus classes' global (over the course of the experiment) and local (given the preceding stimulation) probabilities. If the stimulus matches the expectations well, the P3b amplitude is small. The stronger expectations are violated the larger P3b amplitudes become. Applying this interpretation to our data means that matches were most expected. Expecting matches is a smart strategy as in 50% of all trials matching stimuli appeared and this event therefore had the highest global probability.

More interesting, as P3b amplitude reflects the subjective probability of a stimulus class it can be employed to assess into which subjective classes the different mismatches fell. Confirming our hypothesis that subjects differentiate between mismatches in orientation-independent and mismatches in orientation-dependent information, P3b amplitudes were much larger for mismatches in orientation-independent information than for both types of mismatches in orientation-dependent information with the latter two being of the same magnitude (see Figure 6.5 and Figure 6.6). Notably, mismatches in the two pieces of orientation-dependent information for complex stimuli and the one piece of orientation-dependent information for visually complex stimuli all elicited P3bs of the same amplitude, indicating that these were perceived as belonging to the same class. Importantly, a close examination of Table 6.1 reveals that the amplitude differences between P3bs elicited by mismatches in orientation-dependent and orientation-independent information are not explainable in terms of local (given one stimulus type) or global (over all stimulus types) probability for the three different types of mismatches. The pattern of P3b amplitudes, however, is in line with the global probabilities if probabilities for the two types of mismatches in orientation-dependent information are combined.

To illustrate this point, consider that for trials with visually complex stimuli, local probability for mismatches in orientation-dependent and orientation-independent information was the same; nevertheless, P3b amplitude differed. For trials with complex stimuli, local probability of mismatches in the second piece of orientation-dependent information was twice as high compared with that of the first piece of orientation-dependent information; nevertheless, P3b amplitude did not differ. Averaged over stimulus types, global probability was lowest for a mismatch in the second piece of orientation-dependent information (8.33%) and highest for a mismatch in the first piece of orientation-dependent information (29.17%); nevertheless, P3b amplitudes did not differ. Global probability for a mismatch in orientation-independent information (12.5%) lay in between the probabilities for the two pieces of orientation-dependent information; nevertheless, P3b amplitude was significantly larger for mismatches in orientation-independent information than for mismatches in either piece of orientation-dependent information. However, the combined global probability of mismatches in orientation-dependent information was three times higher than the global probability for mismatches in orientation-independent information. As a consequence, P3b amplitude was larger for the former than for the latter class of mismatches. The pattern of P3b amplitudes consequently supports our claim that participants classify mismatches into those in orientation-dependent and those in orientation-independent information.

Table 6.1

Global and Local Probabilities for Matches and Mismatches in %.

Level	Match	Dep_1	Dep_2	Indep	$\text{Dep}_1 + \text{Dep}_2$
Local					
Simple	50.00	50.00			50.00
V. complex	50.00	25.00		25.00	25.00
Complex	50.00	12.25	25.00	12.25	27.25
Global	50.00	29.17	8.33	12.50	37.50

Note. The observed order of P3b amplitudes is Match < Dep_1 = Dep_2 << Indep. Dep_1 = orientation-dependent mismatch 1 (side of the larger line, the smaller line was attached to); Indep = orientation-independent mismatch (position of the square on the smaller line); Dep_2, = orientation-dependent mismatch 2 (side of the smaller line, the square was attached to).

Taking into account that P3bs peak much later and comparison times are much longer for mismatches in orientation-independent information than for all types of mismatches, we arrive at an even more interesting (though speculative) interpretation. As at the time of comparison stimulus onset orientation-independent information is not actively represented in working memory, a comparison stimulus mismatching in orientation-independent information only is first classified as matching. This early classification is based exclusively on information actively represented in working memory (orientation-dependent information) which perfectly matches for stimuli mismatching in orientation-independent information only. This misclassification delays the process that mediates between stimulus evaluation and response selection (Verleger, et al., 2005) and consequently increases P3b latency and comparison time. The subsequent discovery that the comparison stimulus actually does not match the expected stimulus therefore becomes especially surprising and consequently elicits a large P3b amplitude.

To sum up, the present study indicates very precisely how information in a mental-rotation task is processed: The original stimulus is first encoded into a visual representation, emerging about 200 ms after stimulus onset. This visual representation remains active in working memory for only part of the trial until at least about 1100 ms after the original stimulus disappeared and 1300 ms after the rotation could potentially start. Orientation-dependent information is in a piece-meal fashion extracted, actively and explicitly represented and rotated in working memory. If a second piece of orientation-dependent information is comparison-relevant (as in our complex stimuli), after the first rotation, at about 2800 ms after the onset of the rotation cue, this second piece of orientation-dependent information is extracted from a passive backup representation and also rotated. While the second piece of orientation-dependent information is rotated, the first piece of information continues to be actively represented. At the onset of the comparison stimulus, only orientation-dependent information is actively represented in working memory. That means participants are either unable to or for other reasons refrain to re-activate orientation-independent information or to built up a visual representation before the comparison stimulus appears. Therefore an initial comparison of the active representation and the comparison stimulus indicates a match for both matching stimuli and for stimuli mismatching in orientation-independent information. Only after orientation-independent information is then retrieved from the passive backup representation, mismatches in orientation-independent information are detected. This reactivation delays reactions to mismatches in orientation-independent information by about 60 ms. To our knowledge, this is the most precise empirically founded description of an information processing chain in an equally complex task ever reported.

7. Experiment 3: Parcellation of the Mental Rotation Network via fMRI

A large network of cortical areas is activated in mental-rotation tasks. As detailed above (Chapter 1.6), even when only rotation-specific contrasts are considered, many distributed foci of activation are found (for a review, see Zacks, 2008). These cortical areas purportedly play different roles during mental rotation. For example, it might be possible to differentiate between regions more related to the processing or maintenance of information. It is also possible, that the very same regions are responsible for processing and maintenance. All three experiments reported above indicate that the representation in mental rotation includes only orientation-dependent spatial-relational information. Orientation-independent spatial-relational information in contrast seems to be stored passively for the duration of rotation. That these two types of information are treated differently also indicates that they are processed in different cortical regions. The topographies of slow potentials as observed in Experiment 2 already constitute suggestive evidence in favor of this hypothesis. However, as discussed above (Chapter 6.1) the spatial resolution of these slow potentials was not sufficient to provide conclusive evidence. This gap shall be closed here with the aid of functional magnetic resonance imaging (fMRI). In contrast to EEG the spatial resolution of fMRI should allow identifying the specific cortical regions that process the two types of spatial-relational information.

A similar technique as employed in the three experiments above can also be applied to fMRI data. Activation should be higher for visually complex compared with simple stimuli in regions that process orientation-independent or visual information. An increase in activation that is related to visual complexity should emerge in primary and secondary visual areas of the cortex (BA 17/18, V3), whereas pure orientation-independent information might be processed in other regions. Regions that process orientation-dependent information should show higher activation for complex compared with visually complex stimuli. As spatial-relational information is more abstract than visual information, foci of activation that reflect the processing of orientation-dependent information should lie clearly beyond primary and secondary visual cortex within the dorsal stream of visual information processing (see, e.g., Milner & Goodale, 2008; see also Chapter 1.5.2). As spatial-relational information is apparently stored in the superior parietal lobule (Kosslyn, Thompson, et al., 1998; Trojano, et al., 2002), this area is a likely candidate for showing an effect of the amount of orientation-dependent spatial relational information.

Although considering only rotation-related activations in order to isolate activation due to the process of mental rotation proper is a step into the right direction several difficulties in interpreting the findings reported above (Chapter 1.6) remain. Many authors (including Zacks, 2008) consider the comparison between 0° and a larger angle as rotation-specific. Problematically, 0° rotations are no rotations. For example, when two matching stimuli are shown simultaneously (Chapter 1.3.1) in the same orientation, they can immediately be recognized as the same. A pure template-match would be sufficient. In contrast, even a small rotation already renders the task much more complex. This becomes evident if one considers, for example, the several processing steps assumed by Just and Carpenter (1976; see Chapter 1.3.1). Determining the direction and amount of rotation or initiating a rotation might already elicit rotation unspecific differences between, for example 0° and 60° trials. In addition, as shown above (Experiments 1a, 1b and 2), before mental rotation can start, information must be brought into a specific format. This might not be necessary when no rotation is performed on 0° trials. There are consequently many more differences between trials with rotational angles of 0° and trials that indeed require mental rotation than solely the amount of rotation. The logic of rotation-specific contrasts is to isolate only those processes that become more demanding with increasing rotational angle. This can consequently only be achieved by contrasting at least two rotational angles larger than 0°.

Furthermore, mental rotation proper is not the only cognitive process operating in mental-rotation tasks that becomes more demanding with an increasing rotational angle. Time on task is inherently related to rotation time in mental-rotation tasks. The longer the rotation takes, the longer participants must, for example, focus attention on the task. In addition, when rotation takes longer, information must be maintained for a longer period of time (cf. Milivojevic, et al., 2009). Although the duration of mental rotation can be disentangled from visual stimulation or from execution of button presses (e.g., Ecker, et al., 2006), it cannot be disentangled from time on task. This is where experimentally isolating the process of mental rotation is far superior to purely statistical approaches which must rely on a difference in the time-course of mental rotation and other processes (Ecker, et al., 2006; Richter, et al., 2000; Windischberger, et al., 2003). Activation elicited by processes that have the same timing as mental rotation can to a certain degree be eliminated by constructing a control condition that requires the same set of cognitive affordances as the mental-rotation task but no mental rotation. Subtracting activation in this control condition from activation in the mental rotation condition would then only leave those areas that are involved in mental rotation proper. This is not a trivial goal and might never be fully reached (e.g., Friston, Price, et al., 1996; Price, Moore, & Friston, 1997). However, we believe (and the results reported below prove us right) that a careful design of the control condition can lead much closer to this ideal than the usually employed fixation or 0°-rotation baselines do.

Finally, the difficulty and duration of determining the direction and the amount of rotation might also increase with rotational angle (see above, Chapter 1.3.1 and 1.3.4). This influence can be drastically reduced by employing rotation cues as in the previous three experiments described above. Rotation cues directly indicate the direction and amount of rotation and preparatory analyses of stimulus parts become unnecessary.

7.1 Related Studies

Up to now, only relatively few fMRI or PET studies exist that employ a successive-presentation mental-rotation task as in the present work (Lamm, Windischberger, Moser, & Bauer, 2007; Suchan, Botko, Gizewski, Forsting, & Daum, 2006; Suchan, et al., 2002). Interestingly, one of these studies (Lamm, et al., 2007) tried to examine the influence of the amount of spatial information on brain activation. Lamm et al. (2007) employed two-dimensional block figures (see Figure 7.1). As usual for successive-presentation mental-rotation tasks, participants had first to encode an original stimulus and a rotation cue. After a rotation interval a matching block figure or its mirror image appeared. So far their task is similar to that in many other mental rotation studies. However, these authors rendered their stimuli more complex by adding either of two types of additional information. Within the block figures either an arrow or a dot was shown. These allowed introducing other types of mismatches in addition to mirror images. On part of the trials, the dot appeared in the wrong position within the comparison stimulus. This resulted in an orientation-independent mismatch of the relation between dot and block figure. Similarly, the arrow sometimes appeared in the wrong orientation, resulting in a purportedly orientation-dependent mismatch. Both types of stimuli consequently included two pieces of comparison-relevant information. Specifically, the stimuli with the dot included one piece of orientation-dependent and one piece of comparison-relevant orientation-independent information. If everything had worked out, the stimuli with the arrow would have included two pieces of comparison-relevant orientation-dependent information.

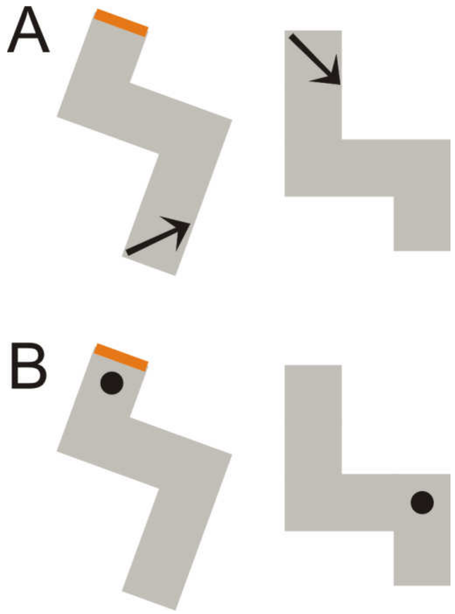


Figure 7.1. *Redrawing of stimuli employed by Lamm et al. (2007). The original stimulus (left) must be mentally rotated so that the stimulus eventually 'stands' on the orange bar. The orange bar consequently is a rotation cue (see Chapter 1.3.4) and indicates a rotation of 160°, clockwise. After rotation the comparison stimulus (right) appears. Can you tell whether the two stimuli in A are matching? Please pay special attention to the orientation of the arrow. What about B? A: Mismatch in the orientation of the arrow. B: Mismatch in the position of the dot. The mismatch in A is very difficult to spot until one realizes that the arrow of the original stimulus points away from the other arm of the block figure and the arrow in the comparison stimulus point towards this arm. This constitutes an orientation-independent encoding of the relation between the arrow and the block figure. Example A does therefore not require a more difficult mental rotation than example B.*

Unfortunately, Lamm et al. (2007) did not closely enough analyze under which conditions participants have to represent orientation-dependent information (see especially Chapter 3.6 and 3.8). The direction of the arrow in isolation evidently is a piece of orientation-dependent information. However, in Lamm et al.'s stimuli this piece of information can easily be encoded in an alternative, orientation-independent way. Consider the example trial given by the authors and which is redrawn here as Figure 7.1. The arrow, which was located in one arm of the figure either pointed towards or away from the other arm. This is not a piece of orientation-dependent information as evident by the fact that the sentence does not include “left/right”, “above/below” or similar terms. This relation does not change when the stimulus is rotated—if, in one absolute orientation of the block figure, the arrow points towards the other arm, it also does so in any other orientation of the figure. This piece of information is orientation-independent. Lamm et al.’s participants consequently did in neither condition have to process a second piece of orientation-dependent information. That means, the authors failed to manipulate the amount of orientation-dependent information. Their contrast between activation in trials employing stimuli with arrows minus trials employing stimuli with dots does not reflect an influence of the amount of orientation-dependent information. Their finding of higher activation in the superior occipital lobe and no activation difference in rotation-related areas does therefore not indicate the brain regions that process orientation-dependent information.

