

ACQUISITION AND CONSOLIDATION OF HIERARCHICAL REPRESENTATIONS OF SPACE

Dissertation

der Mathematisch-Naturwissenschaftlichen Fakultät

und

der Medizinischen Fakultät

der Eberhard-Karls-Universität Tübingen

zur Erlangung des Grades eines

Doktors der Naturwissenschaften

(Dr. rer.nat.)

vorgelegt

von

Wiebke Schick

aus Albstadt-Ebingen, Deutschland

Tübingen

2018

Erklärung / Declaration:

Ich erkläre, dass ich die zur Promotion eingereichte Arbeit mit dem Titel:

„Acquisition and consolidation of hierarchical representations of space“

selbständig verfasst, nur die angegebenen Quellen und Hilfsmittel benutzt und wörtlich oder inhaltlich übernommene Stellen als solche gekennzeichnet habe. Ich versichere an Eides statt, dass diese Angaben wahr sind und dass ich nichts verschwiegen habe. Mir ist bekannt, dass die falsche Abgabe einer Versicherung an Eides statt mit Freiheitsstrafe bis zu drei Jahren oder mit Geldstrafe bestraft wird.

I hereby declare that I have produced the work entitled “Acquisition and consolidation of hierarchical representations of space”, submitted for the award of a doctorate, on my own (without external help), have used only the sources and aids indicated and have marked passages included from other works, whether verbatim or in content, as such. I swear upon oath that these statements are true and that I have not concealed anything. I am aware that making a false declaration under oath is punishable by a term of imprisonment of up to three years or by a fine.

A handwritten signature in black ink, appearing to read 'Wolfgang Huber', written in a cursive style.

Tübingen, den 20.02.2018

Unterschrift /Signature

Datum / Date

ABSTRACT

Navigation – the ability to reach targets which are not visible from the current position - depends on the correct recall of the desired target and the environment between one's current position and this target. The content of these representations are subject to influences from different modalities, e.g. vision, and language. A place can be recognized through different cues, e.g. due to a salient object, but also because of the angles of the routes at an intersection, or a name. The location of places as well as the routes connecting them can be integrated and memorized in an allocentric, survey-like representation. Depending on the amount of detail, the granularity level of a representation can be coarser or finer; the different levels are organized hierarchically. Characteristics of a superordinate category, like a region, can affect the perception of its constituting elements, the places; an inheritance of qualities from region to place levels is possible. The formation of superordinate categories depends both on environmental factors as well as individual ones: what is recognized, what is remembered, and which predictions are drawn from this representation?

In this dissertation I examine the acquisition of representations of space, in order to identify features that are well suited for being remembered and auxiliary for navigation.

I have two research foci:

First, I examine the impact of language by using different hierarchically structured naming schemes as place names. Wiener & Mallot (2003) found that characterizing places only with landmarks belonging to different semantic categories influenced route choice as well as the representations of space. I compare these findings to the impact of different naming schemes. I show that there are naming schemes that may influence behavior in a similar way as a landmark does, but that seeing something and reading its name is by far the same thing.

The second part focuses on the content of representations established during navigation. With three different navigation experiments, I examine the content of the concepts of space that are acquired during navigation. What is remembered - the

location of places, the routes, or the hierarchical structure of the experimental environment? Are there features that are more likely to be consolidated during sleep, e.g., the transfer of concrete knowledge about places and routes into an abstract, survey-like representation? I show that there are improvements in one wayfinding task correlated to sleep. In the other experiments, learning effects were found for both groups. I also address the question of suitable parameters for measuring survey knowledge.

CONTENTS

1.	INTRODUCTION	1
1.1.	What does it take to navigate the world? Representations of space	1
1.2.	The hierarchical organization of spatial knowledge	2
1.3.	Language in the acquisition of spatial concepts	6
1.4.	Consolidation of spatial concepts	10
1.5.	Thesis overview and discussion	13
1.6.	Declaration of contribution	17
2.	LANGUAGE CUES IN THE FORMATION OF HIERARCHICAL REPRESENTATIONS OF SPACE	21
2.1.	Abstract	21
2.2.	Introduction	22
2.3.	Methods	28
2.4.	Results	37
2.5.	Linguistic Analysis of the Cues	45
2.6.	Discussion	49
3.	SLEEP ENHANCES KNOWLEDGE OF ROUTES AND REGIONS IN SPATIAL ENVIRONMENTS	54
3.1.	Abstract	54
3.2.	Introduction	55
3.3.	Methods	57
3.4.	Results	59
3.5.	Discussion	62
3.6.	Supplemental Information	65
4.	EXTENSIONS	70
4.1.	The influence of sleep on navigation and memory consolidation	71
4.2.	The impact of sleep on the consolidation of place and survey knowledge	74

4.3.	Visual priming and the formation of regionalized representations of space	86
5.	REFERENCES	90
6.	ACKNOWLEDGEMENTS	103

1. INTRODUCTION

1.1. What does it take to navigate the world? Representations of space

Day after day, we frequently use mental concepts of the surrounding space and move to our targets with an ease that makes it appear automatic. But in an unfamiliar environment, even additional information - like route directions from a cooperative passerby - may not bring you closer to your target; maybe you did not recognize the house he referred to as a point for orientation, maybe you deduced other actions from his instructions than he had in mind. Your representations of space differ, as one is familiar with the environment, while the other one is not.

What constitutes the differences in our representations, and how are they affected by language, e.g. by the words we use to refer to places? The goal of this work is the analysis of learning processes during the acquisition of spatial concepts. I am interested in the hierarchical organization and interactions both between different granularity levels of one modality, e.g. vision, as well as between perception and language.

I address these questions with two different approaches. The first part, which consists of Chapter 2 and Chapter 4.3, investigates the impact of hierarchically structured naming schemes for places on the spatial representation that is acquired during navigation.

The experiments described in the second part, which consists of Chapter 3 and Chapter 4.1. and 4.2, focus on the content and establishment of mnemonic representations. With three different experiments, we address the question of what is being consolidated during sleep, and what characterizes a feature that is easily remembered.

1.2. The hierarchical organization of spatial knowledge

In this section I describe the entities constituting spatial representations and introduce our definitions of places and routes. The establishment of general representations is mandatory for successful spatial behavior, like navigation and recall on request. The formation of hierarchies is an efficient way to reduce processing effort, and is so intuitive a procedure that sometimes it even occurs without supervision through attention. The employed definition of hierarchy, (from graph theory) as a composition of various nested levels of detail is an essential component in various models of human spatial cognition. A selection of them will be discussed. Spatial cognition has many examples of inheritances from a coarser to a finer level of granularity, one prominent one being regions - larger areas formed through the connection of a number of places.

1.2.1. Places and regions

A place is a location of special significance that is recognized because of certain features. The notion of a place, however, includes a variety of different entities, ranging from a geometrical point to the area occupied by one's body, the firing field of a hippocampal place cell, the current visually accessible environment ("vista space", Montello, 1993), or larger structures such as buildings, neighborhoods, cities, or even countries.

The knowledge we first acquire when exploring a new environment are views of locations as well as the paths we travelled, ergo the routes between them.

A common way for modelling is a graph. The places are symbolized as nodes, and the action that are necessary to get from one place to another are the edges. When entering a new environment, the knowledge about places and routes has to be acquired. At first, there are the visual perceptions, and these views can be organized by being associated as belonging to one place. In the view-graph model from Schölkopf and Mallot (1995), each node corresponds to a snapshot of the scenery, and is connected with other nodes via edges that constitute the behavior necessary to get from one node

to the next one. Gillner & Mallot (2008) showed that even in the absence of landmarks, people are able to navigate based solely on views and snapshots.

Places of an environment can be perceived as belonging to one region, e.g. because of spatial proximity. We denote two levels of spatial granularity as “places” and “regions”, respectively, and assume that a region is made up of a set of places. Thus, places and regions constitute a clear hierarchical order. Note, however, that in general, places and regions or regions of different spatial scales need not be nested, but may also overlap, rendering the hierarchy relations less obvious.

How are region representations constituted in spatial memory? One possibility is to organize regions around important landmarks that are visible from each place within a region. In such cases, the region may be represented in the inhabitants’ representation of space, even after the landmark is removed, as may be the case for many of the towns or neighborhoods named “Beacon Hill”, where the name may survive the destruction of the beacon. Regions may also reflect aggregations of important places separated by voids, in which case the region boundaries might be clearly visible. Again, however, if settlements grow together, the names of the regions and the cognitive boundaries may survive in the mental representations of their inhabitants, even though they are no longer visible in the streets. In this sense, region representations result from abstraction processes which are driven by sensory cues (similarities between places), navigational necessities (a central street hub), or naming conventions. Indeed, assigning names to regions seems like an obvious way to promote the abstraction process underlying the formation of region representations, given the abstraction power inherent in language. In perception and memory, region membership can be created through perceptual and physical boundaries, but also through subjective distinctions, influenced by prior knowledge, underlying assumptions and generalizations, or even non-spatial divisions, e.g. political parties.

Confirmation of the hierarchical structuring of spatial concepts comes from numerous studies (Couclelis, Golledge, Gale & Tobler, 1987; McNamara, Hardy, & Hirtle, 1989; Huttenlocher, Hedges, & Duncan, 1991; Taylor & Tversky, 1992; Strohecker, 2000).

1.2.2. Region boundaries may bias perception and behavior

Construal level theory (Trope & Liberman, 2010) suggests that both objects and actions are represented at different hierarchical levels, and that the formation of high-level concepts leads to a higher degree of abstraction as well as an increase of psychological distance. Psychological distance does not only depend on the metric distance; subjective influences like, for example, a feeling of anxiety, or novelty, also affect the experienced distance.

The different levels of distance - e.g. metric and subjective - are related and influence predictions and concepts. This means that the psychological distance between objects or events that are perceived as being associated with each other appears smaller than the distance when there is no association.

A tendency to overestimate distances that cross regional borders has been reported (Friedman et al., 2005; Friedman & Montello, 2006; Newcombe & Liben, 1982; Maki, 1981), and can remain even if the physical border is not existing any more, i.e. the former Berlin Wall (Carbon & Leder, 2005). Even vaguely defined regions and overlapping borders can affect memorized representations (Montello, Goodchild, Gottsegen & Fohl, 2003). Biased estimations of positions and distances have often been observed, with and without a relation to boundaries, and also for maps (Acredolo & Boulter, 1984; Allen, 1981; Cohen, Baldwin, & Sherman, 1978; McNamara, Hardy & Hirtle, 1989; Maki, 1981; Nelson & Chaiklin, 1980; Newcombe & Liben, 1982; Richardson, Montello & Hegarty, 1999; Stevens & Coupe, 1978; Thorndyke, 1981).

Regional subdivision also influences navigation and route planning. Different strategies have been proposed (Bailenson et al., 1998, 2000). The Road Climbing Principles states that there is the tendency to exit the starting region as soon as possible, and according to the Initial Segment Strategy, there is also a preference for the route with the longest straight initial segment.

Wiener & Mallot (2003) found an interaction between landmarks and regional knowledge that biased route choice: in a hexagonal virtual environment with dead-end-streets, each place was marked with a landmark. The landmarks belonged to three

semantic categories, (animals, paintings and vehicles), and were positioned in such a way that the members of one category stood next to each other, thus partitioning the environment in three districts, but without visible borders. When offered the choice between two equidistant routes that only differed in the number of transgressed regional boundaries, those subjects that reported a region perception preferred the alternative with fewer transgressions, the region-consistent alternative. The fine-to-coarse route-planning algorithm developed from these findings states that fine-grained representations are used at the beginning of routes to distant goals. The target is yet represented on a coarser level, but when it is approached, a finer-grained representation will be used: the shrinking of the metric distance may induce a perceived shorter psychological distance. The demands on working memory are lowered by flexible switches between fine- and coarse-grained representations. Regional boundaries facilitate the shift of focus between representations on different granularity levels.

Wiener & Mallot (2004) reported better recall for regionalized environments.

In a paradigm that questioned the verbal planning of the traveling-salesman-problem, the planning performance was significantly better in the regionalized version (Wiener & Tenbrink, 2008).

The pursuit of a route, as well as the planning of it, is a chain of events. These events include both the recognition of the environment as well as the recall of actions required at certain locations. Entering another region can be regarded as crossing an event-boundary. If the transgression of an event-boundary is obvious, this should facilitate both recognition and route planning.

Summary:

The concepts we establish and use when moving around in the world are structured hierarchically. Depending on the amount of detail that is considered, representations can occur at finer and at coarser levels of granularity. This can lead to interactions, like systematic distortions. Also, features can be inherited, in the sense that qualities

of the parent node in the graph representation of the environment are also assumed to be present in the children node. The consequences on perception of this organization shows us that the spatial concepts we employ are also influenced by prior knowledge; they are not one-to-one objective representations of the world, but subject to influences from knowledge, assumptions, as well as purely situational factors, like a feeling of anxiety.

1.3. Language in the acquisition of spatial concepts

Places can not only be characterized perceptually, but also by a name - though it appears that landmarks are better memorized than words. Here I present findings for interactions between language and perception.

1.3.1. Visual and verbal information

Another influence on human cognition and behavior is language. The American linguist Whorf (1956) proposed what is now known as the Sapir-Whorf-Hypothesis of linguistic relativity, which states that the interpretation of an observation is always, and often unconsciously, influenced and manipulated by the grammar of the maternal language. Thus, the observations and conclusions of users of different languages will never equal completely.

Different suggestions concerning the nature of these interactions between language and perception exist.

Paivio's Dual coding theory differentiates between two independent subsystems: perceptual processing is based on a code analogous to the perceptual stimuli, while linguistic processing is based on symbolic verbal representations (1986).

Barsalou (2008) assumes linguistic understanding to be grounded in simulation processes. A word elicits the representation of what it refers to, including associated physical qualities, thus inducing an "embodied" representation. Landmarks, as well as place names, are representations at the individual level. Though the verbal representation is more abstract, it is by far a-modal, as it is associated with sensory

properties of the mentioned object. The perception-based knowledge, on the other hand, is also influenced by language: propositions are made about the content of a perception, relations to prior knowledge are established, associations may occur, and may affect the subsequent predictions.

Louwerse argues that language encodes both perceptual and embodied relations during conceptual processing (Louwerse, 2008, 2011a, Louwerse & Jeuniaux, 2008, Louwerse et al. 2012). These interactions between perceptual relations and their embodiment are considered as a shortcut that accelerates cognitive processes (Symbol Interdependency Hypothesis, Louwerse, 2011b). To compare linguistic and embodied biases, subjects had to make judgments about semantic or iconic relationships (Louwerse, 2010). For picture pairs, error rates and response times were lower when they were presented in the familiar spatial configuration, e.g. *attic* above *cellar*. For word pairs, the frequency of co-occurrence was a better predictor for performance. According to the authors, this indicates the recall of both embodied as well as linguistic information during conceptual processing.

Miller et al. (2013) postulate context - appropriate memories. They reported that spontaneous recall of an item reactivates its spatial context and name this context reinstatement as the base for recollection. Spatial coding systems are part of a complex that processes spatiotemporal contexts in episodic memory and reinstates them during retrieval, which can trigger other, similar memories.

The advocates of context-availability state that highly imaginable words have stronger connections to contextual knowledge, which is assumed to be stored in semantic networks (Schwanenflugel & Shoben, 1983). These bonds lead to an increased activation, when such a term is mentioned, as well as easier processing. There is evidence supporting both theories (context-appropriate memories, context-availability), but the type of task also has to be considered (dual-coding theory: *Context-availability*: Holcomb et al., 1999; *neuroimaging data*: Mellet et al., 1998; Giesbrecht et al., 2004; Noppeney & Price, 2004; Binder et al., 2005; Sabsevitz et al., 2005; Goldberg et al., 2006).

Different other mechanisms that could explain Whorfian effects have been suggested, among them perceptual ‘tuning’ and a shifting of attention, an influence on category

formation through a re-representation, and changes in the computational costs (Majid & Levinson, 2004).

The activity of place-sensitive neurons observed during verbal recall indicates that there is no strict cerebral separation between non-linguistic and linguistic space-related activities. Both abilities can be seen as part of a contextual coding apparatus (Ekstrom, 2013). The dual coding theory of spatial cognition also assumes independence from the modality (Meilinger & Knauff, 2008).

1.3.2. Landmarks and place names

As mentioned before, a place can be characterized and memorized with different views, with salient objects, with a distinctive angle of route intersection, and also with a name. The representations differ between objects and words.

In a long-term-study, Bahrick (1983) questioned people about the city they had lived in during college, and found a significantly stronger recall of salient landmarks than of street names. Verbal recall has been used to identify what qualifies as a landmark (e.g. Appleyard, 1969). There is one caveat: though an object is easily recalled, this does not mean that is used for navigation, as other features can be used, too (e.g. angles of intersections, Janzen et al., 2000; structure of a building or environment, Stankiewicz & Kalia, 2007).

Reference to a landmark is not the same as referring to an abstract entity like a street name, even if it contains the name of the landmark (Tom & Denis, 2004). Subjects were asked to learn a route direction that either referred to landmarks, mainly buildings, or to street names containing the respective words (“cross the park” vs. “cross Park Street”). Both the sketches of the routes drawn on a given map after the learning as well as the remembered location names were better for the version with reference to the landmarks. This indicates a difference in the mnemonic representation between words and objects.

Landmarks influence recall and memory through their number: Denis et al. (2014) found better recall, tested verbally as well as via drawing of sketch maps, for environments in which landmarks are abundant.