7.2 Construction of the Control Task

The goal of our control task is enabling a differentiation between activation related to mental rotation proper and all other activation that also increases with rotational angle but is not related to mental rotation proper. Angle-dependent activation should be found in the experimental as well as in the control task, but the angle-dependent activation in the control task should only be a subsample of the activation found in the experimental task. The control tasks should therefore, of course, be as similar as possible in terms of perceptual stimulation. In addition, as mentioned above, the control task should require the same set of cognitive processes but no mental rotation. To do so, we basically replaced the rotation interval by a retention interval (see Figure 7.2). Such retention trials were inserted randomly into rotation trials in order to avoid a specific preparation for the respective condition. Another problem was the activation associated with the key press participants gave to indicate that they had finished the rotation. In order to introduce a comparable motor affordance the retention interval was also terminated by a key press. This key press was given as soon as the arcs (which worked as rotation cues in the rotation condition) changed their color from black to gray. As reported in Experiment 1a and b, rotation times differ for different stimuli, rotational angles, participants and phases of the experiment. In order to account for all these variables, the program continuously updated the point in time when this color change happened as to induce the key press at a time equivalent to the current median of the given participant's rotation time in the respective rotation cell of the experimental design.

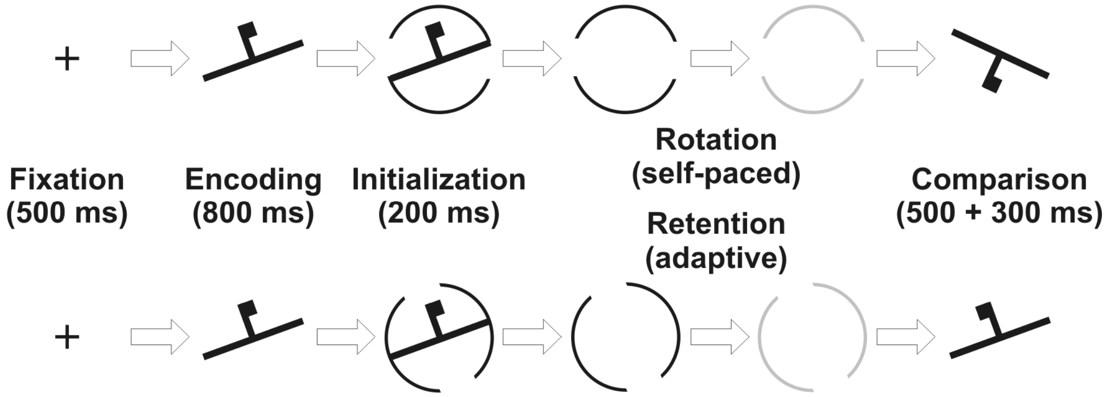


Figure 7.2. *Trial procedure of Experiment 3. On rotation trials (experimental condition, upper row) participants had to rotate the original stimulus along the arcs as in the previous experiments. They indicated having finished the rotation by a key press. The color change of the arcs was irrelevant in this condition. On retention trials (control condition, lower row) rotation cues appeared centered on the main axis of the stimulus. This indicated that no rotation had to be performed and the upcoming comparison stimulus would be in the same orientation as the original stimulus. In this condition, participants waited until the rotation cue changed its color from black to gray and then pressed a key in order to proceed.*

The experiment was conducted with three main questions in mind. Firstly, which brain areas are involved in the process of mental rotation proper? These areas should show stronger activation for larger rotational angles compared with smaller angles and this effect should be clearly stronger for the rotation compared with the retention condition. That means activation in these areas should show an interaction between rotational angle and experimental condition. Secondly, is orientation-depended information (i.e., the type of information that is mentally rotated) represented within the same brain areas that also perform rotation? Following the same logic as in Experiment 2, those areas that show higher levels of activation for complex stimuli than for visually complex stimuli potentially hold orientation-dependent information. We assume that a mental process must have direct access to the processed information and that therefore activation in the same set of brain areas should depend both on the amount of represented information and on the amount of processing (rotational angle in the present study). According to our reasoning, the process of mental rotation is performed on orientation-dependent information only. Consequently, activation in the set of brain areas that show rotation-specific activation should also depend on the amount of represented orientation-dependent information. Thirdly, where is orientation-independent information (i.e., a type of information that is not mentally rotated) stored and which brain areas simply reflect the visual complexity of the rotated stimuli or the amount of represented orientation-independent information? Again following the same logic as introduced above (Chapter 3.8), those brain areas that are activated more strongly during the processing of visually complex compared with the processing of simple stimuli either code orientation-independent information or visual complexity. As we already collected much evidence that orientation-independent information/visual complexity is processed separated from orientation-dependent information (Experiment 1a, 1b and 2), we hypothesize that these two types of information are processed in different brain areas. In sum, the overarching aim of the present study was to identify the cortical network that is employed in mental-rotation tasks and to gain insight into the function of its several parts.

7.3 Methods

7.3.1 Participants

Thirty-eight students recruited at Saarland University (20 women; median age: 23.5 years, age range: 19-30 years) received €8 per hour of participation. Participants reported having normal or corrected-to-normal vision and gave informed consent. As indicated by an informal interview after the testing, one participant did not follow the instructions to proceed to the comparison stimulus as soon as he had finished the rotation and was consequently excluded from further analysis. Additionally, data from one participant with an outlier overall accuracy more than 1½ times the interquartile difference below the group mean (< .7) and one participant with an outlier overall rotation time 1½ times the interquartile difference above the group mean (> 4538 ms) were excluded.

7.3.2 Design

As in the previous experiments, the original stimulus was simple, visually complex, or complex (*stimulus type*). It was displayed in one of four orientations (±150°, ±70°), and took one of the two possible values for each of the maximally three pieces of comparison-relevant information (e.g., for complex stimuli, the smaller line was attached either to the one or to the other side of the larger line, the square was either in the middle or at the top of the smaller line and either to the one or to the other side of it). On one third of trials, no rotation had to be performed. Visual stimulation in this *retention* control condition was kept equivalent to the *rotation* experimental condition by employing the same rotational cues (two arcs, each 45° or 135° in size) with the single difference that the cues were centered on the stimulus' main axis (see Figure 7.2). In order to keep the participants' stay in the scanner within a comfortable duration only trials with rotations of 45° and 135° (*rotational angle*), clockwise and counterclockwise were employed. On 50% of trials, the comparison stimulus differed from the to-be-imagined stimulus in a single piece of information. The two possible mismatches (see Figure 3.4) for visually complex stimuli were equiprobable. As in Experiment 1a and 2, a mismatch in the second piece of orientation-dependent information (on which side of the smaller line the square was located) appeared twice as often as the other two types of mismatches for complex stimuli. All factors were varied within participants and presented in a randomized order. The experiment consisted of two blocks with 144 trials each.

7.3.3 Procedure

Stimulus presentation and response recording was controlled by E-Prime 2.0 (Psychology Software Tools, 2005). Due to a technical error, stimuli were slightly smaller than in the previous experiments, namely about 2.67° of visual angle. They were presented in black against a gray background at the center of the screen of MRI compatible goggles (VisualSystem, NordicNeuroLab). The trial procedure is displayed in Figure 7.2. Each trial began with a 500 ms fixation cross. The original stimulus was then shown for 1000 ms. Two arcs indicating the direction and amount of rotation appeared 200 ms before offset of the original stimulus and remained on screen for the whole rotation interval. In the rotation condition, participants had to perform a mental rotation along these rotation cues. After participants had finished the rotation, they proceeded to the comparison stimulus by a key press with their left or right thumb.

In the retention control condition rotation cues were centered on the main axis of the stimulus. Participants had to press the key with their thumb as soon as the rotation cues changed color from black to gray. The experimental program was designed as to induce this key press at a similar time point in the retention as in the rotation condition. At the onset of each retention trial the median rotation time from all previous trials for the respective cell of the rotation condition was calculated. From this value, the median time from onset of the color change until the key press on retention trials was subtracted. The resulting value determined the time from offset of the original stimulus until the color change of the rotation cue. When participants pressed the button before the color change, the trial was aborted and an error message was displayed. The color also changed in the rotation condition but was irrelevant for the participants. Instructions therefore encouraged participants to ignore the color change on rotation trials.

After the key press, the comparison stimulus was presented for 500 ms. It was always of the same type (simple, visually complex, complex) as the original stimulus. On rotation trials it appeared in the orientation indicated by the rotation cues whereas on retention trials it appeared in the same orientation as the original stimulus. Mismatching stimuli differed from matching stimuli in one piece of information only. Participants had maximally 800 ms to decide whether the comparison stimulus was the stimulus they had imagined or not (*comparison time*). Participants indicated the outcome of their comparison by a press with the left or the right index finger. If this key press was not given within the time limit, the trial counted as a *miss*. Which thumb was used to proceed to the comparison stimulus and whether the left or right index finger were used to give a match or mismatch answer was counterbalanced across participants. Between trials an empty screen was shown for an interval jittered between 2000 ms and 4000 ms.

As in Experiment 1b, participants were informed about all comparison-relevant stimulus characteristics in order to ensure that they were aware of all comparison-relevant information. Participants practiced the task outside the scanner under supervision of the experimenter until the experimenter was convinced that they fully understood the task. During these practice trials participants received feedback on their performance. Inside the scanner they continued practicing until the experimenter had completed the scanner set-up. Participants performed two experimental blocks of 144 (96 rotation and 48 retention) trials each with a break in between.

7.3.4 Scanning procedure

Whole-brain gradient-echo planar images were acquired employing a 3 T magnetic resonance scanner (MAGNETOM Skyra, Siemens Healthcare). A 20-channel head coil was employed for radio-frequency transmission and signal reception. The 3D high-resolution T_1-structural image of the whole brain (3D MPRAGE, 192 slices, slice thickness = 0.9 mm, in-plane resolution = 0.938 × 0.938 mm, repetition time = 1900 ms, echo time = 2.13 ms, inversion time = 900 ms) was acquired during the break between the two functional runs which corresponded to the two experimental blocks. The structural image was later used to normalize the fMRI datasets acquired from each participant into standard MNI space. During task performance, functional EPI images were obtained (repetition time = 2000 ms, echo time = 30 ms, flip angle = 90°, 28 slices, slice thickness = 3 mm, interslice gab = 0.75 mm, field of view = 192 × 192 mm, acquisition matrix = 94 × 94, resulting in a voxel size of 2.04 × 2.04 × 3.75 mm, parallel to the intercommissural (AC-PC) line). Whenever the 105 mm in z-direction were insufficient to include the whole brain, we excluded part of the cerebellum of the respective participant from the functional scan. As the experimental procedure included self-paced intervals (rotation/retention and comparison times) the number of necessary functional scans was not predictable in advance. Each of the two runs was aborted manually several seconds after the participant had finished the 144 trials of an experimental block.

7.3.5 Image analysis

Image analysis was conducted with Statistical Parametric Mapping (SPM8; Wellcome Trust Center for Neuroimaging, 2010) running in MATLAB (The MathWorks, 2008). The first 5 scans of each functional run were discarded in order to allow for the establishment of a steady-state condition of transverse magnetization. Functional images were realigned to the mean image using a least-squares approach and a rigid body spatial transformation (Friston, et al., 1995). The structural scan of each participant was co-registered to the mean functional image, segmented into three tissue classes (gray matter, white matter and cerebrospinal fluid) and spatial normalization parameters were derived by matching gray matter to that of a standard template as provided by SPM8. All functional images were then normalized with these parameters and written at an isotropic voxel size of 2 mm. Finally, the normalized functional images were smoothed with an isotropic 8 mm full-width at half-maximum (FWHM) Gaussian kernel. This relatively coarse smoothing kernel should alleviate effects of structural differences between participants.

Separate regressors were defined for each Condition (rotation vs. retention) × Stimulus Type × Rotational Angle cell separately for each functional run. These regressors of interest were modeled as discrete impulses in the middle of the rotation interval (cf. Postle, Zarahn, & D'Esposito, 2000). Dummy regressors of no interest were modeled at the onset of the original and at the onset of the comparison stimulus in order to suppress variance introduced by these events. In addition, the overall difference between runs was modeled. Finally, the realignment parameters were included as regressors of no interest in order to suppress residual motion-related variance (Friston, Williams, Howard, Frackowiak, & Turner, 1996). All regressors were then convolved with the canonical HRF provided by SPM8 and employed to predict the activation pattern in each single voxel (mass-univariate approach) based on the General Linear Model. Based on the *b* weights from these regressors, statistical parametric maps were created for each subject displaying *t* values of planned contrasts at each voxel. These maps indicate whether a certain voxel was more strongly activated in one compared with another condition. These *t*-value maps were then submitted to a second-level random effects analysis over subjects in order to obtain results which can be generalized to the population from which the subject sample was drawn. Specifically, the following contrasts were analyzed: rotation > retention, rotation, 135° > rotation, 45°, retention, 135° > retention, 45°, (rotation > retention) × (135° > 45°), rotation, visually complex stimuli > rotation, simple stimuli, rotation, complex stimuli > rotation, visually complex stimuli.

In order to correct for multiple comparisons, a cluster extent threshold was determined via Monte Carlo simulations using cluster_threshold_beta (Slotnick, 2006; see also Slotnick, Moo, Segal, & Hart, 2003). The underlying idea is that clusters of contiguous voxels become increasingly improbable as the clusters grow larger. Running 1,000 simulations, for an individual voxel threshold of $p < .001$ and an overall (rather conservative) type I error rate of $\alpha < .001$, a minimal cluster size of 40 contiguous voxels was determined. That means, only clusters of 40 voxels or larger were considered significantly activated. Anatomical labels of activated areas were identified with the SPM anatomy toolbox (Eickhoff, 2011; see also Eickhoff, et al., 2005) complemented by additional literature as indicated and the Talairach client (Research Imaging Center, 2009) with MNI coordinates transformed into Talairach coordinates by mni2tal (Brett, 1999). In addition, MarsBaR (Brett, 2010; see also, Brett, Anton, Valabregue, & Poline, 2002) was used to build functional regions of interest (ROIs) and rfxplot (Gläscher, 2009) to export the ROI data of individual subjects for further statistical analysis.

7.4 Results

7.4.1 Ignored information

In order to obtain an acceptable number of observations per cell for the χ^2-test, we pooled accuracy data from rotation and retention conditions. Following the same procedure as described for Experiment 1a, we excluded 11 participants who ignored at least one type of information in at least one stimulus type. As in Experiment 2, all of these participants ignored the piece of orientation-independent information in complex stimuli. One participant additionally ignored the piece of orientation-independent information in visually complex stimuli, and one participant additionally ignored the second piece of orientation-dependent information. The final sample consisted of data from 24 participants (12 women; median age: 23, age range: 19-30).

7.4.2 Behavioral data

In order to obtain values directly comparable to Experiment 1b (Figure 5.2), rotation and retention times were defined as the times from onset of the rotation cues until the participant's key press. The resulting pattern is displayed in Figure 7.3. We first conducted an analysis to examine whether the algorithm for equating retention to rotation times was successful. A 2 (condition: rotation vs. retention) × 3 (stimulus type: simple vs. visually complex vs. complex stimuli) × 2 (rotational angle: 45° vs. 135°) MANOVA on median rotation/retention times indicated that retention times were on average longer than rotation times, $F(1,23) = 19.65$, $p < .001$, $\eta_p^2 = .46$. However, rotation and retention times did not significantly differ with respect to the effect of rotational angle, $F(1,23) = 2.67$, $p = .11$, $\eta_p^2 = .11$, the effect of stimulus type, $F(2,22) = 2.33$, $p = .12$, $\eta_p^2 = .12$, or the interaction between rotational angle and stimulus type, $F(2,22) = 0.84$, $p = .45$, $\eta_p^2 = .04$. Even though the employed algorithm was not perfectly successful in equating rotation and retention times, the patterns are very similar. Concerning the fMRI analysis, the fact that retention times are longer than rotation times is conservative with respect to the assumption that certain cortical areas should be more active in the rotation condition compared with the retention condition.

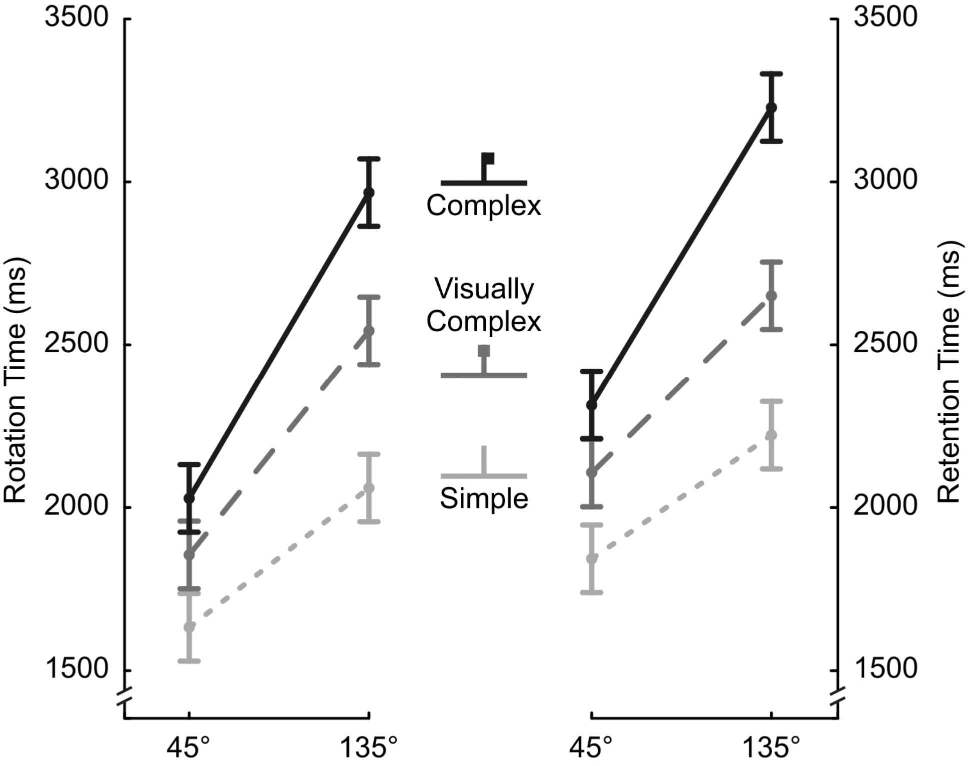


Figure 7.3. *Rotation times (left) and retention times (right) in Experiment 3. Retention times and rotation times show similar patterns, because the experiment was designed to adjust retention times to rotation times for each Stimulus Type × Rotational Angle cell (please refer to Chapter 7.3.3 for details of the adjustment procedure). Confidence intervals are based on the Stimulus Type × Rotational Angle interaction.*

Retention times were artificially influenced by the algorithm of the experimental program. Therefore, rotation times (see left part of Figure 7.3) were also analyzed separately. A 3 (stimulus type) × 2 (rotational angle) MANOVA on median rotation times revealed an effect of stimulus type, $F(2,22) = 10.77$, $p < .001$, $\eta_p^2 = .45$, an effect of rotational angle, $F(1,23) = 42.85$, $p < .001$, $\eta_p^2 = .65$, and an interaction between the two, $F(2,22) = 13.10$, $p < .001$, $\eta_p^2 = .41$. The interaction was driven by a stronger increase in rotation times from 45° to 135° for both visually complex compared with simple stimuli, $t(23) = 2.94$, $p = .007$, and for complex compared with visually complex stimuli, $t(23) = 3.02$, $p = .006$.

Median comparison times for correct answers are displayed in Figure 7.4. Separate Condition × Match Type MANOVAs were conducted for each stimulus type. One participant did not give any correct answer for mismatches in the piece of orientation-dependent information of visually complex stimuli on rotation trials (but did apparently not ignore this piece of information on retention trials). Therefore tests including this cell have one degree of freedom less than comparable other tests. Comparisons took longer in the rotation compared with the retention condition, $F(1,23) = 9.14$, $p = .006$, $\eta_p^2 = .28$, $F(1,22) = 3.19$, $p = .09$, $\eta_p^2 = .13$, $F(1,23) = 18.67$, $p < .001$, $\eta_p^2 = .45$, for simple, visually complex and complex stimuli, respectively. The condition by match type interaction was significant for simple, $F(1,23) = 7.43$, $p = .01$, $\eta_p^2 = .24$, and marginally significant for visually complex, $F(2,21) = 2.93$, $p = .08$, $\eta_p^2 = .17$, but nonsignificant for complex stimuli, $F(3,21) = 1.05$, $p = .39$, $\eta_p^2 = .04$.

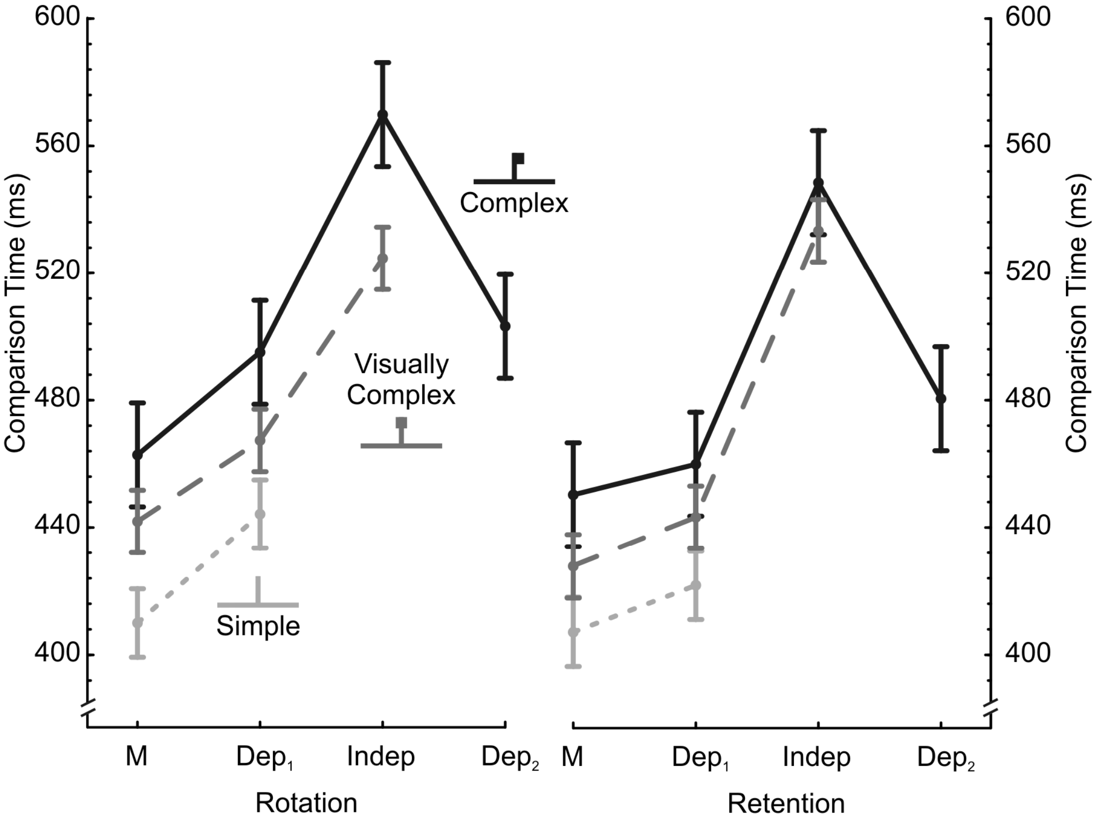


Figure 7.4. *Comparison times in the rotation (left) and retention (right) condition in Experiment 3. Confidence intervals are based on the effect of match type separately for each stimulus type. M, match; dep*$_1$*, orientation-dependent mismatch 1; Indep, orientation-independent mismatch; Dep*$_2$*, orientation-dependent mismatch 2.*

7.4.3 fMRI data

Group brain activation maps for the contrasts of interest are shown in Figure 7.5. The upper-left activation map shows the effect of rotational angle (135° > 45°). Activated areas reach from the earliest visual areas (BA 17/18) through most stages of the dorsal stream (inferior parietal lobule, intraparietal sulcus, superior parietal lobule, left V3; e.g., Goodale & Milner, 1992; see also Chapter 1.5.2 and 1.6.1) and also include left V4 and the somatosensory cortex (BA 1/2/3). The second large cluster includes the inferior part of the dorsolateral premotor cortex (pMd; Schubotz, Anwander, Knösche, von Cramon, & Tittgemeyer, 2010), the ventral premotor cortex (including regions BA 44/45) and the left pre supplementary motor area (pre-SMA, Picard & Strick, 2001).