It appears that place names may support and augment navigation, if they meet the criteria that have been identified for landmark selection: salience, permanence, and relevance (Gillner et al., 2008).

1.3.3. Verbal processing and navigation

Carruthers sees language as the medium of non-domain specific thinking, but with the capacity of transgressing modular borders or combining the information from different modules in a new way (2002). The benefits of intensified processing for memory has been demonstrated in different applications (e.g. Wiener & Mallot, 2004; Basten, Meilinger et al., 2012). Hardiess et al. reported advantages through intensified processing: the consequences for spatial long-term-memory were investigated in the context of trajectory planning under the constraints of different tasks, and the findings led to the proposal of the Thinking-Helps-hypothesis (Hardiess et al., 2011, 2014).

Baumann et al. (2011) used a sparse virtual environment with landmarks, and had the subjects perform secondary tasks in a maintenance period between exploration and test phase. The tasks involved either visual, verbal or spatial working memory. In the subsequent test phase, subjects had to walk back the route they had been led along and stop at a special point. The verbal as well as the spatial secondary task interfered with learning, but good navigators were only disturbed by the spatial secondary task. Bad navigators were disturbed by all interference tasks. This indicates that both the verbal and the spatial subsystem of working memory is involved in navigational tasks (Garden et al., 2002, Meilinger et al., 2008).

Summary:

Place names influence the processing and storage of spatial representations. Like landmarks, they are representations on the individual level. Also, the names can induce propositions which influence behavior.

It appears that visual and linguistic cues differ concerning the ease with which they are remembered and used for navigation. Nevertheless, linguistically induced intensified processing can support recall.

1.4. Consolidation of spatial concepts

1.4.1. Neuronal activation during navigation in humans and rodents

Different processes are involved in guiding attention and storing important information when establishing representations of space. Neuronal activation allows to differentiate between objects that are relevant for navigation and others that are not: in functional imaging studies, the responses were found to be stronger at places that were relevant for route planning, than the response to objects that had not been located at decision points (Janzen & Weststeijn, 2007; Janzen, Wagensveld & van Turenout, 2007). Both types of objects were presented without spatial context and with a white background, and the effect did not depend on attention. The subjects were told beforehand to pay attention to one type of objects, but the stronger responses were also found for the object type that was not told to be important - when it was located at a point where an action like a turn was required. Even for forgotten objects, this neuronal activity, the “decision point effect”, was detected. The mental highlighting of objects that are relevant for navigation seems to be an automatic process, and the effects were still visible in the scans on the following day. The effect in posterior PHG was detected for objects that were located at one decision point, but not for objects that were seen from two different places. This could be a sign that only unambiguous, non-misleading information yields the PHG-activation, which has also been reported for routes learnt in real-world environments.

The source of the information matters: When subjects pictured an internal mental representation built on verbal descriptions, PET scans showed an activation of the language areas and of the angular gyrus when the topographic representation was mentally scanned, but not during learning. When the spatial information had been presented with a map, this activation was not found. The activation was in a region

which is involved in the processing of linguistic spatial information (Mellet, 1998, 2002).

In rodents, associations between hippocampal activity and being at a certain place have been reported, a finding that was rewarded with the Nobel Prize. Other cue-specific cells have been identified, e.g. cells whose activity depends on the turning of the head of the animal ("head direction cells") as well as cell activity associated with the recall of a survey representation of the environment ("grid cells"; O'Keefe, & Nadel, 1978; Moser et al., 2014; Hartley, Lever, Burgess, & O'Keefe, 2014).

The human hippocampus is involved in memory consolidation (for a review see Eichenbaum, 2000). Eichenbaum (2017) names the hippocampal involvement in memory organization as one reason for the activity during spatial tasks. Hippocampal activation during the acquisition of representations of space has also been reported for humans. Effects of intensive route learning and the memorization of spatial layouts has been found in a study with taxi drivers in London: in order to get a license, they need astute knowledge about the locations and streets of London and have to navigate without technical assistance (Maguire et al., 2006). Trained taxi drivers showed more hippocampal grey matter volume than bus drivers, who drive the same streets, but are not required to recall them from memory. The specification of hippocampal cells for locations was also demonstrated in pre-surgery single-cell recording in the medial temporal lobe: from the neuronal activation, it could be inferred at which place in a virtual environment the subjects were located (Mormann et al., 2014).

Proceeding activation including the hippocampus and prefrontal cortex was reported for visual path integration, as well as during the interactions of self-motion processing and spatial working memory (Wolbers et al., 2007).

1.4.2. Establishment and consolidation of representations of space

Siegel and White (1975) described the exploration of a new environment as a process starting with knowledge about places and the routes between them, from which

hierarchically organized and finer-grained representations may emerge - if needed (landmark knowledge, route knowledge, survey knowledge).

Apart from environmental factors, familiarity and purpose also influence the content of the concept. Moeser (1988) observed that nurses working in a complexly constructed hospital did not have survey knowledge of the hospital, even after 2 years of working there. The local information about the location of their station sufficed to get to all the needed targets.

The mental representation is not literally like a map, but sparse for the sake of efficiency. There are surroundings in which direct paths, angles of crossing routes and salient landmarks suffice completely to reach the targets (Golledge et al., 1999). Further, expertise on a local scale does not automatically finally lead to global, or survey knowledge – unlike proposed by Siegel and White (1975).

The consolidation does not only take place during navigation. Neural activity associated with spatial representations has also been observed during sleep.

Sleeping rodents showed the same sharp-wave activation patterns that had also been recorded when the animal was awake and located at a certain place in the maze (Diba & Buzsaki, 2007). In humans, consolidation processes during sleep have been reported for different spatial tasks, e.g. for route-planning, (Peignieux et al., 2004), and landmark-based navigation (Ferrara et al., 2008).

Summary:

There are numerous findings for the role of hippocampal activity in memory consolidation and navigation. This double function may stem from the fact that the content of memories are events, which occur at a specific time – and at a specific place. Knowing what is going to happen where is necessary for predictions. There are, though, still blank spots concerning the interactions between visual and linguistic information, as well as circumstances that favor recall of one form of representation over the other.

1.5. Thesis overview and discussion

When we move, we perceive environmental properties, remember a selection of them, and are able to generate, based on this knowledge, an abstract representation. The current dissertation examines the learning processes during navigation in an unfamiliar environment. I address two main topics: First, I look at the influence of linguistic labels – place and city names, and whether there are interactions between hierarchical structures in the environment and in language.

In the second part, I discuss which forms of knowledge about an environment are extracted and recalled, and what sort of spatial information is consolidated during sleep.

1.5.1. Language and representations of space

The first part consists of Chapter 2 and Chapter 4.3., where the influence of place names on the representation is tested with navigation tasks.

In Chapter 2, we show that the categorization scheme of place names in a virtual environment is not always integrated into the concept of space, and even if this is the case, this does not necessarily suffice to bias route choice behavior. While landmarks belonging to different semantic categories led to such a bias, substituting the landmarks by their names did not. Four different naming schemes were tested, and for two conditions, language-based induction of spatial hierarchies was found. A linguistic analysis of the likelihood of co-occurrence for the place names revealed that a high probability of co-occurrence does not always induce transfer of the linguistic hierarchy into perception. We found similar co-occurrence patterns for two conditions, but only a route choice bias for one of them. There were also differences concerning the reported perception of regional subdivision as well as the quality of the sketchmap which had to be drawn after the navigation experiment.

The results clearly show that place names, which are more abstract than objects, affect both behavior as well as the memorized representations of space. We argue that the differences are also related to the vividness of the place names, as we

did find an influence on route choice in the condition in which place cues of one region were associated in numerous ways – through a shared, prototypical context, through spatial proximity, through likelihood of co-occurrence of the used place names. We assume that the contextual association of the stereotypical scenes facilitates associations with other words occurring in this context.

In Chapter 4.3., adjectives were used as place cues, and subjects were primed with a picture-sorting task that associated the four adjectives of each region with a landscape scenario. We assumed that this might lead to a transfer of the presented grouping scheme of the adjectives into the concept of the environment. We did not find an influence on route choice or recall, though.

In summary, place names belonging to different categories can induce a perception of regional subdivision in a way that facilitates orientation and navigation in a virtual environment, but it is clearly more difficult than with landmarks of different groups. One important factor seems to be proximity in a contextual way, which, in one condition, was also associated with spatial proximity. Another factor is that the place cues can be attributed unambiguously to the different categories. We think that ambiguity and the high level of abstraction explain why we observed no transfer of the grouping schemes suggested by the adjectives: the psychological distance between landscape-pictures and a virtual environment with signposts bearing words was too big.

For further experiments, it would be interesting to identify by means of a co-occurrence analysis nouns with a high probability of co-occurrence which do not share a highly stereotyped context. Also, the use of abstract nouns could shed light on the question of the importance of imagination. As for the priming experiment, it may be promising to replace the adjectives with nouns.

1.5.2. Effects of sleep consolidation on representations of space

In the second part of my dissertation, which consists of Chapter 3, Chapter 4.1. and Chapter 4.2., I address the question whether there are environmental features whose recall is improved after sleep, which would suggest consolidation during sleep.

In Chapter 3, we use a virtual environment that can be perceived as hierarchically structured into regions if the categorization scheme of the landmarks is recognized and integrated in the spatial representation. Sleep improved the navigation performance of the subjects, and there was a stronger report of regional subdivision in this group, too. It did not, though, bias the route choice of the subjects in favor of the region-dependent route choice.

It may be that subjects did not use the regionalization scheme for route planning because the recall of landmarks and the routes connecting them sufficed to perform the tasks. They did recognize the hierarchical subdivision, though. We conclude that the route choice may not be a reliable indicator for an allocentric representation in this task. The explicit forms of knowledge about the location of places and the routes connecting improved in the Sleep-group.

In Chapter 4.1. and 4.2., we tested the integration of place and route knowledge into an allocentric representation.

Both experimental environments were presented with the Head-mounted Display Oculus Rift (DK2). Thus, subjects also experience vestibular information, as they have to turn in the desired directions when they moved through the streets. After the navigation tasks, subjects had to draw a sketch map of the layout.

In the experiment described in Chapter 4.1., a hexagonal environment was used. A learning effect was found for both the Sleep and the Wake group. There was a correlation between the navigation errors in the second session and the quality of the sketch map, which is not surprising.

In Chapter 4.2., subjects had to navigate a virtual inner city. Novel shortcuts were used as a measure for the quality of the spatial representation. The shortest way to a presented target in the test phase required combining familiar route segments in an

unfamiliar way. The improvement of the Sleep group was higher than that of the Wake group, as was the quality of the sketch maps.

This suggests that sleep may support consolidation of route knowledge. We did not find statistical evidence for daytime effects, but it has to be considered that both alertness and learning rate are generally higher in the morning than in the evening (Pomplun, 2012).

For further studies, it could be promising to let one group do a nap in between two sessions, while the other one stays awake; this could reduce possible influences of the daytime.

1.6. Declaration of contribution

This dissertation contains manuscripts that are either published or submitted for publication. Details about the collaboration and the candidate's work are presented in the following.

- *How to construct a linguistic landmark: language cues in the formation of hierarchical representations of space.* Schick, W., Halfmann, M., Mallot, H.A. (2015). Published in: *Cognitive Processing* 16 (S1(1): 383-388).
 - designed experiment: Schick, Mallot
 - setup: Halfmann
 - carried out experiment: Schick
 - analysed data: Schick
 - writing: Schick

- *Sleep enhances knowledge of routes and regions in spatial environments.* Noack, H., Schick, W., Mallot, H.A., Born, J: (2017). Published in: *Learning and Memory* 24 (3), 140-144.
 - designed experiment: Noack, Schick
 - setup: Schick
 - carried out experiment: Schick
 - writing: Schick
 - analysed data: Schick, Noack, Born, Mallot
 - writing: Noack, Schick

- *Language cues in the formation of hierarchical representations of space.* Schick, W., Halfmann, M., Hardiess, G., Hamm, F., Mallot, H.A. (submitted for publication).
 - designed experiment: Schick, Mallot, Hamm
 - setup: Halfmann
 - carried out experiment: Schick
 - analysed data: Schick, Mallot, Hardiess
 - linguistic analysis: Schick, Hamm
 - writing: Schick

Parts of this work were also presented at the following conferences and scientific events:

Talks:

- *The right words to find the right route: interactions between spatial perception and language.* Schick (2017). Interdisciplinary College Günne: Rainbow Session (lecture, 90 min).
- *Language Cues in the Formation of hierarchical representations of space: How to build a linguistic landmark.* Schick (2016). TeaP Heidelberg.
- *Language Cues in the Formation of hierarchical representations of space or the linguistic landmark.* Schick (2015). International Spatial Cognition, Rome.
- *Language Cues in the Formation of hierarchical representations of space.* Schick (2015). TeaP Hildesheim.
- *Language Cues in the Formation of hierarchical representations of space.* Schick (2014). „Gießener Abendgespräche *Kognition und Gehirn*“, Universität Giessen.

Poster Presentations:

- *The Impact of sleep on the formation and consolidation of spatial survey knowledge.* Schick, W., Holzmann, J., Mallot, H.A. (2017). COGSCI 2017: Computational Foundations of Cognition. London.
- *Sleep enhances knowledge of routes and regions in spatial environments.* Schick, W.; Noack, H.; et al. (2017). International Workshop on Models and Representations in Spatial Cognition, Tübingen.
- *The impact of sleep on the consolidation of place and survey knowledge.* Schick, W.; Holzmann, J.; Mallot, H.A. (2017). Interdisciplinary College, Günne.
- *The influence of sleep on navigation and memory consolidation.* Schick, W.; Baumann, M.; Mallot, H.A. (2016). KogWis: Space for Cognition, Bremen.

- *Language Cues in the Formation of hierarchical representations of space.* Schick, W., Halfmann, M., Mallot, H.A. (2016). KogWis: Space for Cognition, Bremen.
- *Language Cues in the formation of hierarchical representations of space.* Schick, W., Halfmann, M., Mallot, H.A. (2016). Spatial Cognition, Philadelphia. (Presented by Mallot, H.A.).
- *Language Cues in the formation of hierarchical representations of space.* Schick, W., Halfmann, M., Mallot, H.A. (2016). 6th IMPRS NeuroCom Summer School, Leipzig.
- *The linguistic landmark: language cues, route planning and recall in a regionalized environment.* Schick, W., Halfmann, M., Mallot, H.A. (2016). Interdisciplinary College, Günne.
- *How to construct a linguistic landmark: language cues, route planning and recall in a regionalized environment.* Schick, W., Halfmann, M., Mallot, H.A. (2016). International Workshop on Models and Representations in Spatial Cognition, Hanse-Wissenschafts-Kolleg, Delmenhorst.
- *Language Cues in the Formation of hierarchical representations of space.* Schick, W., Halfmann, M., Mallot, H.A. (2014). Spatial Cognition, Bremen.
- *Language Cues in the Formation of hierarchical representations of space.* Schick, W., Halfmann, M., Mallot, H.A. (2014). KogWis, Tübingen.

2. LANGUAGE CUES IN THE FORMATION OF HIERARCHICAL REPRESENTATIONS OF SPACE¹

2.1. Abstract

We study the role of verbal cues (place and region names) in the formation of hierarchical, or regionalized, representations of space. Spatial representations were probed behaviorally, i.e. by route choices between two equidistant, alternative routes differing only in the number of regions they touched. Wiener and Mallot (2003) showed that visual objects taken from one semantic category and placed in spatial vicinity induce region representations in the sense that routes reaching the goal region earlier are preferred over equidistant routes entering the region of the goal only later. Here we show that region dependent route preference is no longer found if the landmark objects are replaced by sign posts displaying written object names. Naming schemes with explicit region naming or contextual relation of place names were also tested and led to significant effects on region dependent route choice in some conditions, but not in others. A comparison with word association (pointwise mutual information in deWaC corpus) did only partially explain the differences. We conclude that language cues differ from visual landmark objects in the formation of spatial representations. Region effects based on language cues are found if the place cues imply spatial nearness or allow for common narratives, but not if they are only related by semantic categories.

¹A modified version of this text has been submitted for publication. Preliminary data of this study has been published: Schick, W., Halfmann, M., Mallot, H.A. 2015. How to construct a linguistic landmark: language cues in the formation of hierarchical representations of space. *Cognitive Processing* **16**, 383-388. doi:10.1007/s10339-015-0722-9

2.2. Introduction

When we explore a spatial environment, we learn and memorize spatial concepts such as landmarks, places, routes, or regions. These concepts are formed by processes of abstraction that lead from trajectories travelled in continuous space and time to discrete representations of places and regions defined by their location, extent, and the adjacency to or overlap with other discrete places or regions.

Sensory pattern classified as belonging to one place need not be similar to each other but can be views taken from different viewpoints and approach directions, characteristic houses or shops known to be localized at a given place, acoustic or olfactory cues, or the just experienced walking distance from another, adjacent place. Place recognition is thus not a simple classification of a sensory pattern, but maps many different patterns or cues to one invariant place representation.

Each "place" is therefore an abstract concept activated by a variety of sensory patterns whose communality is not their featural similarity, but their known belonging to the same place. The same holds, *a fortiori*, for regions, i.e. spatial entities of coarser granularity that include a group of nearby places. Sensory cues obtained within a region will be even more diverse than the cues obtained for any individual place. As places, regions are not defined by the communalities of instantaneous sensory inputs, but by knowledge of the sensory inputs that can be expected in each region.