Obviously, these brain areas together are sufficient to visually represent the stimulus, transform it into an appropriate spatial mental representation, perform the rotation and maintain all comparison-relevant information. Indeed, this activation pattern is very similar to that found in mental rotation studies employing a rather loose baseline (e.g., Thompson, Slotnick, Burrage, & Kosslyn, 2009). However, part of this work is also necessary to successfully perform the retention control condition. Consequently, part of the brain areas is also more active for retention times equivalent to 135° rotation compared with retention times equivalent to 45° rotations as displayed in the upper middle part of Figure 7.5. Similar to the previous contrast, all primary and secondary visual areas are activated as well as the inferior parietal lobule, the intraparietal sulcus and the inferior part of the superior parietal lobule. However, the superior part of the superior parietal lobule (SPL), the intraparietal sulcus (IPS), inferior parietal cortex (IPC), left somatosensory cortex (BA 1/2), dorsolateral premotor cortex (pMd) and the left pre-supplementary motor area (pre-SMA) are clearly more activated when rotation has to be performed as evident in the contrast rotation > retention (lower leftmost) and the interaction contrast (rotation > retention) × (135° > 45°) (lower middle). Obviously, these two contrasts, which should show the brain regions that are related to mental rotation proper, provide similar results. Among these, the interaction contrast is the more conservative comparison, because it also takes into account the effect of rotational angle. In the following, we therefore focus on the regions significantly activated in the interaction contrast. As indicated in Table 7.1, only the largest cluster comprises several cortical regions, namely left SPL, left IPS and left somatosensory cortex and is in the following referred to as SPL+. All other clusters are roughly restricted to one cortical region and are therefore referred to by the name of the respective region. In sum, these regions constitute the network of brain areas that is frequently found activated in mental-rotation tasks and is therefore known as the mental rotation network.

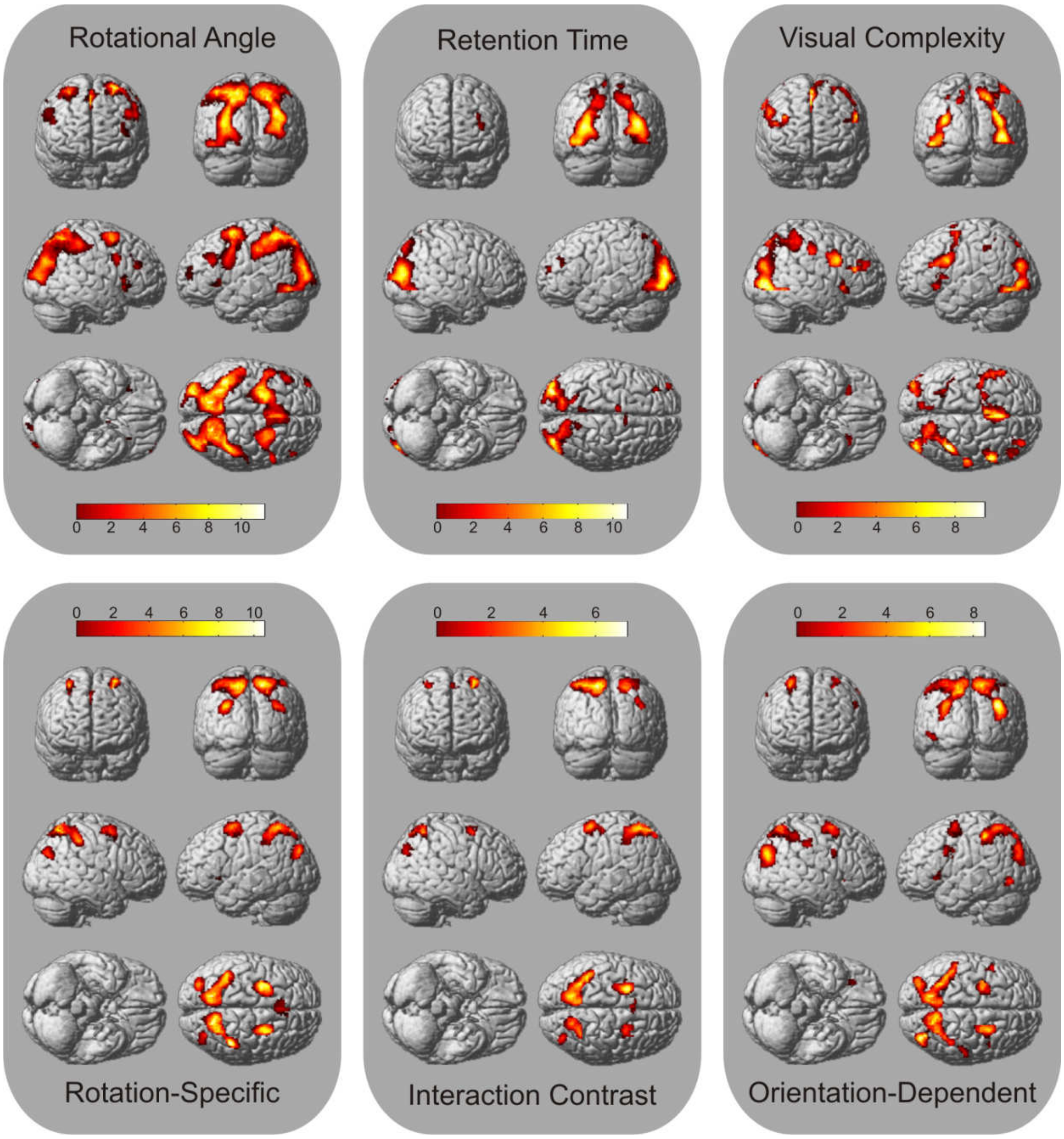


Figure 7.5. *Group brain activation maps overlaid over the single subject render from SPM8. For each contrast we employed an individual voxel threshold of* $p < .001$ *and a cluster extent threshold of 40 contiguous voxels thereby keeping the overall type I-error rate at* $\alpha < .001$ *as determined by a Monte Carlo simulation (please refer to Chapter 7.3.5 for details). Colors code the t value for the respective contrast at the respective voxel. Rotational Angle: rotation, 135° > rotation, 45°; Retention Time: retention, 135° > retention, 45°; Visual Complexity: rotation, visually complex stimuli > rotation, simple stimuli; Rotation-Specific: rotation > retention; Interaction Contrast: (rotation > retention) × (135° > 45°); Orientation-Dependent Information: rotation, complex stimuli > rotation, visually complex stimuli.*

Table 7.1

Areas Activated by Mental Rotation Proper as Identified by the Interaction Contrast (Rotation > Retention) × (135° > 45°).

MNI Coordinates			Volume			
x	y	z	(cm^3)	*t*	Potential Structure	Label
-12	**-64**	**56**	**14.64**	**6.83**	left SPL (7A/7PC), BA 2, IPS (hIP1/2/3), IPC	SPL+,l (A)
-38	-52	60		5.51		
-26	-60	54		5.31		
22	**-68**	**58**	**4.81**	**5.30**	right SPL (7A/7P/7PC)	SPL,r (B)
28	-54	56		5.15		
36	-52	66		3.75		
-26	**6**	**60**	**5.38**	**7.17**	left pMd	pMd,l (C)
-22	-2	54		5.98		
-26	-10	54		5.83		
28	**4**	**58**	**1.92**	**4.45**	right pMd	pMd,r (D)
24	10	48		4.07		
34	10	64		3.94		
42	**-78**	**32**	**1.02**	**4.63**	right IPC	IPC,r (E)
34	-76	40		4.20		
0	**10**	**60**	**0.50**	**4.64**	left pre-SMA	pSMA,l (F)
-10	14	54		3.87		

Note. Coordinates are given for global (bold) and local maxima (more than 8 mm apart) in each cluster. All *p*s ≤ .001.

Six main clusters were significantly activated in the interaction contrast (Rotation > Retention) × (135° > 45°) and are purportedly the cortical areas directly involved in the process of mental rotation. Activations in these areas as a function of Condition × Stimulus Type × Rotational Angle are displayed in Figure 7.6. Respective MANOVAs conducted for each ROI are summarized in Table 7.2. As ROIs were determined by the Condition × Rotational Angle interaction contrast, this interaction is, of course, highly significant for activation in all ROIs, all $Fs(1,23) > 19.75$, all $ps < .001$. In addition, activation in all ROIs showed clear main effects of stimulus type and rotational angle, all $Fs(2,22) > 6.39$, all $ps < .001$, and $Fs(1,22) > 14.68$, all $ps < .001$, respectively.

There was no three-way interaction, all *Fs*$(2,22) < 0.92$, all *p*s > .41. The activation pattern in the pre-SMA differed somewhat from the other, mostly homogeneous activation patterns. Only for the pre-SMA a marginal significant interaction between stimulus type and rotational angle was present, $F(2,22) = 3.01$ $p = .07$, $\eta_p^2 = .13$, in all other ROIs, this interaction was not significant, all *Fs*$(2,22) < 0.29$, all *p*s > .75. In contrast, the main effect of condition was present in all ROIs, all *Fs*$(2,22) > 17.35$, all *p*s < .001, except the pre-SMA, $F(1,23) = 1.52$ $p = .23$, $\eta_p^2 = .06$. Only the interaction between condition and stimulus type showed a rather inconsistent pattern over ROIs (see Table 7.2).

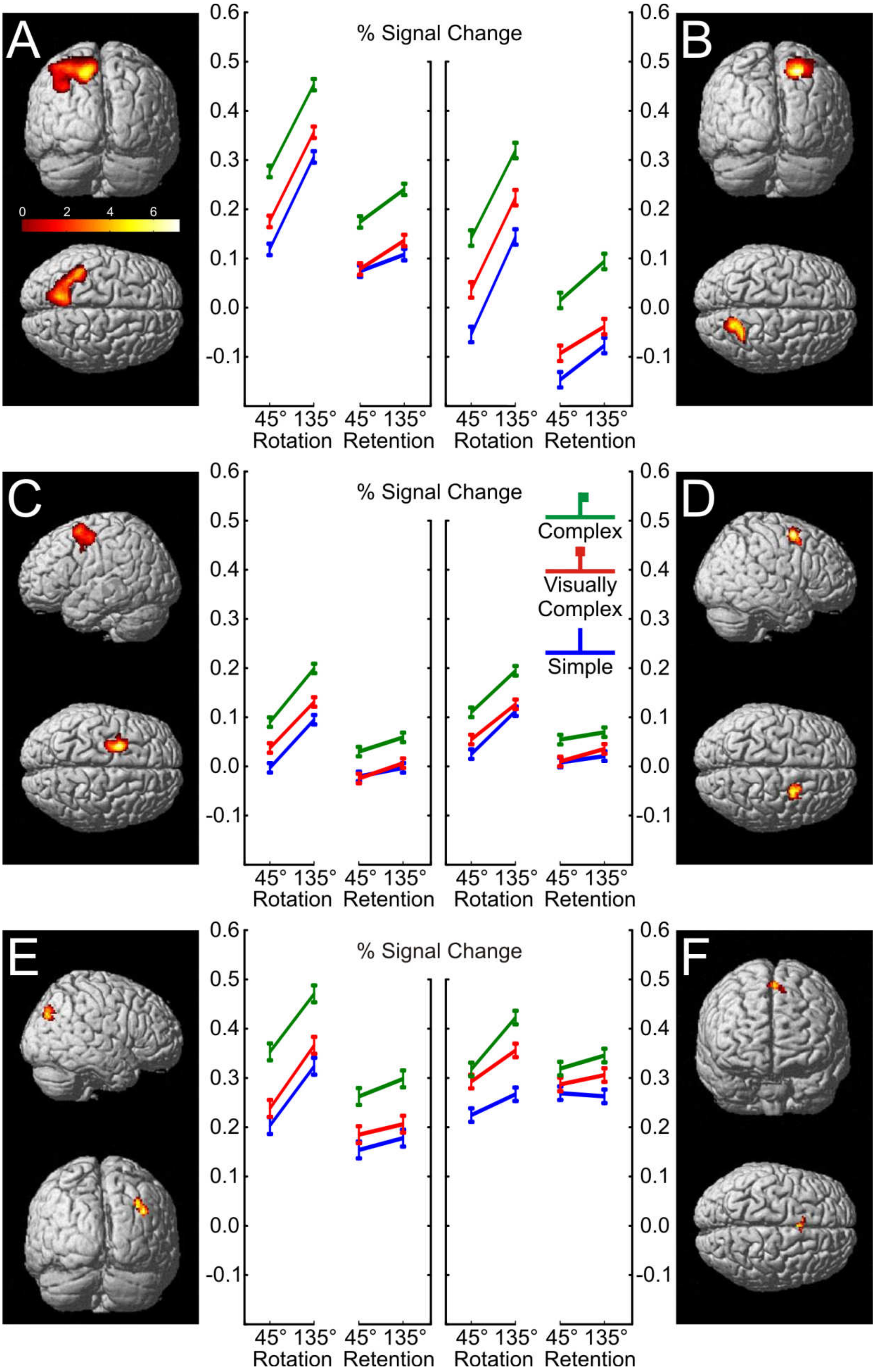


Figure 7.6. *Please refer to the figure caption on the right.*

Figure 7.6. *Brain areas involved in the process of mental rotation proper as identified by the (rotation > retention) × (135° > 45°) interaction contrast overlaid over the SPM single subject render (outside) and their activation pattern in percent signal change as a function of condition, stimulus type and rotational angle (inside), displayed with 95%-confidence intervals based on the Stimulus Type × Rotational Angle interaction. We employed an individual voxel threshold of* $p < .001$ *and a cluster extent threshold of 40 contiguous voxels thereby keeping the overall type I-error rate at* $\alpha < .001$ *as determined by a Monte Carlo simulation (please refer to Chapter 7.3.5 for details). Colors code t values for the displayed contrast at the respective voxel. As a single contrast is displayed, the scale in A is also valid for all other areas. (A) left SPL+; (B) right SPL; (C) left pMd; (D) right pMd; (E) right IPC; (F) left pre-SMA.*

Table 7.2

Summary of Multivariate Analyses of Variance (F Values) on Activation in the Six Regions of Interest.