What are the rules underlying the abstraction processes that lead to the formation of regions or hierarchies in spatial representations? Certainly, places that are to be grouped into one region should be spatially close. In addition, various rules can be formulated:

- (i) Similarity: If places can be grouped by some common feature, this may support their coercion into a region. For example, different suburbs may be defined according to the predominant architectural style of their buildings.
- (ii) Common function: If nearby places play a role in a larger behavioral task, they might be grouped into a region for that task, as would be the case for a university quarter or a harbor.

- (iii) Designation: Neighboring places might also be grouped by a pure convention, i.e. by assigning names to groups of places. These names could be arbitrary, derived from a present or historic function, or refer to a prominent place that is or was present in this region.

Spatial memory can be built without support from language, as is clearly the case in animals. However, with language at their demand, humans not only have improved abilities of communication about space, but might also be able to use the language-immanent mechanisms of concept formation and abstraction to improve the structure of internal spatial representations. We therefore hypothesize that language may play a role in the formation of hierarchical representations of space. Of the three mechanisms mentioned above, designation is only possible with language, i.e. with a name assigned to each region. Similarity and common function can be based on non-lingual cues, but language may help to recognize the common feature or function defining a region.

As the central hypothesis, we can thus formulate the idea that language cues such as place and region names presented in a navigational environment enhance the use of language-based mechanisms of abstraction and therefore the formation of higher hierarchical levels of spatial concepts (i.e. region representations). This hypothesis is tested with route choice as a behavioral indicator of region representations and various naming schemes. To our knowledge, this paper is the first to systematically address this question.

Regions

One basic spatial entity at a fine level of granularity and a low level of abstraction is the place, which we define as a portion of space visually accessible from one position. This is similar to Montello's (1993) vista space which he describes as the "space of single rooms, town squares, small valleys, and horizons". Regions are structures containing multiple places. These can be continuous areas surrounded by a boundary (e.g., Stevens & Coupe, 1978), in which case the distances across the boundary are over-estimated both in vista space (Newcombe & Liben, 1982) and in global geographical knowledge (Friedman & Montello, 2006). Using the example of the

former inner German border, Carbon & Leder (2005) show that overestimation of distance across borders persists even if the borders no longer exist. Another notion of a region as part of a spatial hierarchy (McNamara, 1986) is a connected sub-graph of a larger place graph (Wiener & Mallot, 2003). Here, regions are defined as a higher-level node connected to its places, while the boundaries between regions are not explicitly represented. Still, boundaries have a significance in behavior, since planning a boundary crossing implies graph paths crossing between the place and region levels. This property was used by Wiener & Mallot (2003) as a measure of regionalization: given the choice between two equidistant routes, subjects tended to choose the route entering the target region as soon as possible.

Regions and places can also be distinguished by their local reference frames (Mou & McNamara, 2002), which have been shown to vary with the level of granularity (Wang & Brockmole, 2003). For a cognitive model of spatial representation accommodating both graph structure and local reference frames see Meilinger (2008).

Structured environments are learned easier than random arrangements. In a goal-driven search task, Juliani, Bies, Boydston, Taylor, and Sereno (2016) showed that navigation performance in fractally defined landscapes is better if fractal dimension is low. Wiener, Schnee and Mallot (2004) had subjects learn the contents of an array of four by four showcases that were either grouped by semantic categories or randomly shuffled. Learning was significantly faster in the structured condition. Similarly, route planning in traveling-salesman-task is improved if the environment supports regionalization (Wiener, Ehbauer, & Mallot, 2009; Wiener & Tenbrink, 2008).

The consolidation of regional knowledge during sleep was studied by Noack, Schick, Mallot, and Born (2017) using the paradigm of Wiener and Mallot (2003). Region-dependent route choice was confirmed but did not benefit from sleep consolidation. However, awareness of regions expressed in a questionnaire did consolidate with sleep. This seems to indicate that two different aspects of region representation are addressed in route choice and in sketch map drawing.

Language

Representations of indoor scenes built either from visual perception or from verbal descriptions have been investigated e.g., by Avraamides, Loomis, Klatzky (2004), and Golledge (2004). After studying the view or the verbal description of an indoor scene, subjects were asked to perform egocentric pointings to or exocentric pointings between objects in the scene. Results are rather similar in either condition, suggesting a common, "amodal" representation of space. On a navigational scale, Mellet et al. (2002) asked subjects to imagine traveling spatial representations built either from maps or verbal descriptions ("mental scanning"). PET scans of subjects in this experiment reveal common fronto-parietal activations for both learning modalities but also modality-specific activations in vision or language areas, respectively. Dissociations between language and vision mediated spatial memories was reported from dual task studies of spatial working memory, e.g., by Meilinger, Knauff, and Bühlhoff (2008).

The relevance of language for spatial representations is most obvious in communication, i.e. in giving directions or in reporting about spatial relations. Tom and Denis (2004) asked subjects to memorize a route direction that either named particular landmarks or street names containing the same word, such as in "cross the park" vs. "cross Park Street". Reference to the perceivable object, i.e. the park in the above example, correlated with better sketch quality and better recall of the locations. In a long-term study, Bahrck (1983) questioned people about the city they had lived in during college and found a significantly stronger recall of salient landmarks than of street names. Not only salient landmarks, also the regionalization is stored in long-term memory: On the campus of the Northwestern University in Evanston, Illinois, an environment consisting of three different regions, Uttal, Friedman, Hand, and Warren (2010) studied navigation planning as well as verbal expressions of students while they had to make spatial decisions. They identified two levels, the category, or region knowledge on the superordinate level, and fine-grained or place knowledge on the basis level, and observed a bias of location estimates towards the center of each region which increased with the subjects' degree of familiarity with the environment. There were no clear region boundaries, but the regional subdivision was also present in

communication, though only after the students had lived on campus for about two years.

In summary, navigational experience and language clearly interact in the formation of spatial representations, but some differences seem to exist, for example with respect to memories of knowledge acquisition or the duration of memories about routes or place names.

Spatial Concepts

Spatial concepts are formed from navigational experience in a number of processes such as the categorization of views and landmarks to place memories, the inference of place adjacencies from perceptions of ego-motion and other places, or the grouping of a set of individual places to larger regions. The basic navigational experience is essentially a series of events (Zacks & Tversky, 2001) from which space has to be inferred as a background property of each event, i.e. by discovering spatial communalities across temporally separated events happening at the same place. The resulting representations refer to specific places or regions with a well-defined location in the world and are therefore not abstract concepts in the sense of abstraction theory (e.g. Borghi et al., 2017). Classification occurs on the individual level, i.e. it identifies a specific place, not a class of places or scenes, and need not be based on language. Still, place recognition requires learnt concepts and involves processes of categorization and classification that also occur in more complex abstraction processes known from object or social cognition, in which language is thought to play a role (Barsalou, 2008; Gallese, Keysers, & Rizzolatti, 2004; Xu, He, & Bi, 2017). Indeed, the conceptual system of spatial cognition has been considered as an evolutionary pre-adaptation for more elaborate concept systems and eventually for language itself (Hauser, Chomsky, & Fitch, 2002).

The abstraction levels of spatial concepts can be addressed in the light of construal level theory (Trope & Liberman, 2010), which proposes a correlation between the abstraction level of mental construals and the "psychological distance" currently perceived to the object or issue represented by this construal. Psychological distances can be social, contextual, or spatial. A clear point in case of construal level theory in

the spatial domain is the fine-to-coarse planning procedure suggested by Wiener and Mallot (2003) which states that routes to distant goals use fine-grained representations at the starting point and get coarser as the planning point moves further away. Similarly, recall of distant places depends on the distance from the place where the recall is performed: sketch maps drawn from memory are oriented in the imagined approach direction if the target place is in walking distance, but not if the target place is two kilometers away (Röhlich, Hardiess, & Mallot, 2014). In this sense, views, places, and regions are three spatial concepts of increasing abstraction level.

Purpose of this Study

Here, we investigate the role of language in the formation of spatial concepts on the region level. Visual landmarks and different types of language cues are presented as naming schemes in a simple virtual environment. After learning this environment, subjects carry out a number of way-finding tasks with alternative route options from which spatial representational hierarchies can be inferred. With this paradigm, we address the following questions:

First, are region representations formed on visual landmarks and language cues equivalent in their effects on wayfinding, verbal region report, and sketch map drawing? In many studies of spatial cognition, the equivalence of visual landmarks and written landmark names is tacitly assumed. Here we explicitly address this problem by using visual and textual landmarks with all other parameters being identical.

Second, can region representations be induced by explicitly naming the region ("designation")? This is to be expected if abstractions from the language domain would be directly transferred to the spatial domain to form higher level spatial concepts. Region names could be either arbitrary or contain hints towards the names of places included in each region.

Third, do implicit communalities between the names of adjacent places (that have to be discovered by the subjects) support the formation of regionalized representations? Examples of implicit communality include semantic categories from which the place names of one region might be taken, or expected proximity of the named landmarks in

familiar real world environments. More formally, adjacent places might be grouped into a region if their names have a high probability of co-occurrence in texts.

Finally, can different types of regionalization be distinguished by behavioral data from wayfinding performance, questionnaires, and sketch map production? Regions can be thought of as categories of places, densely connected subgraphs (cliques) of larger place graphs, bounded spatial areas, local vs. regional reference frames, etc. It is well possible that these notions are at least partially dissociable.

2.3. Methods

Participants

In total, 215 subjects participated in the experiment. Most of them were students or employees of the University of Tübingen. All of them were native speakers of German. Age varied between 19 and 43 years. All gave written informed consent and received either course credit or a payment for their participation.

Subjects who produced more than six errors in the test phase were excluded from further analysis. It turned out, however, that in some of the conditions large numbers of subjects had to be excluded by this criterion. This results in the varying number of subjects analyzed in each condition (see Table 1). Altogether, data from 126 subjects were analyzed.

Table 1: Number of subjects in the five conditions. Of the subjects who finished the experiment, only the data of those with less than six errors were further analyzed.

	tested		finished		analyzed	
	m	f	m	f	m	f
Landmarks	20	17	20	17	15	15
City names	16	35	15	29	13	9
Pars-pro-toto	19	26	16	23	9	13
Semantic	10	20	10	19	6	16
Compounds	21	31	21	30	12	18

The experimental setup

The experiment was conducted with a desktop virtual reality setup. The virtual environment was designed with the software Multigen Creator (Multi-Gen-Paradigm). The visual scenery was rendered on a 30-inch screen; instructions as well as the targets for both training and test routes were displayed on a second screen measuring 15 inches. The subjects were seated in a chair in front of a desk with the two screens; they could change the viewing distances by adjusting the chair and the smaller screen (Figure 1b).

The virtual environment in all experiments was a maze with 12 places, six of them arranged in a hexagon, with six adjacent dead end streets (Figure 1a). At each junction point, three streets met with regular angular spacing (120°). Thus, the street raster did not provide positional information of any type except the distinction between dead ends and the inner ring. Small hills between any two places occluded the views to distant places.

Each place was characterized by three cues placed in the corners of the junctions. The cues in the *Landmarks* condition were rendered object models and two sign boards displaying a picture of it (Figure 2a). In the language conditions, all cues were presented on sign boards. Beyond the dead end places, barred street entries were visible but could not be reached (Figure 2b). All place cues became visible as soon as

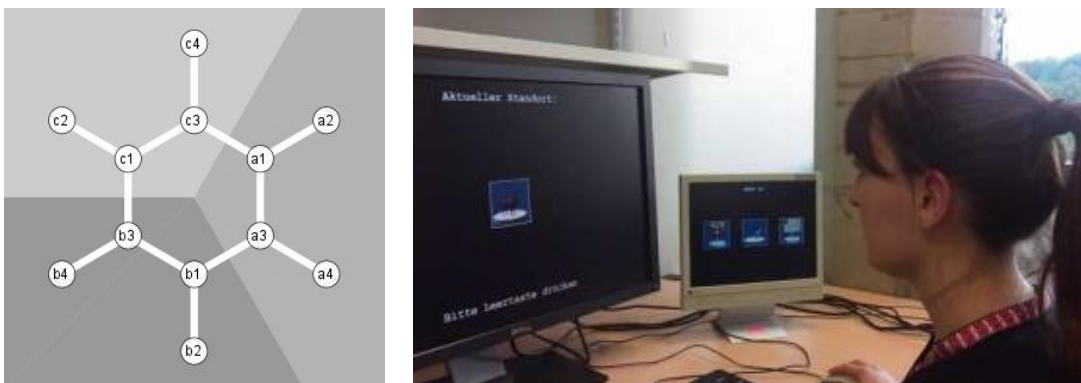
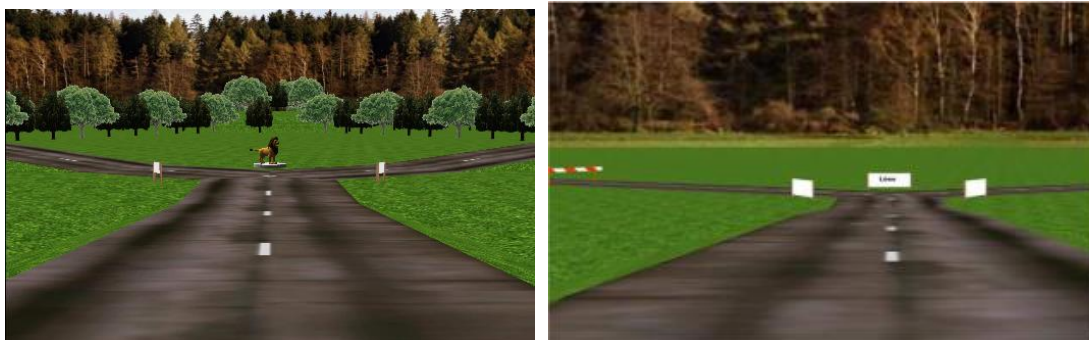


Figure 1: **a.** Schematic survey map of the experimental environment. There are no physical boundaries visible to the subjects. The different background shades depict the categories created through the linguistic cues (here depicted through the three letters a, b, c). **b.** View of the setup with desktop VR (left screen) and presentation of the goals of the current route finding task (small screen to the right).

the subjects reached the top of the hill between places. Subjects navigated the environment in discrete steps, using the buttons of a computer mouse. Clicking the left and the right button led to 60° turns in the respective direction followed by a movement forward to the next intersection. Only in the dead ends, subjects could also turn continuously by keeping the according mouse button pressed. When entering a dead end, subjects were stopped half way towards the place (Fig. 2b) and rotated by 180 degrees. They then needed to click the middle mouse button to move back to the inner ring (Figure 2a).

In the test phase, three goals for each trial were presented as icons or words on the additional small "task screen". Icons or words were moving slowly along elliptic, intersecting trajectories in order not to bias subjects towards a particular work sequence (Figure 1b). The task was to find the shortest route connecting the starting point and the three targets. Whenever a target was reached, it disappeared from the task screen. Note that in the explicit naming conditions (*City names* and *Pars-pro-toto*), only the place names were shown on the task screen while the region names were not mentioned. In this way, we wanted to ensure that the subjects learn the regional structure implicitly, i.e. by exploration.



a.

b.

Figure 2: Sample views from the environment. **a.** *Landmarks* condition, view when approaching an intersection on the inner ring from the adjacent dead end.

b. *Semantic* condition, view of the sign boards in a dead-end street.

Conditions

The place and region cues used in the experimental conditions are summarized in Table

2. The five conditions were:

1. *Landmarks*: This was a repetition of the Wiener and Mallot (2003) experiment, with landmark objects as place cues and no textual cues. Landmark objects were chosen from three semantic categories (a: animals, b: vehicles, c: famous paintings). The object models were included in the Multigen Creator software; a view of the lion is included in Figure 2a. The paintings were *Mona Lisa* by da Vinci, *Composition VIII* by Kandinsky, *Sunflowers* by van Gogh and a detail from the *Marilyn Diptych* by Warhol.

2. *City names*: Here we used arbitrary city names as explicit cues to regionalization displayed together with the place names on the sign boards. Place names were common downtown locations and were randomly associated to the city names. Thus, the city names did not contain any hint to the place names included and vice versa.

3. *Pars-pro-toto*: In this condition, the places names and their distribution were identical to the *City names* condition. Region names were not arbitrary but derived from one of the place names contained in each region. Again, region names were displayed on the signboards together with the place names.

4. *Semantic*: This condition tested the effect of semantic relatedness on regionalization. Place cues were names of objects chosen from one of three distinct semantic categories (animals, vehicles, and buildings). This condition resembled most closely the Wiener and Mallot (2003) experiment and condition *Landmarks*, except that the landmark objects were replaced by signs displaying their names, and that the category "paintings" was replaced by "public buildings", since the names of the paintings will not be obvious to all subjects. Region names were not displayed in the environment or otherwise mentioned (implicit condition).

5. *Compounds*: As an alternative type of word similarity we study contextual or whole-part relation. The environment was structured using distinctive locations from three compounds: Open Air Bath, University, Farm (the compounds, or holonyms). Place cues (meronyms) were names of typical locations that are associated with each compound. Only the place cues were shown, while inferring the containing compound was left to the subjects. The choice of place names was based on a pilot questionnaire with a group of subjects not included in the experiments. They were either asked to name the first associations with one of the compounds or had to name a suitable header for a given word list. As in conditions *Semantic* and *Landmarks*, region cues are purely implicit.

Table 2: Region cues used in the various experimental conditions. The letters and numbering refer to the place labels given in Figure 1a. The *City names* and *Pars-pro-toto* conditions differ only in the region names and are therefore shown in one column. Cues in italics (lion etc.) refer to rendered objects in the *Landmarks* condition. Cues in the language conditions were given as German words included here in brackets. See text for further explanations.

	Landmarks	City names/ Pars-pro-toto	Semantic	Compounds
a	-	Redtown (Rotstadt) / Bridgetown(Brückenstadt)	-	-
1	lion	Cinema (Kino)	Church (Kirche)	Sunbathing Area (Liegewiese)
2	monkey	Fountain (Brunnen)	Hospital (Krankenhaus)	Kid's Pool (Kinderbecken)
3	rooster		Schoolhouse (Schule)	Diving Platform (Sprungturm)
4	dog		City Hall (Rathaus)	Racing Pool (Schwimmbecken)
b	-	Yellowtownm(Gelbstadt) /Churchtown(Kirchenstadt)	-	-
1	tractor	Courthouse (Gericht)	Dog (Hund)	Campus (Campus)
2	car	Schoolhouse (Schule)	Rooster (Hahn)	Mensa (Mensa)
3	motorcycle	Cafe (Café)	Monkey (Affe)	Seminar room (Seminarraum)
4	crane truck	Church (Kirche)	Lion (Löwe)	Lecture hall (Hörsaal)
c	-	Bluetown (Blaustadt) / Operatown (Opernstadt)	-	-
1	Mona Lisa	Hotel (Hotel)	Bus (Bus)	Cowshed (Kuhstall)
2	Composition VIII	Butcher (Metzger)	Car (Auto)	Cornfeld (Kornfeld)
3	Sunflowers	Bakery (Bäcker)	Tractor (Traktor)	Dungheap (Misthaufen)
4	Marilyn Diptych	Opera (Oper)	Motorcycle (Motorrad)	Barn (Scheune)

Procedure

Instructions were given to the subjects in writing. The experiment started with a free exploration phase lasting at least five minutes, in which each place had to be visited at least once. In the subsequent phases, routes to one or multiple goals had to be found. The starting point and the goals were presented by their cues (icons or place names) on the main screen or the task screen, respectively (see Fig. 1b). In the explicit conditions (*City names* and *Pars-pro-toto*), only the place names were used as target specifications. The starting point was always in a dead end with the viewing direction towards the inner ring. When the subject hit the space button, the VR simulation was initiated. The goal cues were removed from the task screen as soon as the respective goal was reached.

The training phase comprised six different route tasks, three of them heading for the dead end in a neighboring arm of the hexagonal maze and three of them heading for the second next arm (Figure 3, Training routes). For each goal there existed just one shortest route which was considered the correct solution. The six routes were selected such that each of the places in the maze was visited at least once during the training phase. The training was finished when each route had been completed correctly two times consecutively. Thus, a minimum of 12 route tasks had to be completed in the training phase.

The test phase consisted of 18 three-goal routes, six A-routes, six B-routes and six distractor routes, presented in the same random order for each subject (Fig. 3). A-routes led to the directly opposed dead end; one of the correct routes passed through two regions, the other one through three. The B-route goals included the two dead ends neighboring the start position the far ring location. Again, two equidistant solutions (nine segments) exist which include an u-turn at one of the dead end goals. One solution crossed two region boundaries and the other one three of them. In both the A- and B-routes alternative correct solutions are equivalently distinguished by the subject's first decision, which can be either within region (less region crossings) or crossing a region boundary (more region crossings). Note that all dead ends were used as starting points; the direction of the first turn is therefore independent of the number of region crossings needed.

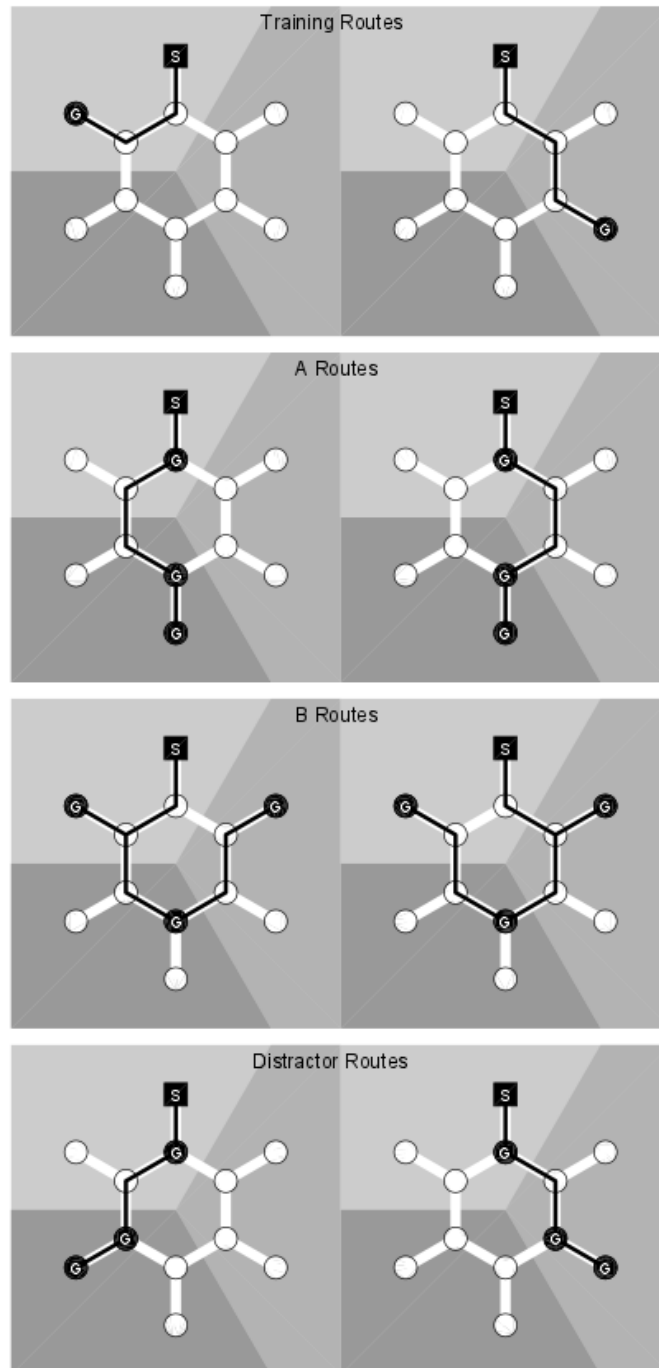


Figure 3: Route types. The black squares indicate the starting point; the black disks indicate the goals. The black lines show the correct solutions. Note that two correct solutions exist for the A- and B-routes used in the test phase of the experiment.

Distractor routes were included to prevent subjects from learning the symmetry of the test routes. They had only one shortest solution with four segments. Again, all dead

ends were used as starting points. Three of the distractors involved a first turn to the right and three to the left.

After the navigation experiment, the subjects had to fill in a questionnaire with eight questions, addressing self-assessment of navigational performance, general feelings about the experiment, and the perception of landmarks and regions. Of these, only the question about region perception was used in later analysis (see below).

Together with the questionnaire, subjects were asked to draw a sketch map of the experimental environment. They were instructed to name all the features they considered important, but region names were not explicitly asked for.

Variables of Interest

The variables of interest of the VR-task were navigational errors, region dependent route choices, and the turning direction of the first route decision, each separately for the A- and B- routes. From the questionnaire, region perception report and sketch maps were analyzed.

Errors. Routes were counted as errors if the traveled distance (number of segments) exceeded the minimally required length. Subjects with more than six erroneous routes out of the 12 performed in the test phase were excluded from further analysis.

Region-dependent route choice (RDRC). For the A- and B- routes, two equidistant paths exist which differ in the number of region boundaries crossed. As a measure for region-dependent route choice, we use the percentage of routes with the smaller number of boundary crossings out of the total number of correctly performed routes for each subject.

First decision. As an alternative measure of region dependence of A- and B-routes that can also be applied to erroneous routes, we also considered the direction of the turn at the first intersection. The measure is the percentage of first decisions staying within the current region, out of the total number of test routes, irrespective of their correctness.

Region report. The questionnaire included the question "Did you have the impression that the environment consists of separate regions?", which the subjects were asked to answer on a scale from 1 (very weakly) to 7 (very strongly). The ratings were analyzed as region report.

Sketch map. The sketch maps were analyzed for five criteria:

(i) detection of hexagonal ring-structure ("Form" in Table 3), (ii) names of places or landmarks ("Places") (iii) indication of regions ("Region"), (iv) number of correct pairs of ring placed and dead ends ("Pairs"), and (v) length of longest sequence of places represented in the correct order ("Order"). For each criterion, up to 1 point could be earned; for the place names, pairs and order criteria, the fraction of correct elements was calculated. In total, up to 5 points could thus be collected.

Statistical analyses were performed in MATLAB.

2.4. Results

Errors

The number of subjects who did not finish the experiment or did not meet the navigation criterion (no more than 6 errors in 12 route tasks) varied widely between the conditions (see Table 1 and the blue line in Figure 1). It was lowest in the *Landmarks* and *Semantic* conditions and highest in the *City names* and *Pars-pro-toto* conditions. The average errors for the subjects included in the analysis are shown as columns in Figure 4. Overall, A-routes have lower error rates than B-routes, which reflects the different length and difficulty of the two route types. There were no gender effects.

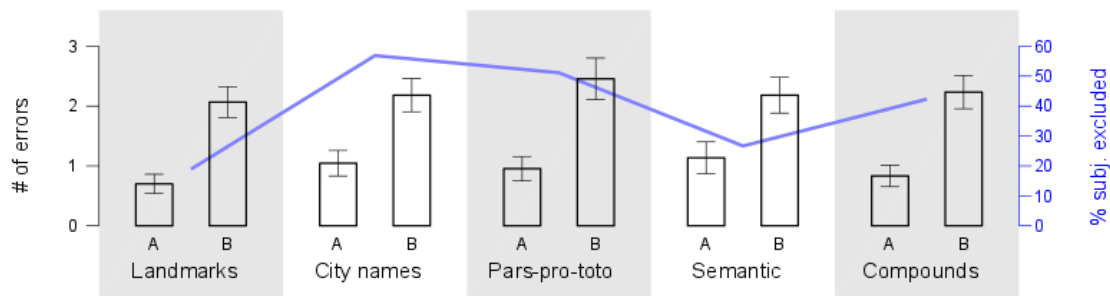


Figure 4: Error rates for A- and B-routes in the five conditions. Error bars are standard deviations of the mean. The blue line shows the percentage of subjects who did not finish the experiment or failed the error criterion in the test phase.

Regions (RDRC and First Decisions)

Figure 5 shows the mean number of region - dependent route choices for each condition and route type, for all subjects. One-tailed sign tests reveal that RDRC values are significantly above the chance level of 50% for the *Landmarks* condition (A-routes: $p < 0.001$, B-routes: $p = 0.002$), the *City names* condition (A-routes: $p = 0.021$), and the *Compounds* condition (B-routes: $p = 0.032$). Gender-dependent analysis did not reveal significant effects except for the B-routes in the *Landmarks* condition (male: mean = 0.56, female: mean = 0.70, Wilcoxon-rank-sum test $p = 0.038$). The results in the *Landmarks* condition reproduce the original results by Wiener and Mallot (2003). Figure 6 shows the percentage of region-consistent first decisions for all included subjects independent of the correctness of the overall route. Effects are slightly weaker than for the route choice reported in Figure 5; one-tailed sign tests revealed significances for the same conditions as before, i.e. *Landmarks* (A-routes: $p < 0.001$), *City names* (A-routes: $p = 0.032$), and *Compounds* (B-routes: $p = 0.026$). No significant gender effects were found.

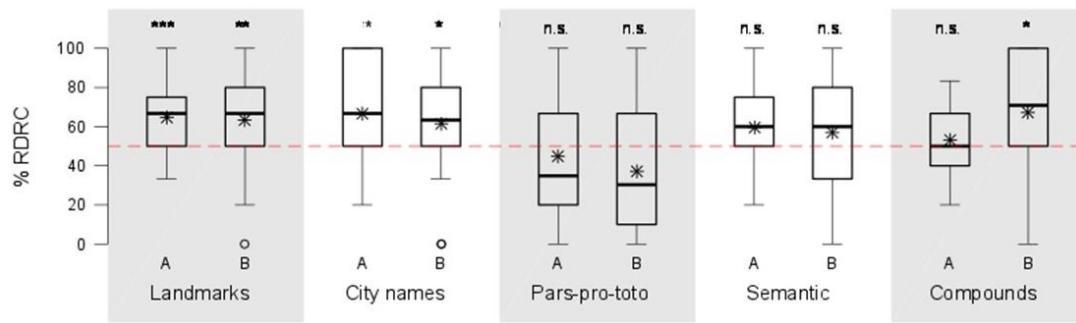


Figure 5: Region-dependent route choice (RDRC) per subject for all conditions. A, B: route types. Boxes include 50% centermost data points. Whiskers show most outlying data point included in a 1.5 inter-quartile-range distance from box. Outliers are shown as circles. The asterisk in the box marks the arithmetic mean. Deviations of the median of 50% were tested with a one-tailed sign test. n.s.: not significant. *: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$.

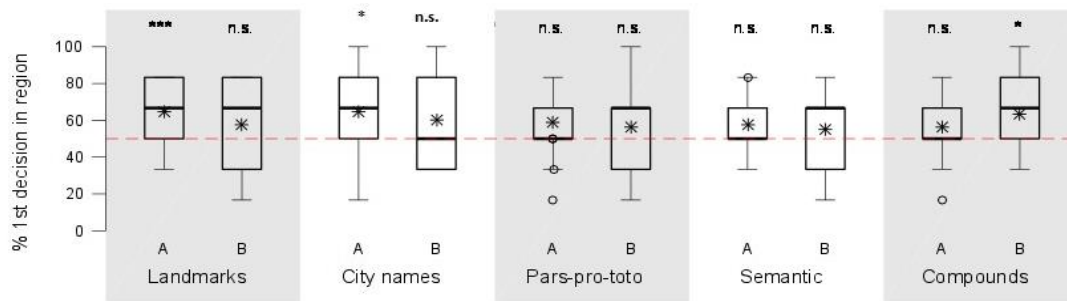


Figure 6: Percentage of region consistent first decisions per subject for all conditions. A, B: Route types. Conventions as in Figure 5.

Questionnaire and Sketch Maps

Average region report and sketch map ratings are shown in Figure 7. Region reports are lowest in the *City names* condition and highest in the *Compounds* condition, i.e. in one of the implicit condition where region names had not been presented. No significant differences between conditions were found. Sketch map ratings were highest in the *Landmarks* and *Semantic* conditions and lowest in the *Compounds* condition. Again these differences were not statistically significant.

Figure 8 and Table 3 show typical sketch maps and average ratings for the five map criteria. Perfect sketches with rating 5 occur in all conditions. Even in the implicit conditions (*Landmarks*, *Semantic*, and *Compounds*), some subjects write down the

implied region names and draw region boundaries. Indeed, region names are mentioned more often in the implicit *Landmarks* and *Semantic* conditions than in the explicit conditions (*City names* and *Pars-pro-toto*); the lowest frequency of region mentioning occurred in condition *Compounds*, which, however, showed the highest region report. Place names are generally well reported with a lowest rating in the *Compounds* condition. As before, these differences between individual measures do not reach statistical significance, but see the multivariate analysis below.

Table 3: Condition means of the sketch evaluation criteria for each criterion.

Condition	Form	Places	Region	Paris	Order	Total
<i>Landmarks</i>	0.98	0.91	0.88	0.86	0.83	4.49
<i>City names</i>	0.88	0.86	0.55	0.70	0.71	3.65
<i>Pars-pro-toto</i>	0.98	0.99	0.56	0.93	0.76	3.80
<i>Semantic</i>	0.90	0.98	0.76	0.83	0.62	4.10
<i>Compounds</i>	0.88	0.70	0.53	0.66	0.53	3.32

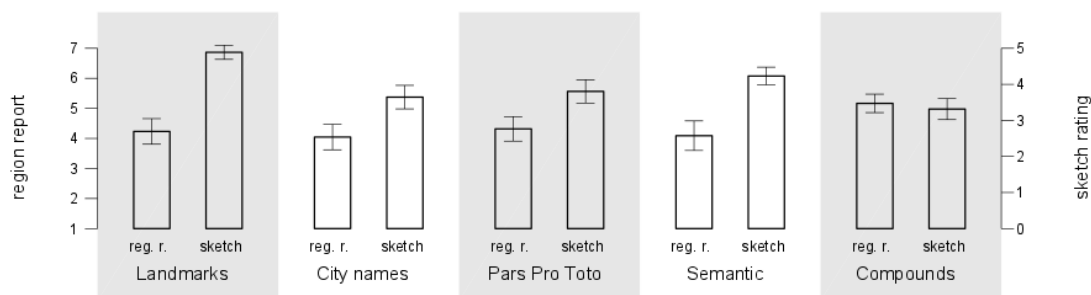


Figure 7: Left columns and scale: region report on a scale from 1 to 7. Right columns and scale: Sketch map ratings on a scale from 0 to 5. Error bars are standard deviations of the mean.

Multivariate Analysis

In total, eight dependent variables were recorded for each subject, errors in A- and B-routes, region dependent route choices in A- and B-routes, first decision in A- and B-routes, region perception, and sketch map score. Pair correlation between these measures did not lead to significant results.