Source	SPL+,l	SPL,r	pMd,l	pMd,r	IPC,r	pSMA,l
Condition	43.86^{***}	67.67^{***}	54.74^{***}	38.25^{***}	17.36^{***}	1.52
Stimulus	68.84^{***}	61.12^{***}	28.35^{***}	26.69^{***}	39.90^{***}	16.39^{***}
Angle	96.53^{***}	92.51^{***}	46.55^{***}	30.26^{***}	22.64^{***}	14.68^{***}
Condition × Stimulus	$3.09^{\dagger}$	1.98	6.31^{**}	$2.84^{\dagger}$	1.82	3.96^{*}
Condition × Angle	32.05^{***}	21.62^{***}	36.65^{***}	19.88^{***}	23.45^{***}	19.75^{***}
Stimulus × Angle	0.18	0.29	0.25	0.01	0.02	$3.01^{\dagger}$
Condition × Stimulus × Angle	0.55	0.54	0.20	0.45	0.15	0.91

Note. l = left; r = right; SPL = superior parietal lobule (+ = and surrounding); pMd = dorsolateral premotor cortex; IPC = inferior parietal cortex; pSMA = pre-supplementary motor area.
$^{\dagger}p < .10$, $^{*}p < .05$, $^{**}p < .01$, $^{***}p < .001$.

We hypothesized that the same regions that are responsible for mental rotation proper also represent the rotated information (orientation-dependent information). Indeed, as summarized in Table 7.3, all ROIs from the interaction contrast show the expected effect of the amount of orientation-dependent information. These regions apparently also show an effect of the amount of orientation-independent information/visual complexity. However, in all ROIs, except the pre-SMA, orientation-dependent information has a clearly stronger effect than orientation-independent information as evident in Figure 7.6 and in the effect sizes given in Table 7.3. This is also apparent when looking at the group brain activation maps in Figure 7.5. Consider the strong similarity in activation pattern of the maps in the lower row of Figure 7.5, which display the regions active during mental rotation proper and the regions mainly processing orientation-dependent information (Figure 7.5, lower right). The brain activation pattern that orientation-independent information/visual complexity elicits (Figure 7.5, upper right), in contrast, differs strongly from the regions active during mental rotation proper.

Table 7.3

Effects (t Values and Effect Sizes, d_zs) of the Amount of Orientation-Dependent (Dep) and Orientation-Independent Information/Visual Complexity (Indep) on Activation in the Six Regions of Interest.

	Dep		Indep	
Region	t	d_z	t	d_z
SPL+, left (A)	5.58***	1.14	3.25**	0.66
SPL, right (B)	5.91***	1.21	4.34***	0.89
pMd, left (C)	4.20***	0.86	2.98**	0.61
pMd, right (D)	4.59***	0.94	2.04†	0.42
IPC, right (E)	6.96***	1.42	1.78†	0.36
pre-SMA, left (F)	2.48*	0.51	5.58***	1.14

Note. All tests have 23 degrees of freedom. SPL = superior parietal lobule (+ = and surrounding); pMd = dorsolateral premotor cortex; IPC = inferior parietal cortex; pSMA = pre-supplementary motor area.

$^{\dagger}p < .10$, $^{*}p < .05$, $^{**}p < .01$, $^{***}p < .001$.

In addition to the rotation-specific areas, the amount of orientation-dependent information influences activation in bilateral insula (maxima: 34/32/-4 and -32/22/2), bilateral BA 44 (maxima: -50/10/32 and 46/6/32), and left

V5/MT (maximum: -42 -68 -10). However, activation in these areas was also influenced with a similar strength by orientation-independent information/visual complexity and therefore might rather reflect the amount of comparison-relevant information in a given condition. Some visual areas as bilateral V4 and right-medial BA 17/18 were specifically activated by orientation-independent information/visual complexity. In addition, the activation cluster in the left pre-SMA was much stronger for this contrast compared with all other contrasts. Table 7.4 gives an overview over the areas activated in the different contrasts.

Table 7.4

Summary of Activated Areas of the Mental Rotation Network in Several Contrasts.

Region	Rot, Angle	Ret, Angle	Cond	Cond × Angle	Indep	Dep
BA 17	l/r	l/r			r (m)	
BA 18	l/r	l/r			r (m)	
V3	l	l/r				
V4	l	l/r			l/r	
V5/MT	l	l			l/r	l
IPC	l/r	l/r	l/r	l/r	l/r	l/r
IPS	l/r	l	l/r	l/r	l/r	l/r
SPL	l/r	l/r (inf)	l/r (sup)	l/r (sup)	l/r	l/r (sup)
BA 1	l/r		l/r	l	r	
BA 2	l/r		l/r	l	l/r	l/r
BA 3	l/r					
pMd	l/r		l/r	l/r		l/r
pSMA	l		l	l	l	
SMA		l/r				
BA 44	l/r				l/r	l/r
Insula	l/r		l		l/r	l/r

Note. Angle = rotational angle; Cond = condition; Rot = rotation; Ret = retention; Indep = orientation-independent information/visual complexity; Dep = orientation-dependent information; l = left hemisphere; r = right hemisphere; m = medial part of the structure; sup = superior part of the structure; inf = inferior part of the structure.

7.5 Discussion

We set out to explore the function of the several cortical regions that form the mental rotation network. First of all, those regions that increase in activation with the amount of performed rotation were identified. These regions, which include mainly visual, parietal and premotor areas, purportedly all contribute to the performance of mental-rotation tasks. Notably, all principal regions discussed in Zacks' (2008) meta-analysis on mental rotation studies (see Chapter 1.6) were also found active in the current study. However, as evident in the comparison of the duration-adjusted 135°- and 45°-retention trials, a subsample of these areas plays a more passive role. Activation in these areas also increases with the duration of retaining information, even when no mental rotation is necessary. With the aid of this very specific control condition, we were able to isolate the regions that are responsible for the process of mental rotation proper as those regions in which the effect of rotational angle was stronger than the effect of retention time (the interaction contrast). These included only a subsample of the areas that form the mental rotation network, namely the superior parietal lobule (including the intraparietal sulcus and somatosensory areas), dorsolateral premotor areas, the right inferior parietal cortex and the pre-supplementary motor area. As predicted, activity in all areas involved in mental rotation proper was also influenced by orientation-dependent information. Except for the pre-SMA, orientation-dependent information had a much stronger effect than orientation-independent information/visual complexity.

Why did orientation-independent information/visual complexity influence activation in these areas at all? Besides the training phase, participants of the current study performed a rather small amount of only 192 rotation trials in total. In comparison, participants of Experiment 1a and 1b performed at least 432 rotation trials and, additionally, incorrectly solved trials were repeated until correctly solved in these latter experiments. The design was reduced for the fMRI study in order to keep the time inside the scanner at a comfortable duration. As evident in the analysis of training effects in Experiment 1b (see also Chapter 3.6), participants need some training before they are able to employ an efficient mental representation. Consequently, participants in the current study might often have represented irrelevant or redundant orientation-dependent information. For example, in addition to representing “the smaller line is above the larger line” they might have represented “the square is above the larger line”. Note that these two pieces of information are redundant, because the square and the smaller line were always on the same side of the larger line. It was consequently sufficient to represent only one of these pieces of information. In line with this reasoning, rotational speed was in the present study not only lower for complex compared with visually complex stimuli, but also for visually complex compared with simple stimuli. If some participants sometimes represented two pieces of orientation-dependent information on trials with visually complex stimuli, visually complex stimuli have caused a stronger activation in the cortical regions that process orientation-dependent information compared with simple stimuli. However, for complex stimuli participants might also have represented this redundant information *and* the additional piece of comparison-relevant orientation-dependent information. Consequently the increase in activation due to the amount of represented orientation-dependent information was much stronger from visually complex to complex stimuli.

As discussed above (Chapter 1.6.3), the superior parietal lobule (SPL) and intraparietal sulcus (IPS) as well as the dorsolateral premotor cortex (pMd), that is, the areas that are activated by mental rotation proper, are also activated when participants observe others performing object-related hand actions (Buccino, et al., 2001) and are therefore considered part of or related to the mirror-neuron system (e.g., Rizzolatti & Sinigaglia, 2010). Object-unrelated hand actions also activate the pMd but not the IPS/SPL. Consequently, these areas might also play differential roles in mental-rotation tasks. The pMd might represent the imagined action of rotation whereas the IPS/SPL might hold the rotated representation (information about the rotated object). However, the fact that in the present study activation in both regions depends on the amount of represented orientation-dependent information and the amount of performed rotation constitutes evidence against a differential role of these regions in mental rotation. In addition, the topography of the negative slow potential that was observed in Experiment 2 and that was taken to reflect the amount of processed orientation-dependent information indicates that the pMd is more strongly involved in processing this type of information compared with the parietal cortex.

Rizzolatti and Sinigaglia (2010) emphasize more the role of the inferior parietal cortex than the superior parietal lobule in the mirror-neuron system. However, they also note that the superior parietal lobule is activated in studies employing proximal arm movements that are directed to a particular spatial location, for example, when observing, executing, or imagining a reaching movement without grasping (Filimon, Nelson, Hagler, & Sereno, 2007). In the working memory literature, it is considered established that spatial information is stored in the superior parietal lobule whereas object information is stored in the inferior parietal cortex (e.g., Wager & Smith, 2003). If the manipulated object (the mental representation in our case)—in contrast to the real objects typically that are employed in the studies reviewed by Rizzolatti and Sinigaglia—is purely spatial in nature, it appears more probable that it is represented in the spatial and not in the object storage system. That the mirror-neuron system is involved in mental rotation is also indicated by the involvement of another classical mirror-neuron area, namely bilateral BA 44/45. However, this area is not specifically involved in representing orientation-dependent information. Its activation increased with the amount of comparison-relevant information regardless of whether the information was orientation-dependent or independent.

Further, activation in bilateral insula depended on the amount of comparison-relevant information. The insula is found active in many mental rotation studies (e.g., Kosslyn, Digirolamo, et al., 1998; Lamm, Windischberger, Leodolter, Moser, & Bauer, 2001; Milivojevic, et al., 2009). Based on a thorough review of the literature reporting insula activation, Sterzer & Kleinschmidt (2010) propose that the activation in this area depends on the level of alertness induced by stimulus or task characteristics. If this is the case, the amount of comparison-relevant information in our task had a uniform influence on our participants' alertness. Also a region close to left V5/MT showed consistently increasing activation with the amount of comparison-relevant information. Activation in this area might correspond to rotation-specific activation in left V5/MT found by Seurinck et al. (2011). These authors found a rotation-specific effect (which was modulated by a rotation aftereffect, see Chapter 1.6.5) on activation in this area and therefore assume that V5/MT is of functional relevance for mental rotation. This interpretation fits well with V5/MT's role in visual motion perception (Barnes, et al., 2000; M. S. Cohen, et al., 1996; Vanrie, et al., 2002). However, according to the present data, V5/MT is not involved in mental rotation proper. Activation in this area is apparently merely related to the passive maintenance of any type of comparison-relevant information for the duration of mental rotation.

We found stronger activation in visual areas for visually complex compared with simple stimuli. This was purportedly due to the higher visual complexity of visual complex stimuli. These areas could in principle provide the back-up representation as postulated above (Chapter 6.5). However, these areas very probably are the source for the positive slow potential observed in Experiment 2 which was also sensitive to the stimuli's visual complexity. This slow potential extinguished long before the comparison stimulus appeared (latest 2600 ms after the original stimulus disappeared). This representation is consequently not sufficient to identify mismatches in orientation-independent information whenever the trial lasts too long.

This might be were the pre-SMA comes into play. Many mental rotation studies report rotation-related activation in the SMA (e.g., M. S. Cohen, et al., 1996; Richter, et al., 2000) or pre-SMA (e.g., Ecker, et al., 2006; Milivojevic, et al., 2009; Windischberger, et al., 2003). Windischberger et al. (2003) found that the posterior part of the SMA (the SMA proper) is more engaged in the button press, while the anterior part (the pre-SMA) is related to mental rotation. Often the differentiation between SMA proper and pre-SMA is not taken into account although these areas are anatomically and functionally clearly separable (for a review, see Picard & Strick, 2001). Consequently, also studies reporting SMA activation might, similar to the present study, actually have found pre-SMA activation. The pre-SMA is not as directly related to motor planning as the SMA proper (Picard & Strick, 2001). It is apparently involved in establishing or retrieving sensory-motor associations (Kurata, Tsuji, Naraki, Seino, & Abe, 2000;

Sakai, et al., 1999). Pre-SMA seems to be activated when participants are preparing for selecting a motor response based on retained information (Petit, Courtney, Ungerleider, & Haxby, 1998).