In order to detect differences between the conditions we first normalized each measure by subtracting its mean and dividing by its standard deviation. Next, we calculated similarities between the eight-dimensional data vectors of each pair of conditions as the p -values of eight-dimensional two-sample Hotelling T^2 tests. Using these p -values as proximities, we performed a classical multidimensional scaling (MDS) of which we considered the first three dimensions. This results in a three-dimensional coordinate vector for each condition in MDS space. Next, we calculated a matrix projecting the condition means as closely as possible (in a mean square sense) to the MDS position of each condition (Procrustes analysis). Finally, the individual data sets for each subject were also projected to the three-dimensional MDS-space using the same matrix. The result is a linear, orthogonal transformation of our eight-dimensional data space to a three-dimensional space in which differences between the conditions will be best represented.

The result appears in Figure 9. Fig. 9 a - c show score-score plots of the individual data points (one per subject) together with 95 % confidence regions for the condition means. The confidence regions overlap in all three projections for the *City names*, *Pars-pro-toto*, and *Semantic* conditions, indicating that differences between these conditions are low.

This is confirmed by three-dimensional two-sample Hotelling T^2 test on the projected data which did not reach significance between these three conditions (Table 4).

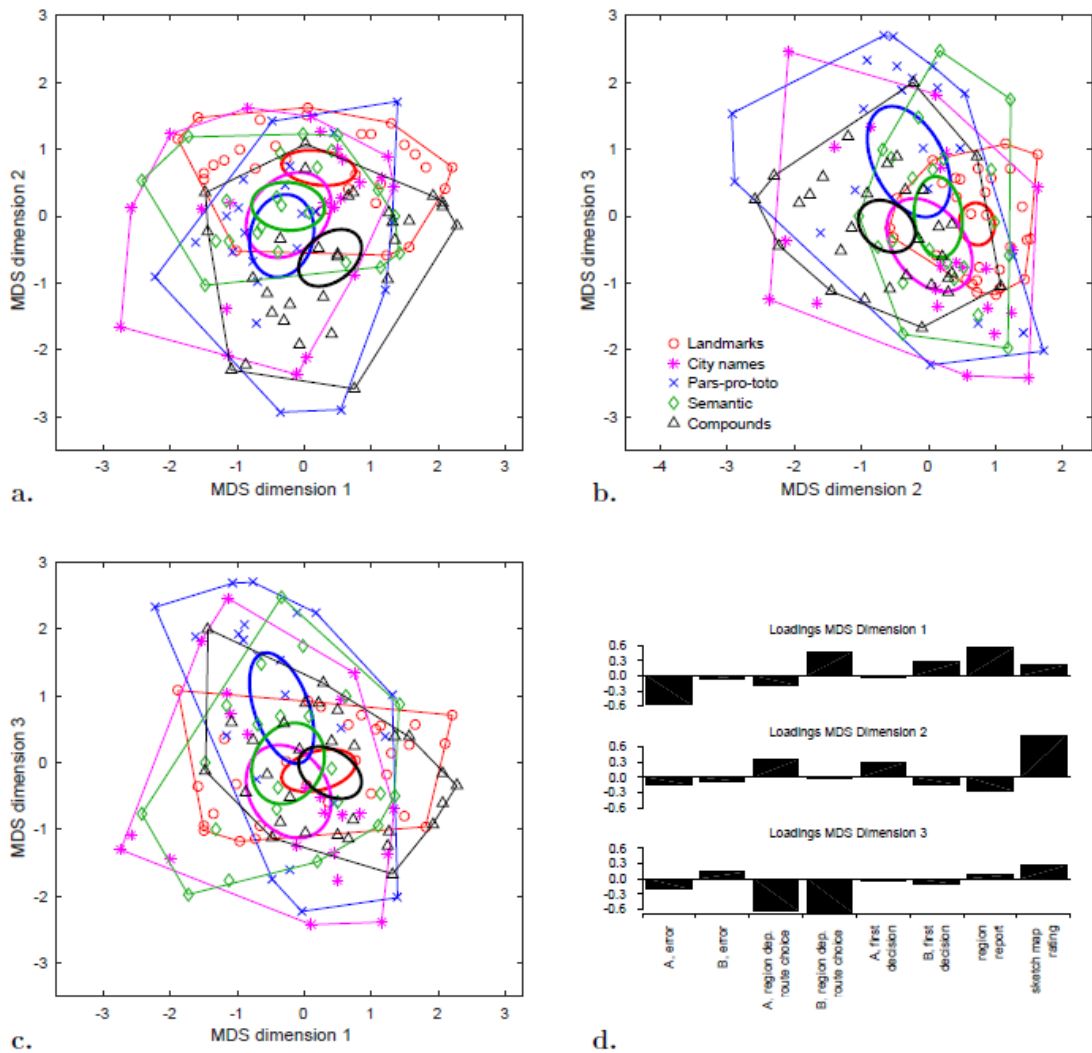


Figure 9: Projection of multivariate data vectors on a three-dimensional subspace generating the strongest separation between conditions (MDS plus Procrustes analysis, for details see text). **a. -c.** score-score plots. **d.** Loadings of the first three MDS dimensions. Dimension 1 reflects overall performance while dimensions 4 and 5 emphasize contrasts between region awareness, map knowledge, and navigational performance.

In contrast, both the *Landmarks* and *Compounds* conditions show non-overlapping confidence areas with all other conditions in at least one of the projections. This pattern is confirmed by the Hotelling tests appearing in Table 4. Note that the p -values appearing in the Table are not corrected for multiple testing. To do so, they have to be multiplied by 4.

The loadings of the three MDS dimensions appear in Figure 9d. Dimension 1 is a factor for overall performance with negative loadings on the errors and positive loadings on region report and sketch maps. Scores for this factor are highest in the *Landmarks* and *Compounds* conditions. Dimension 2 shows a contrast between region report (negative loading) and sketch map ratings (positive loading). It separates condition *Landmarks* with superior sketch maps and weak region report from condition *Compounds* with a strong region report and poorer sketch map. Dimension 3 has strong negative loadings on region dependent route choice and separates the two explicit naming conditions *City names* and *Pars-pro-toto*: region dependent route choice was lowest in the *Pars-pro-toto*-condition.

Table 4: Uncorrected Hotelling significances between the conditions, calculated from the scores on the MDS dimensions depicted in Figure 9.

	City names	Pars-pro-toto	Semantic	Compounds
Landmarks	.0120	.0005	.0064	$<10^{-6}$
City names		n.s.	n.s.	.0114
Pars-pro-toto			n.s.	.0031
Semantic				.0011

2.5. Linguistic Analysis of the Cues

The general idea of this paper is that commonalities of the words used as names of adjacent places support the integration of these places into a common region representation. The various naming schemes discussed above use different such commonalities and their effects on region induction differ substantially. In this section we present a statistical analysis of the commonalities occurring in the naming schemes used in the experiments.

According to Firth (1957), "a word is characterized by the company it keeps". Since in our experiments, grammatical "collocations" do not occur, we can restrict the analysis of the "company" of a word to contextual aspects, i.e. the likelihood of co-occurrence in close textual proximity (see Manning & Schütze, 1999). For this we use Pointwise Mutual Information (PMI) in combination with Information Retrieval (PMI-IR) as introduced by Turney (2001), see also Henrich (2008) and Bailey (2008). PMI is zero if the words occur independently, i.e. if the joint probability equals the product of the individual word probabilities. It takes positive or negative values if co-occurrence is more or less likely than in the independent case.

Co-occurrence probabilities of word pairs were obtained from the deWaC² corpus. This corpus comprises 1.7 billion words, derived from the ".de"-domain of the Internet starting from word lists taken from the *Süddeutsche Zeitung* and basic German schoolbooks (Baroni, Bernardini, Ferraresi, & Zanchetta, 2009). The documents of the corpus were segmented ("tiled") into topical segments using the open source search software ApacheLucene³ with the TextTiling algorithm proposed by Hearst (1997). Place names are lemmatized, so that they are counted independent of their genus and casus (e.g., "house" and "houses" count equally). The analysis resulted in a matrix of the frequencies of co-occurrences n_{ij} of each word pair i, j in the topical text segments defined by the TextTiling algorithm. In addition, the plain occurrence frequencies of each single word n_i are also returned.

Word similarities were calculated as the pointwise mutual information (Turney, 2001),

² <http://wacky.sslmit.unibo.it/doku.php?id=corpora>

³ lucene.apache.org

$$s_{ij} = 1 + \frac{\log_2 (n_{ij}/n_i n_j)}{\log_2 n} \quad (1)$$

for $i \neq j$, where n is the total number of topical text segments which was estimated as $n = 0.5 \times 10^8$. For $i = j$, we assume $s_{ii} = 1$ which assured the condition $s_{ij} \leq s_{ii}$ for all i, j . Finally, the resulting similarity values were converted to distances by the operation $d_{ij} = \sqrt{1 - s_{ij}}$.

The PMI-IR analysis resulted in distance matrices for each of the naming schemes used in the various conditions. Only the similarities between the 12 place names were calculated.

The region names of the two explicit conditions (*City names* and *Pars-pro-toto*) were not used because they were artificial words; the region names of the two implicit conditions (*Semantic* and *Compounds*) were not expressed in the experiment at all. The results are shown as MDS-embeddings in Figure 10.

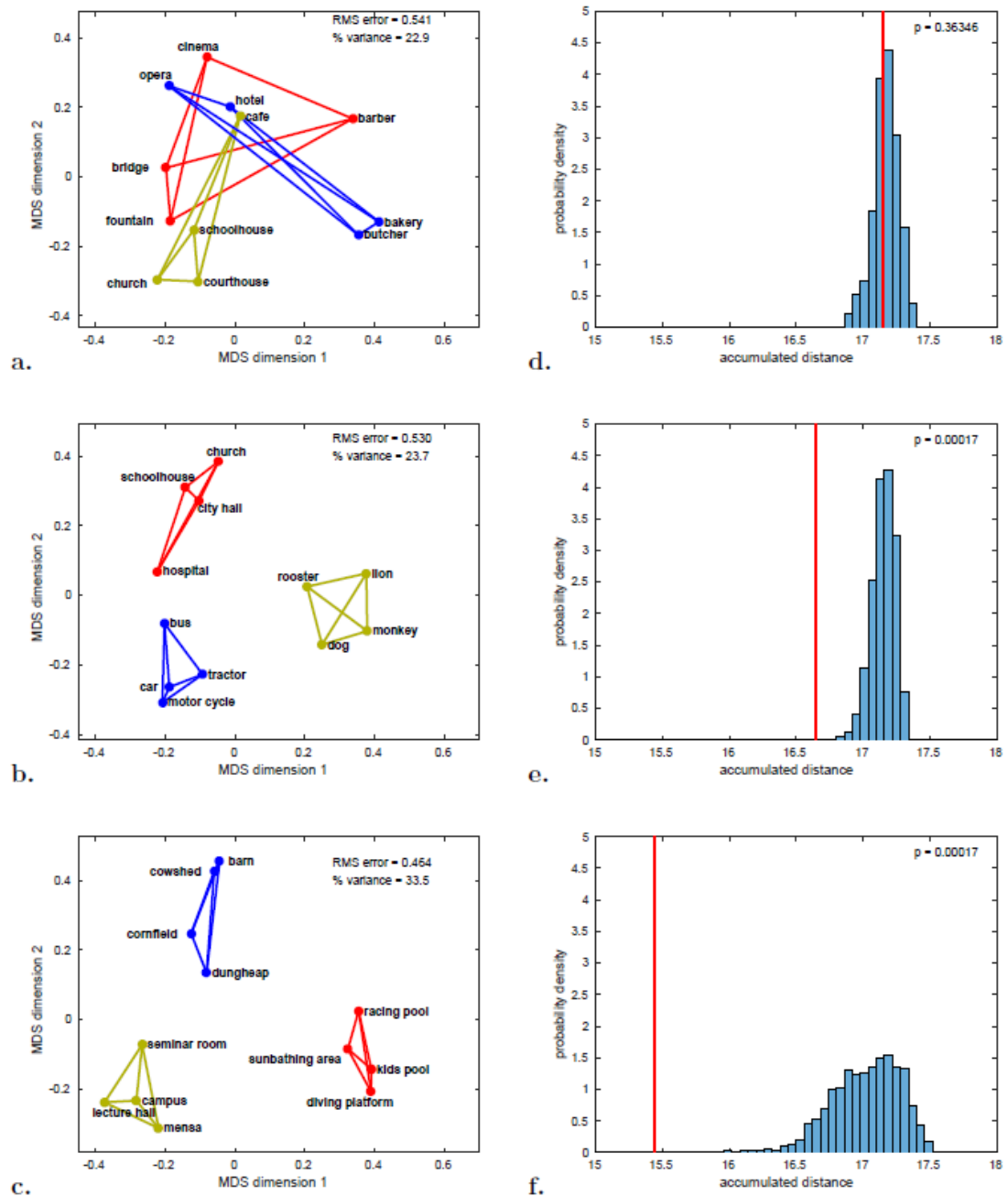


Figure 10: Left column: MDS analysis for the place name PMI-similarities. Right column: Accumulated within-region distances for all possible groupings of the place names to regions. The red bar shows the value for the naming scheme used in the experiment, p is the probability of getting this or a smaller accumulated distance by chance. **a.,d.**, *City names* and *Pars-pro-toto* conditions **b.,e.** *Semantic* condition, **c.,f** *Compounds* condition.

In the *Semantic* and the *Compounds* condition, there are clusters that correspond to the intended regionalization scheme. The statistical significance of clustering was tested by accumulating all within-region word-word similarities in a given naming scheme. For each condition (i.e. each set of 12 place names), we constructed all possible regionalization, i.e. all possible clustering of the 12 names into groups of four. Simple combinatorics shows that the number of possible regionalized naming schemes that can be derived from a set of 12 place names equals

$$k = \binom{11}{3} \times \binom{7}{3} = 5775 \quad (2)$$

For each of the 5775 naming schemes we calculated the accumulated distances of all within-region-pairs, i.e. for the pairs connected by lines in Figure 10 a-c. Note, however, that the line lengths in the Figure show only the projection of d_{ij} on the first two MDS dimensions. The distributions of the true cumulated distances appear in Figure 10 d-f together with the accumulated distance of the actually used naming schemes (red line). For the *Semantic* and *Compounds* conditions, the used naming scheme takes the single smallest value of accumulated distance. In contrast, the naming scheme used in the *City names* and *Pars-pro-toto* conditions has an average value of accumulated distance. These results agree with the clustering found in the MDS analysis. The distributions for the *Semantic* and *Compounds* conditions differ in that the separation between the actual accumulated distance (red line) and the peak of the distribution is much larger in the *Compounds* condition. This may mean that the clustering is stronger or more reliable in this condition and may be one reason for the presence of a region effect in the *Compounds* but not in the *Semantic* condition.

2.6. Discussion

The starting point of this paper is the idea that regions are abstract spatial entities that have to be inferred by the observer from the relations between places which in turn are recognized by local cues. Regions are abstract in the sense that the place cues are not generally present on region level. It has been demonstrated (Wiener & Mallot, 2003) that semantic relatedness of landmark objects at adjacent places can induce regionalization. Our main hypothesis is, therefore, that regionalization can also be induced by relations of naming cues of adjacent places. Indeed, one might expect that this is even more powerful than the semantic relatedness of objects, since language seems to be the natural tool for abstraction processes.

However, the direct comparison of the *Landmarks* and *Semantic* conditions, in which the visual landmark objects are replaced by object names with a similar semantic relationship, indicates that this replacement leads to the extinction of region-dependent route choice (Figures 5, 6), poorer sketch map quality (Figure 7), and increased overall difficulty of the experiment, as indicated by the number of subjects needed to fill the groups (blue line in Fig. 4). The multivariate data vectors collected from the two conditions differ significantly at the $p = 0.0064$ level (Table 4). In this sense, language cues are clearly not more efficient than - and indeed not even equivalent to - visual landmark cues in the induction of spatial hierarchies. This result is in line with the dual coding of spatial concepts (Paivio, 1978, 1986) in a verbal and an image system. If navigational behavior is assumed to be driven by the image system, language cues would have to be transferred to the image system and might therefore have weaker effects.

Some language-based induction of spatial hierarchies was found in the *City names* and *Compounds* conditions (Figures 5, 6), again with poorer sketch maps than in the *Landmarks* condition (Figure 7) and increased overall difficulty of the experiment (Figure 4). Still, the two conditions are significantly different in the multivariate analysis ($p = 0.0011$, Table 4).

Separation of data is clearest in MDS dimensions 1 and 2 (Figure 9a), which reflects contrasts between A and B routes and between region report and sketch map quality.

Specifically, region-dependent route choices are associated with high region report and relatively poor maps in the *Compounds* condition and with low region report and higher quality sketch maps in the *City names* condition.

Which factors can be identified that support the representation of regions? One such factor which is present in all conditions is spatial adjacency, which however is ambiguous with respect to the specific partition of the environment perceived by the subjects. The specific region cues fall into two groups: explicit region naming in conditions *City names* and *Pars-pro-toto* and implicit regionalization that has to be discovered by the subjects from regularities in the cue arrangement in the other conditions. In the explicit conditions, regions have to be learned as sets of places which are mostly (*Pars-pro-toto*) or completely (*City names*) arbitrary with respect to the region names. I.e. neither can place names be predicted from region names nor the other way round. The situation is slightly different in the *Pars-pro-toto* condition where one place name from each region is used to build the region name. It appears that this naming scheme did not support region learning, probably because the region names generate expectations about upcoming place names which, however, remain unfulfilled in most cases.

In the implicit conditions, regularities in the spatial arrangement of place names exist that have to be detected by the subjects. In the language case (*Semantic* and *Compounds*), these similarities are reflected by the word co-occurrences in the deWaC corpus (Figure 10). If subjects would generate associations to the names of neighboring places based on these co-occurrence probabilities, the expected regionalisations should be perceived. Surprisingly, this worked only for the *Compounds* condition, but not for the *Semantic* condition which shows similar clusters in word co-occurrence probability. One possible explanation for this difference is that the names used in the *Compounds* condition by themselves imply a spatial nearness (e.g., between a seminar room and a library) which is not implied by objects from a common semantic category. Also, place names in the *Compounds* condition share a common function through which they can be connected into simple narratives. A visit to a farm, an open air bath, or the university makes a better story than connecting four types of vehicles into a common plot. Interestingly, some subjects from the *Semantic*

condition reported during debriefing that they had built rural narratives including the place cues tractor, dog, rooster, and car, i.e. objects that belonged to different semantically defined regions in our design. This may be one reason for the missing region effects in this condition. No such between-region narratives were reported in the *Compounds* condition.

Region transitions correspond to clear event boundaries which is not necessarily the case in the *Semantic* condition. This distinction seems to apply only to the language conditions, since region effects are clearly present in the *Landmarks* condition. Semantic groupings occurring in a visual scene representation as is formed in the *Landmarks* condition supports region formation whereas semantic groupings occurring in language-based representations (*Semantic*) does not.

Regions as a spatial concept thus appear to be related to a number of similar representational formats including events (Zacks & Tversky, 2001; Zacks, Speer, Swallow, Braver, & Reynolds, 2007), idealized cognitive models (Lakoff, 1987), and narratives (Bower & Morrow, 1990). All of these formats allow predictions about upcoming places in a navigational sequence; boundaries will be perceived when these predictions fail.

Region-dependent route choice is a clear indicator of the representation of some sort of regional knowledge. However, our results also show some differences in the hierarchical structuring of spatial representations based on visual and verbal cues or on different types of verbal cues. Region-dependent route choice can be associated either with high region report and relatively poor sketch map quality (*Compounds* condition) or with high sketch map quality and weaker region report (*Landmarks* and *City names* conditions, cf. 7). The same contrast is found for the "region" criterion in the sketch map ratings (Table 3): regions may be reported but not marked in the map (*Compounds* condition) or marked in the map but not reported, as was frequent in the *Landmarks* and *Semantic* conditions. The contrast between region report and sketch map quality is reflected by the opposite signs of the corresponding loadings in the MDS-dimension 2 (Figure 9d). This contrast is in line with a recent report by Noack et al. (2017) who used the same behavioral paradigm to show that region awareness is consolidated during sleep while region-dependent route choice is not.

In conclusion, the data presented in this paper clearly show that language and visual object cues act differently in the formation of hierarchical spatial representations. The effects on route planning (region-dependent route choice), region report, and sketch map drawing are partially independent, indicating that the representations differ not only in the amount or quality of the stored information, but also in the kind of knowledge included.

3. SLEEP ENHANCES KNOWLEDGE OF ROUTES AND REGIONS IN SPATIAL ENVIRONMENTS ⁴

3.1. Abstract

Sleep is thought to preferentially consolidate hippocampus-dependent memory, and as such spatial navigation. Here, we investigated the effects of sleep on route knowledge and explicit and implicit semantic regions in a virtual environment. Sleep, compared to wakefulness, improved route knowledge and also enhanced awareness of the semantic regionalization within the environment, whereas signs of implicit regionalization remained unchanged. Results support the view that sleep specifically enhances explicit aspects of memory, also in the spatial domain. Enhanced region knowledge after sleep suggests that consolidation during sleep goes along with the formation of abstract, schema-like representations.

⁴ A modified version of this was published in *Learning and Memory* 24(3), 140-144, 2017.

3.2. Introduction

Sleep supports memory consolidation in humans (Diekelmann & Born, 2010; Rasch & Born, 2013). Consolidation during sleep does not only strengthen memory traces but is also thought to help transform new detailed episodic representations into more generalized semantic representations containing just the common invariant features shared by multiple experiences (Dudai et al., 2015; Inostroza & Born, 2013; Lewis & Durrant, 2011). Thus, compared to wakefulness, sleep after learning enhances the extraction of categories from objects sharing general features (Friedrich et al., 2015) and of statistical regularities and grammatical rules in complex stimulus patterns (Wagner et al., 2004; Durrant et al., 2011; Durrant et al., 2013; Nieuwenhuis et al., 2013), such that participants after sleep were better able to explicitly express these regularities they had acquired implicitly before sleep (Fischer et al. 2006; Wilhelm et al., 2013). Indeed, sleep is thought to preferentially support the formation of explicit memory that crucially depends on hippocampal function (Marshall & Born, 2007; Robertson et al., 2004; see Weber et al., 2014).

Here, we examined whether the assumption of sleep preferentially supporting the formation of explicit memory in the hippocampus-dependent system also holds for the spatial domain. This is important, since the presumed memory function of sleep has been conceptualized based centrally on observations of activity of hippocampal place cells encoding spatial experience in rats. Patterns of activity in such place cell ensembles during encoding of a spatial maze have been consistently found to be reactivated during slow wave sleep after the encoding experience (Pavrides & Winson, 1989; Skaggs & McNaughton, 1996; Wilson & McNaughton, 1994). This neural replay during sleep is considered to cause a strengthening and transformation of the spatial representation. Evidence showing an impact of sleep on spatial memory performance in humans is mixed, however, showing either beneficial (Ferrara et al., 2008; Nguyen et al., 2013; Wamsley et al., 2010) or no effects of sleep (Javadi et al., 2015; Orban et al., 2006; Peigneux et al., 2004; Rauchs et al., 2008).

In fact, rather than representing a unitary hippocampal function, spatial navigation in humans derives from a multitude of explicit and implicit processes and representations (e.g. Wolbers & Hegarty, 2010), including, amongst others, knowledge about the semantic structure of space. Specifically, in this context, the term “regionalization” is used to refer to the observation that humans cluster spatial landmarks (hierarchically) on the basis of nonspatial attributes and that this clustering affects distance judgments (Hirtle & Jonides, 1985; McNamara, 1986; Stevens & Coupe, 1978) and navigation (Balaguer et al., 2016; Schick et al., 2015; Wiener & Mallot, 2003). In essence, these studies show that distances tend to be overestimated when routes cross regional barriers – both perceived and just imagined ones - compared to when they do not (Carbon & Leder, 2005; Newcombe & Liben, 1982; Kosslyn et al., 1974; Hirtle & Jonides, 1985; Balaguer et al., 2016).

Thus, to demonstrate regionalization, Wiener & Mallot (2003) asked participants to find the shortest path connecting three landmarks in a virtual maze (travelling-salesmen problem). Importantly, all landmarks within the maze pertained to one of three semantic categories (vehicles, animals, buildings) and were arranged such that landmarks of the same semantic category clustered together to form semantic regions. To investigate the effect of these regions on navigational planning, the authors constructed problems where two equidistant solutions to the navigation problem existed, which only differed in the number of - non-visible - region boundaries between semantic regions that had to be crossed (Figure 2A and B). As predicted, participants reliably preferred the routes passing fewer region boundaries to routes passing more boundaries (though both routes had the same length), with this bias indicating that the participants acquired an implicit knowledge of the regions (regionalization) that informed their navigation decisions.

Importantly, for the investigation of sleep’s effect on spatial memory, the regularities among landmarks, which give rise to semantic regions must be extracted from navigation experience, suggesting a beneficial role for sleep in the formation of these semantic regions.

Here, we adapted this travelling-salesman paradigm to measure, apart from route memory (accuracy in finding the shortest path), implicit region memory (by the

navigation bias for the route with fewer region crossings) and explicit region memory (by explicit recall of the semantic regions). We expected that sleep preferentially supported explicit memory for routes and regions, and we explored the effect of sleep on implicit regional bias.

3.3. Methods

Participants

Thirty-eight participants (20 female; mean age = 25 years; range: 18-42 years) performed on a virtual navigation task adapted from Wiener & Mallot (2003; see above) before (Pretest) and after (Posttest) a 12 h retention interval either filled with nighttime sleep (Sleep condition) or daytime wakefulness (Wake condition). All participants performed in both conditions but at different schedules with a minimum delay of 2 weeks between conditions (range 14-45 days). Twenty participants slept during the first retention interval (FirstSleep group) and stayed awake during the second, and 18 other participants (FirstWake group) stayed awake during the first retention interval and slept during the second (see Fig. 1A and Supplemental Methods for a detailed description).

Procedure

Different environments (forest and desert) and different semantic categories (animals, artwork, and vehicles, or musical instruments, tools, and furniture) were used to minimize learning effects over repeated testing (see Fig. 1B).

A

	Session 1	Retention Time	Session 2		Session 3	Retention Time	Session 4
FirstWake	9:00 a.m.	wakefulness	9:00 p.m.		9:00 p.m.	sleep	9:00 a.m.
FirstSleep	9:00 p.m.	sleep	9:00 a.m.	> 2 weeks absence from the lab	9:00 p.m.	wakefulness	9:00 a.m.
	Control Measures - PVT - SSS - DSS - SBSOD Experimental Task 1. Familiarization with the environment 2. Training in the environment 3. Pre-test (18 trials)		Control Measures - PVT - RWT - SSS - (SF-A/R) Experimental Task 1. Post-test (18 trials) Explicit Retrieval - sketch - questionnaire		Control Measures - PVT - SSS Experimental Task 1. Familiarization with the environment 2. Training in the environment 3. Pre-test (18 trials)		Control Measures - PVT - RWT - SSS - (SF-A/R) Experimental Task 1. Post-test (18 trials) Explicit Retrieval - sketch - questionnaire

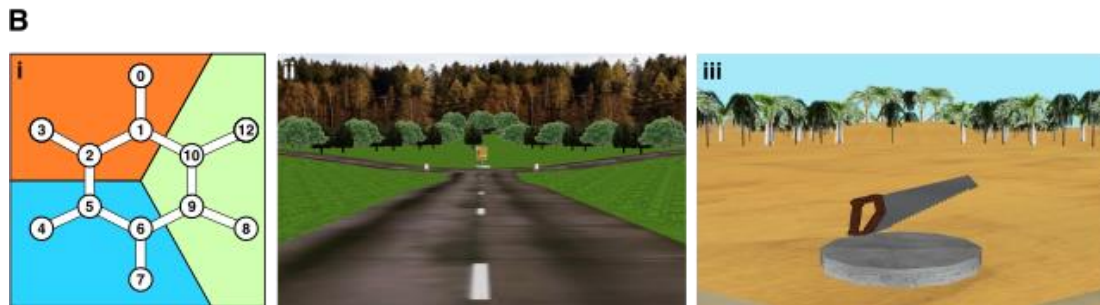


Figure 1: Study Design (A). Sequence of experimental conditions (Sleep / Wake) for two groups: “FirstSleep” and “FirstWake”. Different control measures were assessed at each session. Measures in brackets were only administered in the Sleep condition: PVT, Psychomotor vigilance test; SSS, Stanford Sleepiness Scale; DSS, Digit-Symbol-Substitution; SBSOD, Santa-Barbara Sense of Direction Scale; RWT, Regensburger Wordfluency Test; SF-A/R, sleep questionnaire (see Supplemental Methods); Virtual Environment (B): (i) Iterated y-maze structure of the virtual environment. Numbered circles refer to crossroads marked with a landmark. The 3 implicit regions correspond to clusters of landmarks belonging to the same semantic category. (ii) Example view at a decision point (crossroad) within the forest environment; (iii) Example view at one landmark (saw) within the desert environment. Both environments featured the same spatial layout but only differed in surface characteristics and landmarks.

After familiarization with the virtual maze at pretest, participants solved 3 types of Travelling-salesman-problems (A, B, and C; 6 trials each), where they were asked to find the shortest path connecting three landmarks in the virtual world. Problem type A and B were symmetric and, thus, offered two equidistant solutions of the problem (Fig. 2A and B).

However, one solution would demand passage of more region boundaries than the other (A: 1 vs. 2 boundaries; B: 2 vs. 3 boundaries). The third problem type (C) was

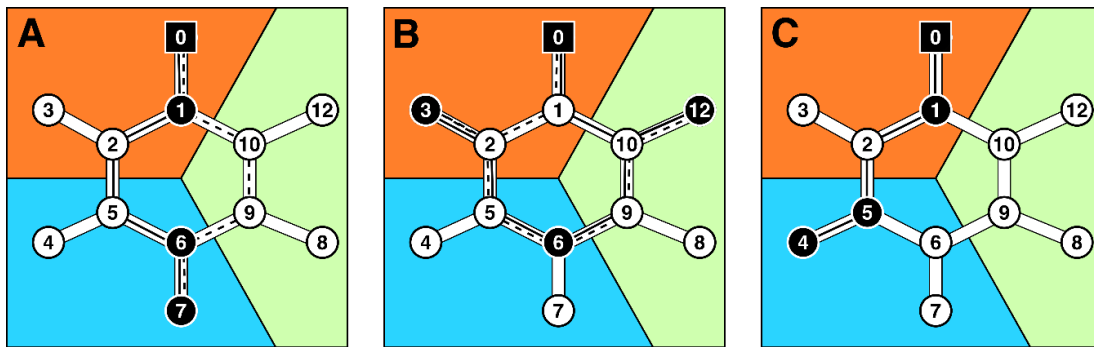


Figure 2: Problem types A, B, and C of the Test phases. On each trail, participants were asked to connect 3 landmarks (filled circles) taking the shortest possible route from the starting point (0). Problem types A and B are symmetric and allow for two equivalent solutions. *Solid lines* represent the solution with fewer boundary crossings (A1: 1,2,5,6,7; B1: 1,10,12,10,9,6,5,2,3) and *dashed lines* the solution with more boundary crossings (A2: 1,10,9,6,7; B2: 1,2,3,2,5,6,9,10,12). Importantly, the decision for one route or the other was always taken at decision point 1. Problem type C allows for only one correct solution. The starting point was rotated on a trial-by-trial basis, such that each dead-end road was the starting point once in every problem type and route decisions were independent of left-right decisions.

asymmetric and thus featured only one correct solution to the problem (see Figure 2 and Supplemental Methods).

3.4. Results

Using four different measures, the performance results were as follows:

(1) Route memory (i.e. the number of correctly solved problems over the total number of problems) was based on data originating from all three problem types (A, B, and C). We found route knowledge generally improving over the 12-hour retention interval ($F(1,34) = 7.81$; $p < 0.01$, $\eta^2 = 0.01$, for Pretest/Posttest main effect). Importantly, this improvement was greater across the sleep than wake retention interval ($F(1,34) = 6.92$, $p < 0.01$, $\eta^2 = 0.01$, for Pretest/Posttest x Sleep/Wake; Fig. 3).

To further investigate potential time of day effects on navigation performance (i.e., differences between evening and morning sessions), we looked at performance during Pretest only. We found no Sleep/Wake (evening/morning) main effect in this analysis

for navigation accuracy ($F(1,34) < 1$) excluding a strong confounding circadian effect. Note there were also no accompanying differences in vigilance, word fluency, or self-reported sleepiness (see Supplemental Results) ruling out confounding influences from such non-specific factors.

(2) Implicit memory of regions was assessed by the directional decision taken at the first decision point in problem types A and B. The region preference index is the number of trials where the participants turned towards the route with fewer boundaries relative to the number of all trials of type A and B problems ($n = 12$), with an index of 1 indicating perfect preference for the routes crossing fewer region boundaries, and an index of 0.5 indicating random choices. In fact, we found a general preference for the routes crossing fewer region boundaries ($M = 0.61$; $SEM = 0.02$, $t(37) = 5.54$, $p < 0.01$). However, at Posttest this preference did not depend on whether subjects had slept or stayed awake after learning ($F(1,34) = 1.07$, $p > 0.250$, for Pretest/Posttest x Sleep/Wake; Fig. 3).

(3) The reaction time at the first decision point in problem types A and B was taken as a measure of the fluency with which the decision was made. Reaction times (at the first decision point) generally decreased from Pretest ($M = 4660$ ms; $SEM = 350$ ms) to Posttest ($M = 3810$ ms; $SEM = 294$ ms; $F(1,34) = 26.28$, $p < 0.01$, $\eta^2 = 0.04$) but were not modulated by sleep during the retention interval ($F(1,34) = 1.68$, $p = 0.204$).

(4) After Posttest, we used an exit-questionnaire to assess explicit knowledge of the environment and its regionalized structure by asking the participants to draw a sketch and by asking them to answer two questions with a response scale ranging from 1 (“not at all”) to 7 (“very strongly”):

1.) “Did you mentally group the landmarks in the environment?”

2.) “Did you have the feeling that the environment consists of different regions?”