In this role the pre-SMA might be programmed on each trial with visually complex or complex stimuli to elicit a mismatch response when the square of the comparison stimulus appears on the wrong position on (the middle or the end of) the smaller line, that is, in case of an orientation-independent mismatch. This programming could already take place during the encoding phase and might therefore explain the prolonged encoding times for complex and visually complex stimuli compared with simple stimuli as found in Experiment 1b. In addition, eliciting a response via the sensory-motor association of the pre-SMA might take longer than via the comparison of actively maintained information, explaining the prolonged comparison times for mismatches in orientation-independent information. It consequently appears probable that the pre-SMA is the back-up store for orientation-independent information.

We assume that the orientation-independent information/visual complexity-related slow potential observed in Experiment 2 and the here observed visual system activation reflect the same process. In Experiment 2, this slow potential lasted only for a fixed amount of time. It might therefore be surprising that visual system activation was stronger for 135° trials compared with 45° trials in both the rotation and retention condition of the present study. However, note that the slow potential in Experiment 2 was present for at least 1100 ms after the original stimulus had vanished. In the present study the average rotation time on 45° trials measured from onset of the rotation cues (200 ms before offset of the original stimulus) was about 1840 ms. That means, 45° trials often ended before the visual representation was extinguished. If this representation was discarded after onset of the comparison stimulus, it was consequently upheld for a longer time period in 135° trials (which lasted about 2520 ms on average) compared with 45° trials.

8. General Discussion[19]

8.1 The Content of the Rotated Representation

Results from each of the four experiments constitute strong evidence for the claim that only orientation-dependent spatial-relational information is explicitly represented during mental rotation.

1. Rotational speed is influenced by the amount of orientation-dependent information but not by the amount of orientation-independent information, the amount of comparison-relevant stimulus parts or by the stimuli's visual complexity as found in Experiment 1a and 1b. These studies made use of and further validate the generally accepted assumption that rotational speed slows down whenever the rotated mental representation becomes more

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[19] Part of this chapter is adapted from Liesefeld and Zimmer (2012). See also the credit line in Footnote 4.

complex. As hypothesized, representational complexity in mental rotation and therefore rotational speed depends exclusively on the amount of orientation-dependent information, indicating that only this type of information is explicitly represented.

2. Only the amount of orientation-dependent information influences the amplitude of a slow potential during a time-interval when purportedly the second piece of orientation-dependent information is rotated as found in Experiment 2. This study made use of and further validates the generally accepted assumption that the amplitude of slow potentials measured during a retention period reflects the amount of information stored in working memory. Our finding consequently indicates that during mental rotation only orientation-dependent information is explicitly represented in working memory.
3. Only the amount of orientation-dependent information influences activation in cortical areas that are responsible for performing the process of mental rotation proper as found in Experiment 3. This study supports our hypothesis that the very same brain areas that perform a mental process are also involved in maintaining the processed representation.

8.2 Representational Content is not Recoded for Comparison

Above, we already discussed in detail that even after mental rotation is finished, the representational content remains the same. Orientation-dependent information continues to be explicitly represented in the active mental representation whereas orientation-independent information remains implicit. This observation is supported by three findings.

1. In all four experiments reported here, comparison times are prolonged for mismatches in orientation-independent information. The processing of this type of information is purportedly delayed, because it is not explicitly represented in the active mental representation employed for comparison.
2. P3bs to mismatches in orientation-independent information are delayed relative to P3bs to mismatches in orientation-dependent information, fur-

ther supporting that orientation-independent information is processed delayed compared with orientation-dependent information.

3. P3bs to mismatches in orientation-independent information are enlarged relative to mismatches in orientation-dependent information, indicating that mismatches in orientation-independent information and mismatches in orientation-dependent information belong to different subjective classes. The critical difference purportedly is that orientation-dependent information is explicitly represented in the active representation and therefore directly accessible whereas orientation-independent information is not.

Further supporting the assumption that orientation-independent information was not actively represented in the representation employed for comparison, some participants did apparently make the comparison only according to actively represented orientation-dependent information. From the total of 28 participants who were excluded for ignoring information over all four Experiments, 25 ignored at least the piece of orientation-independent information in complex stimuli. Among these, 21 participants detected a mismatch when the square switched sides in the complex stimuli, but not when the square moved on the smaller line (see Figure 8.1). In other words, these excluded participants selectively ignored the piece of orientation-independent information (whether the square of the comparison stimulus was in the middle or on top of the smaller line) whereas they processed the second piece of orientation-dependent information (on which side of the smaller line the square was attached), even though both pieces of information describe the spatial relation between the same stimulus parts. We assume that this systematic error could only occur, because participants did not actively represent orientation-independent information at comparison stimulus onset. Those participants who ignored orientation-independent information might, in contrast to the more successful participants, not make use of a passive backup representation for comparison.

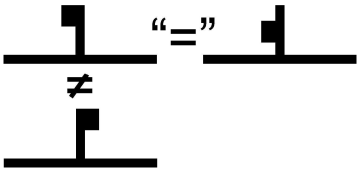

Figure 8.1. *Illustration of a typical mistake. For 25 of the 28 participants who were excluded for ignoring information over all reported experiments, the stimulus in the upper left was indistinguishable from the stimulus on the right. Differentiating between the upper left and the lower stimulus, in contrast, did not pose a major challenge to 21 of them. For the reader this mistake seems rather surprising when looking at the figure, because the figure is a visual representation of the stimuli. Participants in contrast purportedly held a nonvisual representation of the stimulus in the upper left. This representation apparently is identical for the upper two stimuli, because it only specifies selected pieces of orientation-dependent information.*

As indicated by the patterns of comparison times, in three (Experiment 1b, 2 and 3) out of the four experiments and the P3b-pattern in Experiment 2, mismatches in orientation-dependent information were obviously treated similarly independent of whether the smaller line and the square changed to the other side of the larger line (change in the first piece of orientation-dependent information) or the square changed to the other side of the smaller line (change in the second piece of orientation-dependent information). Only for Experiment 1a a mismatch in the second piece of orientation-dependent information elicited longer comparison times than a mismatch in the first piece of orientation-dependent information. An explanation might be based on the (plausible) additional assumption that the several pieces of information are compared sequentially. Participants of Experiment 1a might then have preferentially started the comparison with the first piece of orientation-dependent information, whereas participants of the other three experiments apparently did not have such a clear preference. Fortunately, our interpretation of the observed comparison time patterns that orientation-independent information is held in an alternative, more passive representation does not depend on equal comparison times for the two pieces of orientation-dependent information but only on prolonged comparison times for mismatches in orientation-independent information. An explanation for the divergence in Experiment 1a from the predominant pattern might be found in subtle differences in instructions and would need further research for confirmation.

8.3 The Format of the Rotated Representation

Although we can make an affirmative statement about the representational content (what is represented) mental rotation works on, we cannot tell what the format (how it is represented) of the representation in mental rotation is. Equating representational format and representational content would be the same fallacy as to assume “that the best way to explain data with property P is to assume a representation with property P” (Anderson, 1978). That is, on intuitive grounds it might appear plausible to assume that a representation has the same format as its content, but such an assumption is, of course, not logically justified.

Nevertheless, we can definitely tell what the format is not. As detailed above (Chapter 3.8), we deliberately constructed our task and stimuli in such a way that no visual representation of our complex stimuli, neither a sketch on a sheet of paper nor a visual mental image, can represent the second piece of orientation-dependent information separately from the piece of orientation-independent information. However, all our data—rotation times, comparison times, slow potentials, P3bs and brain activation patterns—indicate that precisely this happens in mental-rotation tasks. Orientation-dependent information and orientation-independent information held by the smaller line and the square in our complex stimuli (see Figure 3.4) were represented separately even though any visual representation of the employed stimuli would have inextricably encoded these two pieces of information together. It is consequently safe to conclude that the representation on which the process of mental rotation works has a nonvisual format. This strongly contradicts implicit and explicit held beliefs that the rotated representation is visual. Mental rotation does not work on a visual mental image.

As already discussed above (Chapter 3.4), Anderson (1978) logically proofed that the behavior of any representation-process pair can be mimicked by an alternative representation-process pair. This might be a last refuge from the ultimate rejection of visual mental images in mental rotation. What could this alternative pair be in the present studies? Of course, it is theoretically possible to extract orientation-dependent information from the visually presented stimulus and to remap this information onto a visual representation, for example, in the form of arrows. That would mean that participants actually rotate visually represented arrows, one arrow to represent orientation-dependent information from simple and visually complex stimuli and two arrows to represent orientation-dependent information from complex stimuli. For the comparison participants then must also extract orientation-dependent information from the second stimulus and recode it into visually represented arrows in order to match both sets of arrows. Recoding from visual to nonvisual and back to visual comes very close to Anderson's "$\mathrm{T}^* = f \cdot \mathrm{T} \cdot f^{-1}$", that, is a recoding from one representational format to the other via an intermediate representation that is of the same format as the original stimulus, which as Anderson himself notes has to be rejected on grounds of parsimony considerations.

There is no possibility to directly recode the implicitly represented orientation-dependent information from the visually presented stimulus into such a set of visually represented arrows without an intermediate nonvisual representation of explicit orientation-dependent information, because the only common property of arrows and the presented stimulus actually is orientation-dependent information. Nevertheless, even if there was such a direct possibility, this recoding would violate parsimony considerations. Participants would recode visual representation A into visual representation B, whereby visual representation B includes less task-relevant information than the original visual representation A (which additionally includes orientation-independent information). This appears so outrageously inefficient (cf. Anderson, 1978) that we initially did not even bother to consider this possibility. Participants could have saved the trouble of recoding and visually represented the stimulus parts directly. They thereby even had represented the piece of orientation-independent information for free. In addition, what strange algorithm would be able to rotate visually represented arrows, but unable to rotate arrows with an additional mark for orientation-independent information? Given our knowledge about the representational content in mental rotation (orientation-dependent information), a visual image is not parsimonious and not plausible as the representational format in mental rotation (cf. Anderson, 1978). The arguments put forward here do not only apply to arrows, but to all conceivable visual representations of orientation-dependent information.

As no affirmative statement about the format of the rotated representation can be derived from our data, they cannot be interpreted as support for a propositional representation in mental rotation. The fact that orientation-dependent information can in principle be expressed isolated and explicitly in a propositional format merely shows that propositional representations are more flexible than analog representations; they do not commit themselves to a certain represented content. On the contrary, findings of nonvisual factors like the difficulty of the comparison influencing rotational speed (Förster, et al., 1996; Pylyshyn, 1979), can no longer unambiguously count as evidence in favor of propositional theories, because, as discussed above (Chapter 3.6), the nature of the comparison can also influence which information is comparison-relevant or how efficiently comparison-relevant information is discriminated from comparison-irrelevant information. Therefore, the predominant interpretation of the classical mental rotation effect that is that a mental representation is rotated similar to an analog rotation is rather strengthened by our results.

It appears at least possible that not only the content of the rotated representation is spatial, but also its format, that is, rotation might work on *spatial* mental images. In contrast to the assumption of a propositional representation, spatial mental images would intuitively explain why the mental rotation effect exists at all. The most plausible transformation of a propositional representation would work like “with a 180° rotation ‘to the left’ becomes ‘to the right’” or “with a clockwise 90° rotation ‘to the left’ becomes ‘above’”, that is, it would be similar to a direct matrix transformation. These transformations would not take longer for larger rotational angles compared with smaller angles. Even though transformations on propositional representations (there is no doubt that humans do possess propositional representations) are obviously a possible strategy in mental-rotation tasks, mental rotation of a purely spatial image might simply take less time than applying complicated rules on propositional representations. This spatial image might, similar to a visual image, be rigid in certain ways and therefore allow only certain types of transformations, as detailed below (Chapter 8.7.3). As a consequence, the typical angle-dependency of rotation times (the mental rotation effect) emerges.

8.4 Experimental Control over Mental Representations

An intricacy of the experimental manipulation of mental representations (see Chapter 3.6) is that control over people's mental representations is never fully possible. Nevertheless, we here introduced several techniques that improve experimental control over mental representations. Among these is a careful choice of stimuli. Comparison-relevance can be directly manipulated by including mismatches in the respective piece of information into the task design. However, participants will represent these pieces of information only if they know or at least presume that they are relevant. Furthermore, they must also know which pieces of information are irrelevant in order not to represent them. Applying this knowledge increases the efficiency of and thereby experimental control over participants' mental representations. An efficient representation can to a certain degree be induced by employing stimuli that do not contain many irrelevant features and by instructions that explain the relevant pieces of information to the participants. However, even then participants obviously represent irrelevant information during early trials of an experiment. As shown in Experiment 1b, only after a certain amount of training participants are able to employ a really efficient representation.

8.5 Limitations of the Present Studies

We developed and employed a task especially suited to obtain evidence for our hypothesis about the mental representation in mental rotation. Both trial procedure and stimuli employed in this task are new and different to other mental-rotation tasks. Although we cannot think of a plausible reason why our results should not generalize to other mental-rotation tasks and stimuli, this generalization has yet to be proved.

The stimuli employed here are (a) visually rather simple, as they contain only few elements, clear geometric shapes and few detail, (b) pre-experimentally unknown, and (c) two-dimensional.