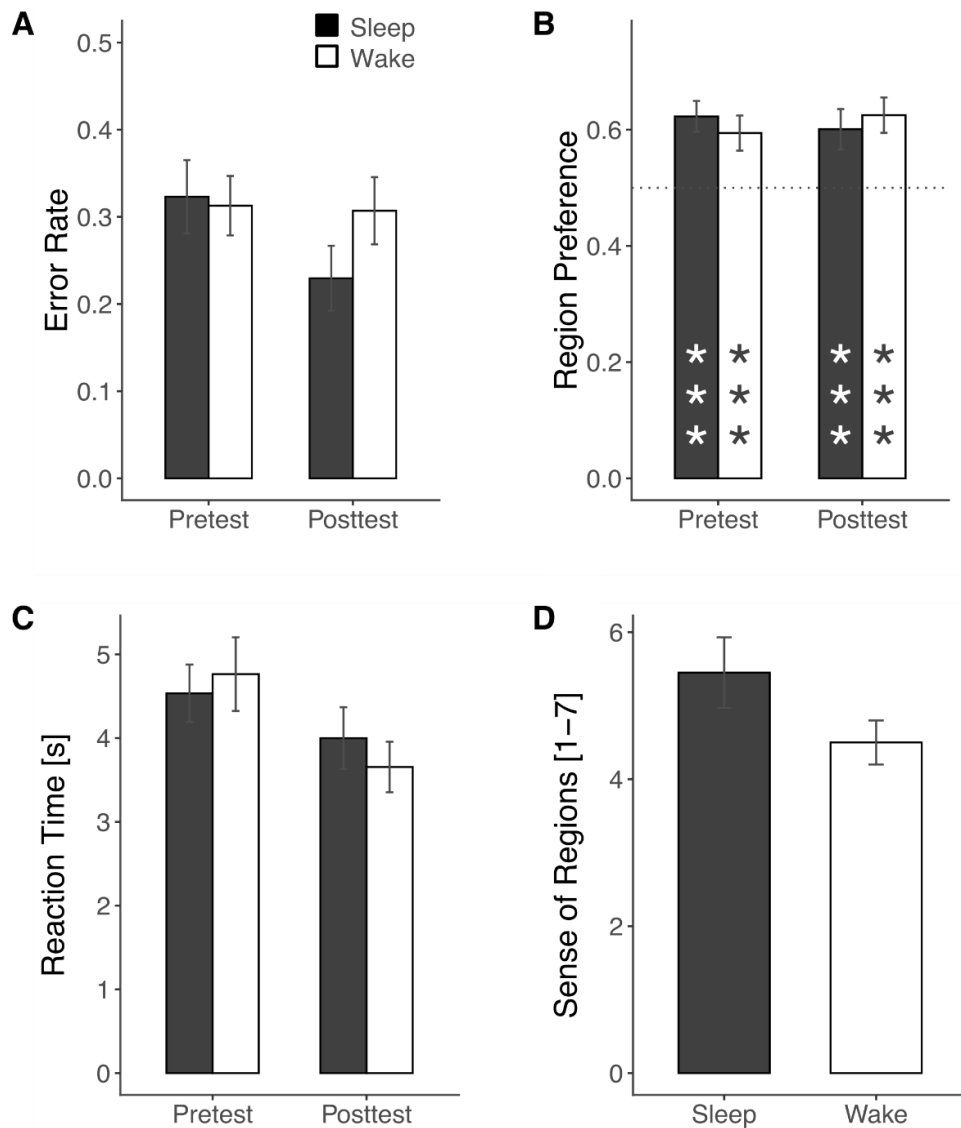


Figure 3: The effect of sleep on route memory and region preference. (A) Route knowledge assessed by error rates (number of trials where participants departed from the shortest path per total number of trials). (B) Region preference represents the decision to choose the route that crosses fewer region boundaries over route that crosses more. Chance level is denoted by the dotted line at a region preference of 0.5. Deviation from chance level was tested for each retention condition at Pretest and Posttest ($***p < 0.01$). (C) The effect of sleep on reaction time at the first decision point. (D) The effect of sleep on awareness of regionalization (by ratings between 1 - 7, no vs. strong awareness).

Of these items, question 2 was the only one allowing for differentiating sleep-related effects, because the sketch drawing task and question 1 revealed clear ceiling effects

inasmuch as at least 74% of participants of participants in both the Sleep and Wake conditions drew correct sketches and recognized the semantic landmark categories (see Supplementary Results). For question 2, we found that participants in the Sleep condition expressed a distinctly stronger awareness of the regionalization ($M = 5.45$, $SEM = 0.48$) than in the Wake condition ($M = 4.50$, $SEM = 0.30$), $F(1.36) = 5.98$, $p = 0.02$, $\eta^2 = 0.05$).

3.5. Discussion

Here, we assessed the effect of sleep on two aspects of spatial memory, i.e., the memory for routes and for regions in a virtual environment. The regionalization of the environment has recently been revealed to be an important factor contributing to human spatial navigation behavior (Balaguer et al., 2016; Schick et al., 2015; Wiener & Mallot, 2003). We found that sleep, compared with post-learning wakefulness, improved route memory, with the participants committing fewer errors after sleep compared to wakefulness. Sleep also improved subjective awareness of the regionalized structure of environment, as a measure of explicit region memory. However, the preference for routes that crossed fewer region boundaries, which we used as a measure of implicit region memory, remained unaffected by sleep. These results support the notion that sleep preferentially enhances explicit over implicit memory representations. Additionally, that sleep enhanced the awareness of regions is consistent with the view of an active consolidation process during sleep that supports the abstraction of spatial structure from incidentally encoded landmarks.

The benefit from sleep in route-knowledge is in agreement with several previous studies, showing that sleep enhances spatial memory in virtual navigation tasks (e.g. Nguyen et al., 2013; Ferrara et al., 2008; Wamsley et al., 2010), but in disagreement with others that failed to reveal spatial performance benefits after sleep (Javadi et al., 2015; Orban et al., 2006; Peigneux et al., 2004; Rauchs et al., 2008). We have argued above that human spatial navigation is a highly complex behavior, which depends on a variety of different processes (Wolbers & Hegarty, 2010), strategies (Iaria et al., 2003; Hartley et al., 2003) and representations of space (Hartley et al., 2014). The

differentiation of strategies, e.g., whether subjects relied on a landmark-oriented stimulus-response strategy or on a survey strategy that takes the overall layout of the maze into account, was not in the focus of this study, but might have contributed to the negative outcome of some previous studies.

The finding of a sleep-induced increase in awareness of regionalization corresponds with the literature in several ways. To the extent that the regions within our environment are not a matter of direct experience but rather must be inferred from the continuous stream of episodic experience, the formation of representations of environmental regions constitutes a process of abstraction of superordinate (semantic) categories in a hierarchical spatial representation (Balaguer et al., 2016; Stevens & Coupe, 1978; Wiener & Mallot, 2003).

Our findings are, thus, in line with current models of an active systems consolidation of memory, which posit that, based on neural reactivation processes during sleep, hippocampal representations of episodic memory become redistributed to neocortical sites, thereby undergoing a transformation into less contextual and more abstract semantic representations (Inostroza & Born, 2013; Lewis & Durrant, 2011; Dudai et al., 2015). The supporting effect of sleep for the formation of abstract representations has been similarly demonstrated for the non-spatial domain of knowledge. Payne and colleagues (2009) showed, for example, that sleep favored false memory of words, when these words pertained to the superordinate semantic categories of previously learned, semantically structured word-lists (see also Diekelmann et al., 2010). Moreover, our finding of a sleep-induced increase in awareness of regionalization corresponds with findings showing that sleep supports the conversion of implicit into explicit sequence memory in serial reaction time tasks (Fischer et al., 2006; Wilhelm et al., 2013). Indeed, the conversion into explicit memory can be considered a kind of semantization of implicit task representations formed before sleep.

At the implicit level, we replicated earlier findings showing a preference for routes that cross fewer region barriers (Wiener & Mallot, 2003). The stronger awareness of regionalization of the environment in the sleep condition did not result in stronger route preferences, however. Such a dissociation of sleep effects for explicit and implicit memory further suggests that sleep has a particular effect on the formation of

explicit memory representations (Fischer et al., 2006; Wilhelm et al., 2013; Zander, T., et al., 2017). However, although indicating a sleep-dependent benefit for explicit memory formation, the present results do not exclude that sleep might also benefit implicit memory. First, the measure of route preference might not sensitively reflect implicit region memory. Specifically, our premise that the route preference scales with the strength of a unique region representation may not hold. In fact, correlations of route preference with explicit judgments of the regionalization across individuals were basically absent ($|r|$'s < .1).

Second, the influence of superordinate spatial categories may scale with the knowledge of the actual spatial relationships between the subordinate spatial items (McNamara 1986). That is, the better the spatial relationship between two locations is known, the lower the bias resulting from their respective superordinate categories should be. Our data does not support this hypothesis, however: To the contrary, we found that better navigation performance (i.e. committing fewer errors) was associated with stronger route preference across individuals ($r = -.53$, 95% CI = [-.72, -.25]). Absent differences in implicit region memory may therefore not be explained by the sleep related differences in route knowledge at posttest.

In summary, we showed that sleep supports consolidation of explicit spatial memory for routes and regions, whereas measures of implicit region memory remained unchanged. These findings further support the idea that sleep preferentially enhances the formation of hippocampus-dependent explicit memory. Our findings shed new light on the role of sleep in spatial memory consolidation by suggesting that abstraction processes during sleep favor the formation of non-spatially defined superordinate clusters. In combination with similar findings in other domains, the present data corroborate theories of sleep supporting an active systems consolidation process in the formation of superordinate (abstract) categories from interrelated experiences.

3. 6. Supplemental Information

Supplementary Methods

Detailed Participant information

Forty-six participants were recruited for the study. Data of eight participants could not be reported in the study because of technical issues ($n = 4$) or because participants withdrew their consent to participate ($n = 4$). Participants of the final sample reported normal or corrected to normal vision, a good spatial sense of direction in *Santa Barbara Sense of Direction* questionnaire (SBSOD; Hegarty et al., 2001, $M = 5.41$, $SEM = 0.22$), and demonstrated normal processing speed in the digit symbol substitution test (DSS) of the WAIS-III ($M = 64.39$, $SEM = 2.21$).

Participants were assigned to the FirstWake or the FirstSleep group in alternating fashion upon their first contact with the experimenter. Participants of the two groups did not differ with respect to self-rated sense of direction (SBSOD: $M = 5.37$ and 5.44 ; $t(36) < 1$) and processing speed (DSS: $M = 61.7$ and 67.4 ; $t(36) = 1.30$, $p = 0.202$).

All participants were instructed to abstain from caffeine, alcohol, and nicotine on experimental days and during the retention period, gave their written informed consent, and were paid 8 €/h for participating. The study was approved by the local ethics committee.

Detailed task procedures

All participants performed an overnight Sleep condition and a daytime Wake condition with a minimum of two weeks between the two conditions. Eighteen participants were first tested on the Wake condition, and 20 participants first on the Sleep condition. In the Wake condition, participants reported to the lab in the morning (8:00 or 9:00am) for Familiarization, Training and an immediate Test phase (Pretest) and returned to the lab 12 hours later (8:00 or 9:00pm) for a delayed Test phase (Posttest). During the Sleep condition, they came to the lab at the same times of the day, but encoding took place in the evening and retrieval took place 12 hours later the next morning.

Specifically, participants first freely explored the environment for at least 5 minutes for Familiarization. This phase only ended when every decision point in the environment was visited once. Then, the Training phase started, where participants were asked to find one single landmark, which was either located in the neighboring or second neighbor dead end from the starting point. Participants performed on 6 problems of each type repeatedly until each problem was correctly solved twice in succession.

Thereafter Pretest phase started: Participants solved 18 problems, 6 of each of the 3 different types (A, B, C). The Posttest phase was identical to the Pretest phase.

In addition, several control measures were assessed to control for potential general effects of time of the day on performance levels. Specifically, we assessed Sleepiness and vigilance before and after the retention intervals with the Stanford Sleepiness Scale (SSS; Hoddes et al., 1972) and the Psychomotor Vigilance Test (PVT, Dinges & Powell, 1985). Additionally, word fluency was tested (Regensburger Wortflüssigkeitstest, RWT, Aschenbrenner, Tucha, & Lange, 2000) at Posttest, to assess the process of retrieving information from long-term memory.

Sleep, in the Sleep conditions, was evaluated using standardized self-reports (SF-A/R; Görtelmeyer, 2011). Participants slept 396 minutes ($SEM = 12$) on average and reported good sleep quality (Mdn = 2, range = 1-4, on a scale ranging from 1 excellent to 7 very poor).

Virtual Environment and Task Structure

Two virtual reality environments (desert, forest) were created with Multigen Creator (Multigen-Paradigm, CA). Both environments featured the same spatial structure, representing an iterated y-maze (Fig. 1A) consisting of 12 “decision points” (Fig. 1B): 6 at three-road crossings on a hexagonal ring and another 6 at the ends of 6 dead end streets. Each of the 12 decision points was marked with one distinctive landmark pertaining to one of 3 different semantic categories (e.g. animals, artwork, and vehicles, or musical instruments, tools, and furniture; Fig. 1C). Importantly, the landmarks were distributed over the map such that the 4 exemplars of each category

clustered together, thereby forming 3 semantic regions of the map. Participants always entered the maze at one of the dead ends facing towards the next crossing. They navigated the maze using the mouse buttons: pushing the left or right mouse button initiated a 60° turn in the corresponding direction and pushing the mouse wheel initiated a forward movement to the next decision point.

The task was presented on two adjacent monitors. The central monitor (30 inches) displayed the virtual environment and a small monitor at the side (15 inches) displayed the landmarks that showed the list of landmarks to be reached. Whenever a person crossed one of the landmarks of the list, this landmark disappeared from the list.

Statistical analyses

Analyses were based on repeated measures analysis of variance (ANOVA) including factors for the Retention conditions (Sleep/Wake) and the Test phase (Pretest, Posttest,). Additionally, Order factors (FirstSleep, FirstWake, FirstForest, FirstDesert) were introduced as group factors to control for potential effects of the order of sleep vs. wakefulness condition as well as the order of environment. Results from these analyses will be reported only if the respective Order main or interaction effects indicated significance. Generally, post-hoc tests were applied to clarify significant interaction effects. A p-value < 0.05 was considered significant. ANOVA were performed with ezANOVA (Lawrence 2013, <http://CRAN.R-project.org/package=ez>) implemented in R (R-Core Team, 2013) using orthogonal contrasts and type-III sums-of-squares. Effect sizes of simple between group comparisons were estimated using Cohen's *d* for unequal group sizes. Effect sizes of single ANOVA effects were estimated using generalized Eta-Square, η^2_G , (Bakeman, 2005; Olejnik & Algina, 2003).

Supplementary Results:

Target measures

Despite of an attempt to balance the design with respect to the order of Sleep and Wake condition as well as to the effect of the order of Environment (desert, forest), we included these design variables as nuisance variables in our statistical models. Note that all results presented in the main text were derived with the nuisance variables present in the models.

We found reliable effects of Sleep-Wake-order for route knowledge, where participants of the FirstWake group performed better than participants of the FirstSleep group ($F(1,34) = 7.81, p < 0.01, \eta^2 = 0.11$ for Sleep-Order main effect). Moreover, performance was generally better in the subject's second session ($F(1,34) = 22.53, p < 0.01, \eta^2 = 0.12$, for Sleep/Wake x FirstSleep/FirstWake which translates to a Session main effect).

Similarly, we observed a trend for a session effect for implicit region memory showing stronger preferences during the second session ($F(1,34) = 3.42, p = 0.07, \eta^2 = 0.02$) as well as a reliable effect of environment ($F(1,34) = 8.02, p < 0.01, \eta^2 = 0.005$, for FirstDesert/FirstForest x FirstSleep/FirstWake x Sleep/Wake, which translates to an Environment main effect).

Control measures

We did not observe any reliable effects for our control measures, which suggests that general performance levels were similar at all testing occasions. More specifically, there was no difference in subjective sleepiness between the Wake and Sleep condition at Pretest (Sleep: $Mdn = 3$, range = 1-6, Wake: $Mdn = 3$, range = 1-6) or Posttest (Sleep: $Mdn = 3$, range = 1-6, Wake: $Mdn = 3$, range = 1-5). Also, reaction times on the PVT (Sleep: Pretest $M = 334, SEM = 5$, Posttest $M = 330, SEM = 4$; Wake Pretest $M = 338, SEM = 5$, Posttest $M = 333, SEM = 5$) or word fluency at Posttest (Sleep: $M = 18.08, SEM = 0.79$; Wake: $M = 17.32, SEM = 0.79$) did not differ between the retention conditions.

4. EXTENSIONS

Some of the questions that arose during these experiments led to experiments conducted by students, e.g. as a Bachelor thesis. All of them are VR-experiments in which subjects have to solve wayfinding problems.

Two of them are conducted with the virtual reality headset Oculus Rift and test with navigation tasks whether sleep consolidation facilitates finding novel shortcuts in a previously explored environment. This would be an indicator that consolidation of generalized, allocentric representations of space also occurs during sleep.

The third experiment is an extension of the linguistically induced perception of hierarchical subdivision. In this study, adjectives are used as place cues, and subjects are primed visually before the navigation tasks.

4.1. The influence of sleep on navigation and memory consolidation⁵

Purpose:

Spatial navigation is a complex process that includes the integration of different sources of information and draws on different memory systems. Beneficial effects of sleep have been reported for navigation (e.g. Peigneux et al, 2004; Wamsley, 2010). Here, we investigate the influence of sleep on memory consolidation in the process of learning a new environment and establishing a generalized representation of it. The experimental environment was an iterated, hexagonal y-maze in a VR design, the same in both testing sessions (Gillner & Mallot, 1998; Fig. 1).