1. By keeping stimuli as visually simple as possible comparison-irrelevant information is kept at a minimum. Thereby extracting comparison-relevant information and ignoring comparison-irrelevant information becomes relatively easy (see Figure 3.2). However, it might be of interest to show that the effects reported here also emerge for visually more complex stimuli. For visually more complex stimuli more training should be necessary before an efficient representation is developed. However, assumedly, the training task does not necessarily need to be a mental-rotation task, but any other task that nudges participants to only process comparison-relevant and ignore comparison-irrelevant information.
2. Consequently, for pre-experimentally known stimuli like alphanumeric characters this training-phase is purportedly rather short, because participants already possess profound knowledge on the stimuli's structure. That is, they already have had abundant training on the stimuli before they even enter the laboratory. By applying this knowledge, it should become easier to classify the potential types of mismatches and thereby to differentiate between comparison-relevant and comparison-irrelevant information. Note, however, that in usual character-rotation tasks (see Figure 1.2C) only one piece of (orientation-dependent) information is comparison-relevant.
3. In a first step, we employed two-dimensional stimuli. However, three-dimensional stimuli would allow independently manipulating three pieces of orientation-dependent information. After training, that is, when participants employ an efficient representation, a linear effect of the amount of comparison-relevant orientation-dependent information on the slope of the function relating rotation time to rotational angle should emerge. Such a parametric modulation of activation should also emerge in brain areas supporting the representation of orientation-dependent information as measured by means of fMRI or slow potentials.

We employed a successive-presentation mental-rotation task with rotation cues (see Chapter 1.3). Although this type of mental-rotation task has some important advantages, it is actually employed rather seldom. As certain cognitive processes involved in mental-rotation tasks can only begin after the appearance of certain stimuli (see Chapter 1.3.4), successive presentation allows separating these processes to a certain degree. In addition, this type of mental-rotation task has an advantage that was especially crucial for our purposes. In all other types of mental-rotation tasks, mismatches in orientation-independent information can be identified before mental rotation starts. This is because in simultaneous-presentation, single-stimulus as well as successive-presentation (without rotation cue) mental-rotation tasks rotation is performed when the comparison stimulus is already shown on the screen (see Chapter 1.3 and Figure 1.2). Smart participants would check for mismatches in orientation-independent information prior to conducting mental rotation. If such a mismatch is found, a mismatch answer can be given without the need for mental rotation. If no mismatch is found and obviously all orientation-independent information matches between the to-be-compared stimuli, there is no need to represent orientation-independent information during rotation (cf. Takano, 1989). That means the question of how orientation-independent information is stored during mental rotation cannot be addresses by these tasks. Nevertheless, effects of the amount of orientation-dependent information can also be examined by these other types of mental-rotation tasks.

8.6 Employing the Developed Techniques to Other Tasks

Apart from mental rotation, humans purportedly employ mental representations in many other cognitive tasks. The techniques to manipulate (Chapter 3.6) and measure (Chapter 3.7) the amounts of represented information and thereby to identify the nature of the representational content should also be adoptable to these other tasks. These techniques can, of course, be applied to all types of working-memory tasks. Additionally, these techniques might be fruitful in research on perception and consciousness, as exemplified in Experiment 2. The slow potential measured during the perception phase of our task was sensitive to the visual complexity of the stimuli. This effect began only about 200 ms after the eliciting stimulus was shown, that is, at the time when it was purportedly perceived consciously. Among many other remaining applications of the developed techniques might also be an examination of the content of the mental representations known as attentional sets (e.g., Adamo, Pun, Pratt, & Ferber, 2008; C. L. Folk & Anderson, 2010).

8.7 Further Implications of the Present Results and Future Directions

As cognitive psychologists have carried the false belief of visual mental images in mental rotation over decades, it has produced a number of misleading assumptions and interpretations of experimental results. In the remaining paragraphs, we will briefly address some of these issues in order to give the interested reader an impression of the more general implications of the present work. The re-interpretation of empirical results given below is of course inherently post-hoc. Further empirical testing therefore appears appropriate in order to substantiate these speculations.

8.7.1 A common explanation for effects on rotational speed

Studies supporting the holistic hypothesis did not find any influence of visual complexity on rotational speed (Cooper, 1975; Cooper & Podgorny, 1976). Studies supporting the piece-meal hypothesis (M. D. Folk & Luce, 1987; Heil & Jansen-Osmann, 2008), in contrast, found such an influence even when the same type of stimuli was employed as in the studies supporting the holistic hypothesis (polygons constructed according to an algorithm by Attneave & Arnoult, 1956). As discussed above (Chapter 3.6), only information that is comparison-relevant must be represented in order to solve mental-rotation tasks successfully. Consequently, representational complexity is not necessarily determined by the visual complexity of the stimuli. Recall that, in contrast to the present study, most mental rotation studies include only mirror images as mismatching stimuli and that two-dimensional mirror images can be distinguished by comparing one single piece of orientation-dependent information. Therefore, if participants in these mental rotation studies always performed most efficiently—that is, if they used the sparsest effective representation—their rotational speed would be independent of visual complexity. Exactly this pattern of results is usually misinterpreted as support for the holistic hypothesis.

However, as discussed in the introduction and as the analysis of training effects (the increase in rotational speed from the first to the second block of trials) in Experiment 1b has confirmed, participants do not always perform most efficiently and often represent more than just the comparison-relevant information. For polygons with many vertices, for example, certainly more information is available and might consequently be represented than for polygons with fewer vertices. The amount of available information might render a differentiation between comparison-relevant and comparison-irrelevant information harder with the more complex than with the less complex polygons. Visually very complex stimuli might therefore mislead participants to represent much more than just comparison-relevant information. As the unnecessarily represented comparison-irrelevant information would also contain orientation-dependent information, rotational speed would decrease accordingly. In line with this reasoning, rotational speed is higher when participants are informed about comparison-irrelevant (redundant) information in a given stimulus (Yuille & Steiger, 1982).

The probability of accurately discriminating between comparison-relevant and comparison-irrelevant information in a given stimulus set and consequently the probability that only comparison-relevant orientation-dependent information is represented should additionally increase with participants' familiarity with the employed stimuli. Indeed, when stimuli are well known to participants (as in Cooper, 1975; Cooper & Podgorny, 1976) no influence of visual complexity on rotation rate is found. In light of the present results, it appears that when stimuli are familiar, only the single piece of comparison-relevant orientation-dependent information is rotated in usual mental rotation studies employing two-dimensional stimuli. Consequently, rotational speed increases with practice on the rotated stimuli (e.g., Heil, Rösler, et al., 1998; Pylyshyn, 1979; Tarr & Pinker, 1989; see also our analysis of training effects in Experiment 1b) and rotational speeds for visually simple and visually complex stimuli converge as these stimuli become familiar (Bethell-Fox & Shepard, 1988).

The tendency to represent comparison-irrelevant information should on the other hand increase with the difficulty of determining which information is comparison-relevant, for example, with the difficulty of the comparison (see M. D. Folk & Luce, 1987; Pylyshyn, 1979). This explains why mental rotation sometimes occurs even when the task does not include any comparison-relevant orientation-dependent information at all. Förster et al. (1996) found a mental rotation effect even though they employed hard to discriminate polygons as mismatching stimuli instead of mirror images. It appears that Förster et al.'s participants did not use the most efficient representation but represented and rotated comparison-irrelevant orientation-dependent information. With training on Förster et al.'s stimuli or with appropriate instructions the mental rotation effect should disappear.

In addition to the effects of visual complexity, familiarity, and task-difficulty, our results can also explain the effect of dimensionality on rotational speed (Bauer & Jolicoeur, 1996; Jolicoeur, et al., 1985). One piece of orientation-dependent information is sufficient to differentiate between two-dimensional mirror images. Without restrictions on the possible rotational plane, rotations in three-dimensional space must, in contrast, take two pieces of orientation dependent information into account (cf. Figure 1.3A). We suppose that it is this difference in the amount of relevant and therefore mentally represented orientation-dependent information that influences rotational speed and not dimensionality per se.

8.7.2 Inability to rotate

Rock, Wheeler & Tudor (1989) convincingly demonstrated that observers are actually unable to imagine how an object looks after a rotation (see also Parsons, 1995). Participants were unable to draw complex irregular three-dimensional objects in a new perspective; in addition, they were unable to recognize these rotated objects when recognition time was limited to 4 s and consequently time-consuming alternative strategies (other than mental rotation) were suppressed.

Rock et al. argue that these results make a clear case against the assumption of mental rotation in general. However, actually, their data only show that their subjects were unable to mentally rotate full-blown visual mental images of objects. This finding leaves open the possibility that in usual mental-rotation tasks only orientation-dependent information is rotated. As we have shown, processing of one piece of orientation-dependent information is sufficient to successfully perform most mental-rotation tasks. The complex and exceptionally irregular forms employed in the experiments by Rock et al., in contrast, purportedly rendered much more information comparison-relevant than manageable by inexperienced subjects. Consequently, in the light of the present article, Rock et al.'s data do not disprove the ability of mental rotation in general, but only the ability to rotate full-blown visual mental images.

8.7.3 Possible rotation mechanisms

The idea of visual mental images in mental rotation took much of its appeal from the fact that a certain degree of rigidity is intuitively ascribed to such representations. Visual mental images apparently cannot be submitted to just any type of transformation. Mental rotation might be performed incrementally, because people simulate how the presented object looks like when rotated. This simulation must go through a series of intermediate steps because participants can tell how an image looks like when slightly rotated but the image loses its inner structure when rotated around too large an angle. In order to prevent such lost, Kosslyn (1994) reasons that the structure must be updated after each rotational step. However, a similar rigidity might also apply to a spatial mental representation. Maybe people lack a direct mapping of the values of orientation-dependent information for large rotational angles. They might however be able to perform small changes in orientation-dependent information and achieve larger rotations by concatenating these small manipulations.

That the process of mental rotation itself is spatial or simulates a spatial behavior is rather self-evident; the present article shows that also the representation this spatial process works on specifies only spatial information. Even more, we can further constrain the information which is rotated, namely to orientation-dependent spatial-relational information. The smaller the informational content of the processed representation the more efficient the process that manipulates this representation can be (cf. Just & Carpenter, 1985). An algorithm that manipulates a pictorial representation, for example pixel-wise, must employ much more resources than a mechanism that works on pieces of abstract spatial-relational information, that is, on much less information than is included in an image. Future models and theories of mental rotation should be based on the active representation and manipulation of orientation-dependent information only (cf. Morgan, 1983), while all other relevant information can be stored passively for the duration of the rotation process.

8.7.4 The special situation of 180°-tilts

An important yet unanticipated outcome of the preliminary experiment, was that mental manipulations of 180° appear to be (at least by some participants) solved in a qualitatively different way (cf. Cooper & Shepard, 1973). Specifically, participants appear to be solving these trials not by mental rotation, but by *mental flipping* a representation first along the horizontal and then along the vertical axis (see Figure 8.2). The response pattern of one participant who was excluded for consistently erring on 180° trials (6.5% correct for 180°[20], 96% correct for other tilts) may be best explained if she flipped the mental representation along the horizontal axis. Critically, she apparently did not execute the second flip which would have been necessary to arrive at a 180°-rotated representation (see Figure 8.2). In fact, a second participant reported having realized committing this error during practice trials and having adjusted his strategy by also executing the second flip in the remaining trials.

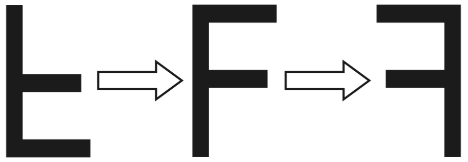

Figure 8.2. *Illustration of a 180° transformation using mental flipping instead of mental rotation.*

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[20] While guessing would lead to a 50% correct rate.

This complements response time data collected by Murray (1997). In a first experiment he could show that subjects indeed can flip a representation around the horizontal axis when they are instructed to do so. This process takes less time than a 180° rotation. Using this difference in speed, in a second experiment, Murray could successfully classify part of the subject sample as using a flipping strategy while the other part used a rotation strategy in an identification task with upside-down stimuli. Our two participants may have employed a flipping strategy without being instructed to do so. We suppose that more participants may have employed a flipping strategy for 180° trials in the preliminary experiment, but without making the mistake which would have brought their strategy to light, namely omitting the second flip.

One important implication for research on mental rotation is that data in 180° trials should be interpreted with caution. These data might not be comparable to other rotational angles, because (1) the amount of mental effort necessary for flipping two times could differ from the amount of mental effort for rotating 180°, that means flipping and rotating could differ quantitatively and (2) the process of flipping may be qualitatively different to the process of rotation. For example, flipping might not necessitate representations in intermediate orientations (Kanamori & Yagi, 2002), while just this characteristic is quite important for the claim of mental rotation being an analogue process (e.g., Cooper, 1976). Compounding this problem is the possibility that part of the subject sample in a given mental rotation experiment uses rotation and the remaining part uses flipping for performing 180° trials, thereby inflating the error variance and undermining the validity of the obtained measures.

How this alternative strategy might work becomes evident when considering the main finding from Experiments 1 to 4 that the mental rotation process works on pure orientation-dependent information. With this knowledge it becomes apparent why flipping in contrast to rotation in the picture plane does not involve intermediate representations of the stimulus (Kanamori & Yagi, 2002). In order to flip a stimulus only one processing step on orientation-dependent information is necessary: “to the left of” directly becomes “to the right of” for a flip around the vertical axis and “above” becomes “below” for a flip around the horizontal axis. This mechanism would clearly differ from a 180°-rotation of a mental image in the depth-plane as assumed by Murray (1997). If this is the case, mental rotation would not be the only process that manipulates orientation-dependent information.

8.7.5 Imagery and perception

The finding that an active mental representation can specify spatial information without being visual has important implications beyond mental rotation. Mental representations of this type certainly play a role in many other cognitive tasks and in daily life. It is rather uncontroversial that imagery and visual cognition are closely related and that findings from both areas should be explainable in a common framework (e.g., Kosslyn, 1994; Palmer, 1999). Especially questions concerning the format of representations, shape recognition and the interface between perception and cognition might best be approached from both perspectives (Pinker, 1984). If, as was the case in the present study, a type of spatial-relational information between stimulus parts can be factored apart and be represented detached from other spatial relations, this shows that it is at least possible to represent stimuli in a purely structural way as structural description theories of object recognition assume (for an overview, see Palmer, 1999; Pinker, 1984). A weakness of structural description theories has been that the elements (primitives and relations) employed by structural descriptions were not sufficiently specified (Palmer, 1999; Pinker, 1984). The present findings constitute evidence for the existence of one such presumably elementary relation (orientation-dependent spatial-relational information) and a process specialized to manipulate it and only it (mental rotation) within our cognitive system. The idea of mutually specialized representation-process pairs is in line with Anderson's (1978) note that “well designed systems tend to have special representations for the kinds of information they have to process frequently. These representations are designed to facilitate the kind of computations useful for this kind of information.” However, note that orientation-dependent information apparently can also be flipped (Chapter 8.7.4) and potentially also translated horizontally and vertically (e.g., a stimulus part that was to the right of might be moved leftwards until it is to the left of another stimulus part).

8.7.6 Orientation-dependent information in applied contexts

If orientation-dependent information is indeed an elementary type of information employed by the human cognitive system, it purportedly is of importance for a huge variety of tasks in daily life.

In general, when perceived from an imperfect perspective (i.e., not aligned with an egocentric reference frame of the viewer), orientation-dependent information is much more difficult to process than orientation-independent information, because mental rotation is necessary to determine how it looks from the canonical perspective. Therefore in situations in which the same object must be recognizable from different perspectives as few orientation-dependent information as possible should be rendered important. Such situations arise, for example, when a client sits in front of a consultant's desk while the consultant sits behind it or in conferences where participants sit around desks. Whenever some material is spread out on the desk, the different participants perceive it from different orientations, and this causes difficulties whenever orientation-dependent information is critical. For example, text is more difficult to read and some graphs are more difficult to interpret when seen bottom up.

In addition, there is strong interindividual variability in the ability to differentiate between left and right (e.g., Hirnstein, Ocklenburg, Schneider, & Hausmann, 2009) which might also drive the variability in mental rotation ability and the respective intelligence factor (W. Johnson & Bouchard, 2005). People ranking low on this ability are therefore potentially less suited for jobs with strong affordances on processing orientation-dependent information (e.g., flying an aircraft, driving a taxi or mechanical engineering). In neuropsychological patients suffering from orientation agnosia the parietal lobe is damaged. That is, these patients might have lost part of the brain regions for processing orientation-dependent information (e.g., Fujinaga, Muramatsu, Ogano, & Kato, 2005; Harris, Harris, & Caine, 2001; Karnath, Ferber, & Bülthoff, 2000; Turnbull, Beschin, & Della Sala, 1997). Indeed, the patient of Harris et al. (2001) showed reduced metabolism in the superior parietal and mid-dorsolateral frontal lobe (potentially premotor cortex). These might be the same areas which we found specifically sensitive to the amount of mental rotation and the amount of orientation-dependent information (see Chapter 7.4.3; but see Turnbull, Della Sala, &

Beschin, 2002). Furthermore, children often confuse letters that differ in orientation-dependent information only (e.g., *b* and *d*; e.g., Dehaene, et al., 2010). Potentially, children would benefit from a preparatory course on orientation-dependent information before they start learning to differentiate between these letters; such a skill might additionally alleviate problems in geometry. In sum, it might be of high ergonomic, diagnostic and pedagogic interest to examine how the necessity to process orientation-dependent information can be avoided and how the ability to process orientation-dependent information can be assessed and improved.

8.7.7 Disoriented object recognition

One remarkable capability of humans is the ability to recognize an object even when encountered in a new perspective in which it was never seen before (see Chapter 1.4). This capability is usually examined by asking participants to name or categorize objects shown disoriented from upright (for reviews, see Jolicoeur, 1990; Leek & Johnston, 2006). On early trials, the slope of the function relating identification time to angular displacement of to-be-identified disoriented objects is of similar magnitude as the slope found in mental rotation studies (e.g., Corballis, et al., 1978; Jolicoeur, 1985; Jolicoeur & Milliken, 1989; Jolicoeur, et al., 1987). However, there are two important differences between these slopes.

Firstly, objects disoriented by 180° are identified much faster than would be expected under the assumption of a linear relation between identification time and angular displacement. Compared with trials with disorientations of 120°, 180° trials are solved only slightly slower (e.g., Jolicoeur & Milliken, 1989; Murray, 1995b) or even faster (e.g., Jolicoeur, 1985; Murray, 1995a, 1995b). Considering the findings for 180°-mental rotation trials as discussed above (Chapter 8.7.4) this indicates that one flip is sufficient for object recognition (cf. Murray, 1997). The 'to the left/right of' piece of orientation-dependent information is apparently ignored. For most objects it does not matter whether they are seen from one or the other side—this information is habitually ignored in object recognition, because it actually is unimportant; it does, however matter whether an object is seen standing upright or upside-down.

Secondly, on later trials, identification time becomes nearly independent of the angular displacement from upright (e.g., Corballis & Nagourney, 1978; Corballis, et al., 1978). Apparently, participants perform mental rotation on earlier but not on later trials (e.g., Jolicoeur, et al., 1985). In order to explain why mental rotation occurs, Jolicoeur (1990; see also, Jolicoeur & Milliken, 1989) assumed that on earlier trials participants are unable to recognize objects presented in a noncanonical orientation and therefore have to rotate a visual mental image of the objects into an upright orientation. The recognition process then is a template-match comparison between the resulting visual mental image and upright oriented long-term memory entries. On later trails, the recognition process changes from a template-match comparison into a comparison of orientation invariant features. As a consequence of this qualitative change of the recognition process, mental rotation becomes superfluous.

According to our reasoning, the fact that mental rotation takes place indicates that (in addition to other information) orientation-dependent information is processed. Apparently, participants in these object recognition tasks assume that orientation-dependent information is of importance. Orientation-dependent information is important for determining how an object is oriented with respect to any frame of reference that is not centered on the object itself. However, for the recognition of an object, the importance of orientation-dependent information is rather low. Usually objects do not appear to change identity by a mirror-reversal, meaning that orientation-dependent information is usually comparison-irrelevant for object recognition. In the seldom case that objects can be differentiated from each other only based on orientation-dependent information, identification times show the usual mental rotation effect. This is, for example, the case for the characters *q*, *p*, *b*, and *d* (Corballis & McLaren, 1984).

In our Experiment 1b, participants apparently processed some comparison-irrelevant orientation-dependent information during the first block but were able to nearly exclusively focus on comparison-relevant orientation-dependent information during the second block of trials. In a similar fashion, participants in experiments on disoriented object recognition might process comparison-irrelevant orientation-dependent information during earlier trials and thereby waste time and cognitive resources. With practice on the task and with increasing familiarity with the employed stimuli participants obviously discover that they can identify the presented objects without considering orientation-dependent information (see also Chapter 3.6 and Figure 3.2). Participants consequently stop processing and comparing this type of information. When no orientation-dependent information is processed, no mental rotation takes place, because there is no information the mental rotation process could potentially process. Participants, however, continue to compare comparison-relevant orientation-independent information between the presented stimulus and long-term memory entries. The feature-based comparison process employed for object recognition is the same on later as on earlier trials, but a certain type of features, namely orientation-dependent information, is simply not taken into account anymore.

In order to explain, why mental rotation occurs on earlier but not on later trials, Jolicoeur (1990; see also, Jolicoeur & Milliken, 1989) had to postulate two qualitatively different recognition processes, namely a template-match comparison and a comparison based on abstract orientation-invariant features. Postulation of a template-match becomes unnecessary and a theory of object recognition becomes much more parsimonious by simply dropping the false assumption that the mental representation in mental rotation is a visual mental image.

9. Conclusions

The main topic of the present work is the mental representation that is rotated in mental rotation. We developed the hypothesis that this representation specifies a potentially elementary type of spatial relation only, namely orientation-dependent information. By developing a new mental-rotation task and carefully controlling the amount of comparison-relevant information, we were able to find abundant converging evidence in favor of this hypothesis from which we here repeat only the most striking.

In Experiment 1a and 1b, rotational speed depended on the amount of represented orientation-dependent information only. As participants of Experiment 1b became experienced, which we argue increases the experimental control over their representations, we even found a strict linear relationship between the amount of represented orientation-dependent information and rotational speed—doubling the amount of represented orientation-dependent information resulted in halving rotational speed. The amount of represented orientation-independent spatial-relational information, the amount of comparison-relevant stimulus parts and visual complexity in contrast did not influence rotational speed at all.

Employing the same stimuli as in the previous experiments, in Experiment 2 we extracted slow potentials from the EEG measured during the rotation interval. These were exploited as an online-measure of representational content. In an early processing phase slow potential amplitude was sensitive to orientation-independent information/visual complexity whereas it was sensitive exclusively to the amount of orientation-dependent information during a later phase. We concluded that the employed representation is visually encoded but then recoded into a format suited for the process of mental rotation.

In Experiment 3, we went one step further and identified the cortical regions that hold the mental representation in mental rotation. This was achieved by searching for those cortical areas that become more active with an increasing amount of orientation-dependent information. We reasoned that in order to be manipulated, a mental representation should be available in the same areas that also perform the manipulation proper. As predicted, rotation-specific and orientation-dependent information-specific activation was found in a fully overlapping set of cortical areas.

Comparison times from all four Experiments as well as P3bs observed in Experiment 2 further indicate that the representation employed for the comparison process which follows mental rotation proper also explicitly represents orientation-dependent information only. This indicates that the mental representation is not recoded after mental rotation. Apparently, the same type of information is explicitly represented for the comparison as during rotation.

In sum, we were able to show that, in contrast to introspection and in contrast to implicit and explicit beliefs of most researchers in the field, the mental representation manipulated by the process of mental rotation is not visual in any sense but exclusively represents orientation-dependent spatial-relational information. As a side effect, we developed and validated several new techniques to manipulate and measure mental representational content. Furthermore, the insights into the nature of the representation in mental rotation as gained by the present work help dissolving discrepant findings about the influence of stimulus complexity on rotational speed and are instructive for theories on the process of mental rotation proper as well as for theories of object recognition.

10. Appendix

As mentioned above (Chapter 4.2.4), accuracy data did not add to an understanding of the processes or representations involved in mental rotation. As a consequence, we did not report any analysis on accuracy data for Experiment 1a, 1b, 2 or 3. Instead, all accuracy means for each Stimulus Type × Rotational Angle- and each Stimulus Type × Match Type cell are given in Table A1.

Table A1

Mean Accuracies and 95%-Confidence Intervals (CIs) from Experiments 1a, 1b, 2 and 3.

Cell	1a	1b	2	3, rot	3, ret
Simple, 45°	.98	.95	.98	.95	.96
Simple, 90°	.97	.97	.97		
Simple, 135°	.95	.91	.94	.93	.96
V. Complex, 45°	.94	.94	.92	.89	.89
V. Complex, 90°	.91	.94	.91		
V. Complex, 135°	.90	.94	.91	.88	.86
Complex, 45°	.91	.92	.92	.86	.92
Complex, 90°	.87	.89	.90		
Complex, 135°	.79	.80	.84	.79	.86
CI (interaction)	*±.02*	*±.02*	*±.02*	*±.02*	*±.03*
Simple, match	.96	.95	.96	.95	.95
Simple, dep_1	.97	.95	.96	.92	.96
CI (match type)	*±.01*	*±.01*	*±.01*	*±.06*	*±.02*
V. Complex, match	.94	.95	.93	.93	.92
V. Complex, dep_1	.96	.92	.96	.90	.95
V. Complex, indep	.83	.89	.83	.77	.71
CI (match type)	*±.03*	*±.03*	*±.04*	*±.07*	*±.06*
Complex, match	.88	.90	.91	.88	.91
Complex, dep_1	.93	.85	.92	.85	.93
Complex, indep	.73	.83	.77	.67	.72
Complex, dep_2	.83	.84	.87	.77	.92
CI (match type)	*±.05*	*±.05*	*±.04*	*±.06*	*±.06*

Note. CIs are calculated according to the procedure described by Jarmasz and Hollands (2009) and are corrected for violations of the sphericity assumption by ε (Greenhouse & Geisser, 1959) as suggested by Loftus and Masson (1994). CIs are given for the Stimulus Type × Rotational Angle interaction and for the effect of match type, separately for each stimulus type. V. Complex = visually complex; $dep_{1/2}$ = mismatch in orientation-dependent information 1/2; indep = mismatch in orientation-independent information.

11. References

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