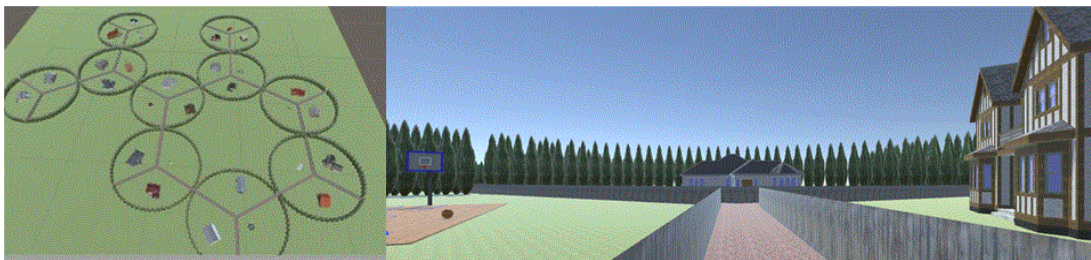


Figure 1: Left: Survey of the experimental environment. Right: View of an intersection.

Procedure:

The virtual environment was presented with the virtual reality headset Oculus Rift (DK2). The environment contained 10 places, each of them characterized by 2 houses and another typical inner-city object, e.g. a bus stop. Participants performed two sessions of wayfinding tasks. Sleep was manipulated through 12-hour-retention intervals: One group performed the first session in the evening and slept (at home) in between the two sessions, the other group was tested in the morning and in the evening of one day. Subjects had to navigate routes in the second session that could be performed in the shortest way by combining segments of the first session in new ways.

⁵ The candidate presented this work as a poster presentation: Schick, W.; Baumann, M.; Mallot, H.A. (2016). KogWis: Space for Cognition, Bremen.

After the second VR-session, subjects had to fill in a questionnaire and draw a sketch of the environment.

Participants

22 subjects were assigned to one of the two conditions. Each group consisted of 11 subjects (6 male, 5 female).

Variables of interest

The navigational performance was evaluated with the errors, the error rate, the relation between wrong and right decisions as well as the time it took to complete all tasks. An error was defined as passing a place that increased the distance to the next target. The error rate was the amount of wrong decisions in proportion to the total number of decisions. The sketch quality was measured by predefined criteria (e.g. the recall of the general layout, the number of correctly recalled places).

Results:

In both conditions, the error rate (Fig.2) and the time needed for the navigation tasks improved. For the time, this improvement was significant ($p < 0.05$, effect size: $\eta^2 = .813$). There were no time-of-day effects.

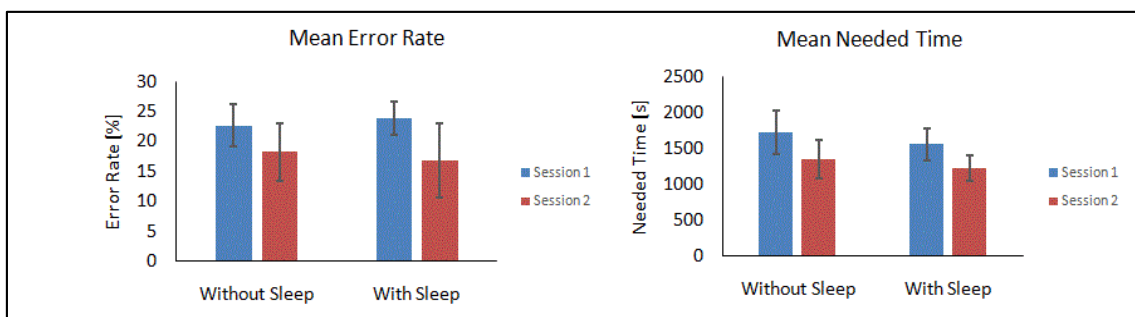


Figure 2: Mean navigation errors per session.

The quality of the sketches of the experimental environment after the second session correlated with the required time and the navigational errors ($r [20] = -0.575$; $p = 0.005$; Fig. 3).

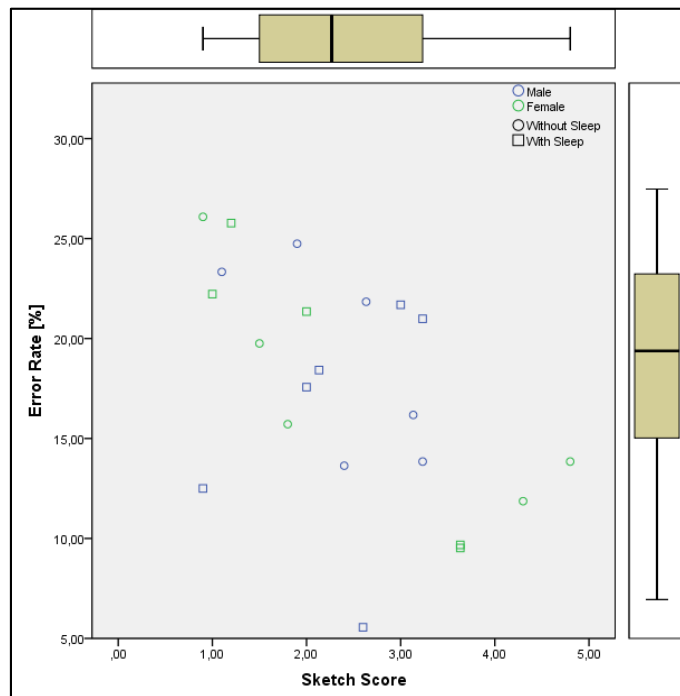


Figure 3: Correlation between the navigation performance, represented through the errors, and the quality of the sketches, represented through the scores in the fulfilment of predefined features.

Conclusions:

1. A lower error rate and thus an improvement of the navigational performance was observed in the second session in both conditions.
2. The quality of the navigation and the sketch map correlated.
3. A significant improving effect of sleep was not found.

Whether these findings indicate that sleep has no beneficial effect on the consolidation of survey knowledge or whether this is caused by a lower learning quality in the evening sessions cannot be deferred from these results.

More data is needed for a better differentiation between all factors influencing learning and memorization processes.

4.2. The impact of sleep on the consolidation of place and survey knowledge⁶

4.1. Abstract

A beneficial effect of sleep on consolidation of spatial memory was reported in several studies (e.g. 1, 2). Here, we investigated the influence of sleep on place and route memory and on the transfer into more abstract representations, like the emergence of survey knowledge.

The experiment was conducted with 20 participants in a virtual reality setup and presented with the Head-Mounted Display Oculus Rift (DK2). The subject was seated on a rotating chair and conducted the movements in the VR via an X-Box-360 Controller. Each subject had to participate in two sessions and was assigned to one of two groups (10 per group): The Wake-group performed the first session in the morning and the second in the evening of the same day; the Sleep-group had the first testing in the evening, slept at home, and performed the second session in the following morning. During the first session, subjects had to learn routes by following a guiding object to a target and finding the way back to the starting point on their own (wayfinding task). In the second session, the previously learned targets were presented in a different order, and the shortest route required the combination of familiar route segments in a new order. The required time and covered distance served as dependent variables for the navigational performance.

⁶ The candidate presented this work as a poster presentation at the COGSCI : Computational Foundations of Cognition. London: Schick, W., Holzmann, J., Mallot, H.A. (2017). *The impact of sleep on the formation and consolidation of spatial survey knowledge*; as well as at the Interdisciplinary College, Günne: Schick, W., Holzmann, J., Mallot, H.A. (2017): *The impact of sleep on the consolidation of place and survey knowledge*.

The alertness as well as the sleep quality in the night before the morning testing were evaluated with the Stanford sleepiness scale and the SF-A-R sleep-quality questionnaire.

We found a significant difference between the Sleep- and the Wake-group concerning the learning success when comparing the performances of the first and the second session:

a 2x2 Anova with the factors Session-Number (1 and 2) and Group (Sleep and Wake) showed an impact on the covered distances ($F = 12,386$; $p = 0,002$, $\eta^2 = 0,408$).

4.2. Introduction

A beneficial effect of sleep on the consolidation of hippocampus-dependent memories such as spatial memory was found in several studies (e.g. Diekelmann & Born, 2010). It is assumed that in this process, contents can also undergo a transformation into more abstract representations, for example the attribution of objects to categories (Friedrich et al. 2015).

As for human spatial behavior, the reported effects of sleep are mixed, as improvements of different forms of spatial knowledge have been reported (*navigation + survey knowledge*: Ferrara et al., 2008.; Peigneux et al., 2004; Nguyen et al., 2013; *route learning*: Hartley et al., 2003; Wamsley et al., 2010; *landmark knowledge*: Javadi et al., 2015; *consolidation of spatial and contextual memories*: Rauchs et al., 2008).

In this pilot study, we investigated the establishment of mental spatial representations and the role of sleep in this process with active navigation in a virtual reality.

4.3. Methods

The virtual environment (VE) was an inner city road network, established with the software City Engine from ESRI (Fig. 1). It was displayed presented with the Head-Mounted Display Oculus Rift (DK2). The subject was seated on a rotating chair and conducted the movements in the VR via an X-Box-360 Controller (Fig. 2). Movement speed and gaze direction were controlled with the left joystick, the right one was used for turns. The instructions and the target points were superimposed on the environment

and disappeared when the subject pressed the A-button to confirm that he had read the text.

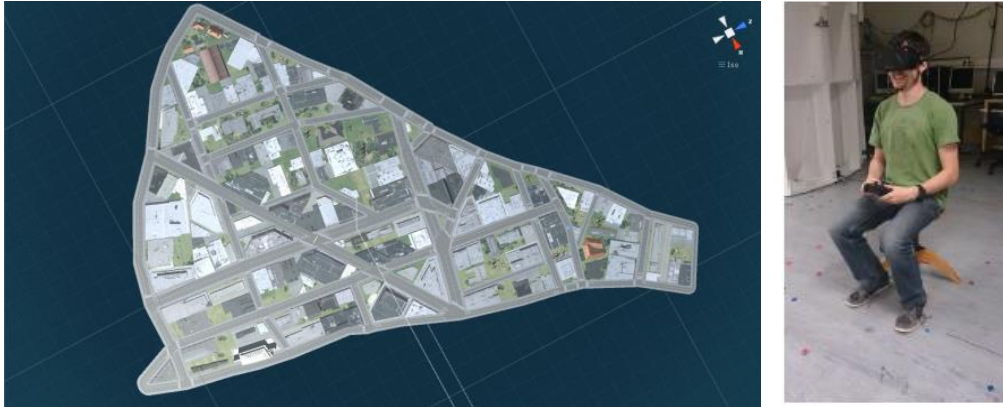


Figure 1: Aerial view of the virtual environment. Figure 2: The experimental setup.

Each subject was assigned to one of two groups and participated in two sessions: The Wake group performed the first session in the morning and the second in the evening of the same day; the Sleep group completed the first session in the evening, slept at home, and performed the second one in the following morning (Table 1).

	Wake Group	Sleep Group
1 st session	declaration of consent task instructions SF – A - R sleep – quality questionnaire	declaration of consent task instructions
Retention interval (12 hours)	Awake	Sleep (at home)
2 nd session	task instructions Stanford sleepiness scale drawing of the sketchmap	task instructions Stanford sleepiness scale SF – A - R sleep – quality questionnaire drawing of the sketchmap

Table 1: Experimental procedure

A starting point and five target places were defined in the VE (see Fig. 4). During the first session, subjects had to learn routes by following a guiding object to a target (Fig. 3 + 4) and finding the way back to the starting point on their own (return task). In the outbound routes, the guiding object moved with constant speed but waited if the distance to the subject exceeded 6 meters. In the inbound (return) routes, the guiding object was absent, but reappeared if the subject did not find the starting point on his own within 5 minutes.



Figure 3: Street view with the guiding object. Figure 4: Target Nr. 1.

In the second session, the guiding object was absent. It started with 5 minutes of free exploration time. Then, the targets from session 1 were presented in a different order, and the subjects had to find the shortest path (wayfinding task). This required the combination of familiar route segments in a new order. The route length grew in the course of the experiment, which comprised 10 routes. Each target was presented twice, but from different starting points (Figure 5).

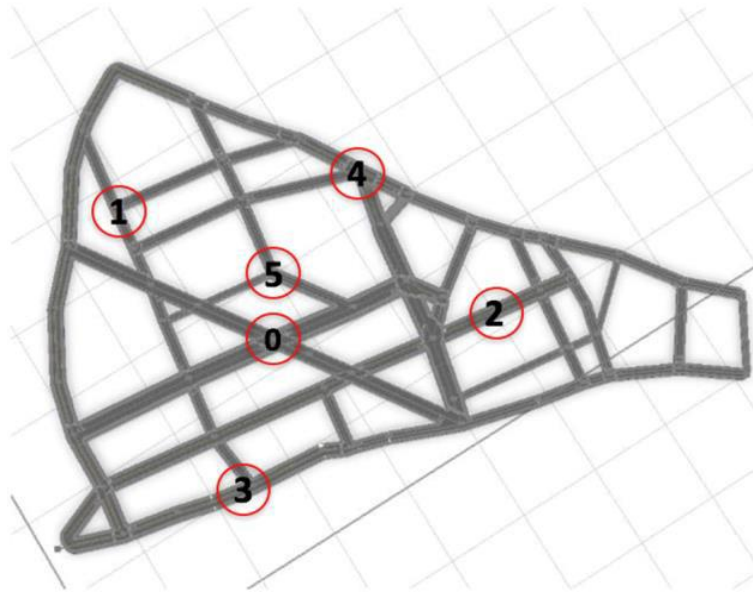


Figure 5: Map with the starting point (0) and the targets (1 – 5).

Variables of interest

The required time and covered distance served as dependent variables for the navigational performance. For both variables, route-specific minima were defined: the shortest path connecting starting point and target was the minimum for the path length; the time minimum was the time needed to complete this path in a continuous movement. The measurement began once the subject pressed the joystick and started to move. From the actual values and these minima we calculated the percentage above optimum (PAO) (*distance*: $[(\text{actual length} - \text{optimal length}) / \text{optimal length} * 100]$; *time*: $[(\text{actual time} - \text{optimal time}) / \text{optimal time} * 100]$).

After the second session, the subjects were asked to draw a sketch of the environment: The alertness as well as the sleep quality in the night before the morning testing were evaluated with the Stanford sleepiness scale and the SF-A-R sleep-quality questionnaire (Görtelmeyer, 1981).

4.4. Results

Navigational performance

As can be seen from the Figures 6 and 8, both travelled distance and required time decreased in the second session of the Wake as well as the Sleep condition. However this difference reached significance only for the Sleep group (distance: $p=0.002$; time: $p=0.004$) while the learning effects were not significant in the Wake group. For the distance measurements, a 2-by-2 ANOVA of session vs. group revealed a significant main effect of session ($F = 12.386$; $p = 0.002$; $\eta^2 = 0.408$), but no main effect of group and also no significant interaction. For the time measurements, the same ANOVA revealed no significant effects. We found a significant difference between the Sleep and the Wake group concerning the learning success when comparing the performances of the first and the second session (Fig. 6 and 8).

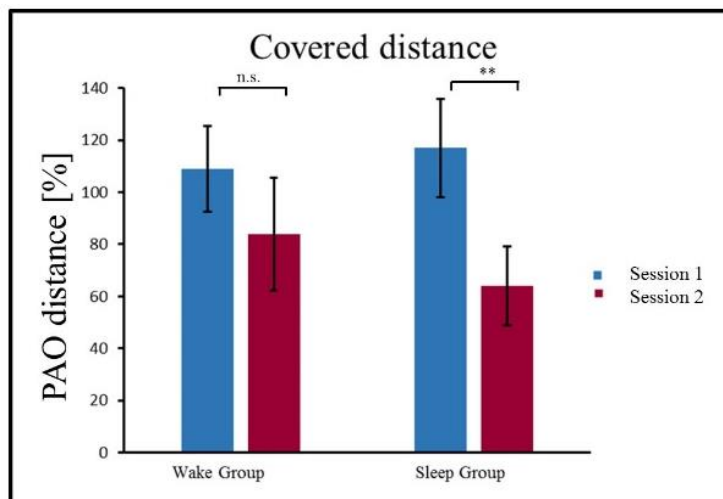


Figure 6: Covered distances (PAO) of the mean, incl. standard error).

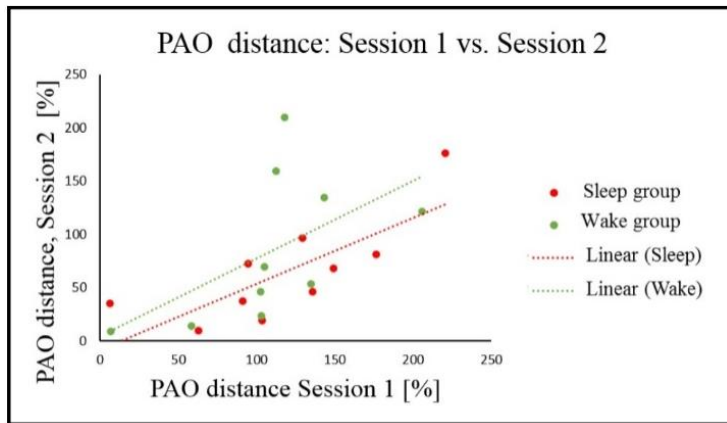


Figure 7: Covered distances (PAO, for each subject, Sleep and the Wake group in both sessions with regression lines.

We found a positive correlation between the covered distances in both sessions on subject level: participants who navigated well in the first session also did so in the second one (Spearman-correlation: $r(18) = 0.734$; $p < 0.05$). Note that the regression lines for the Sleep group fall below the one for the Wake group, as is consistent with the large reduction of travel distance in session 2 in the Sleep group (Fig. 7).

Although the overall pattern for required times looks similar, the effect did not reach significance here ($F = 2.985$; $p = 0.101$; $\eta^2 = 0.142$; Fig. 8).

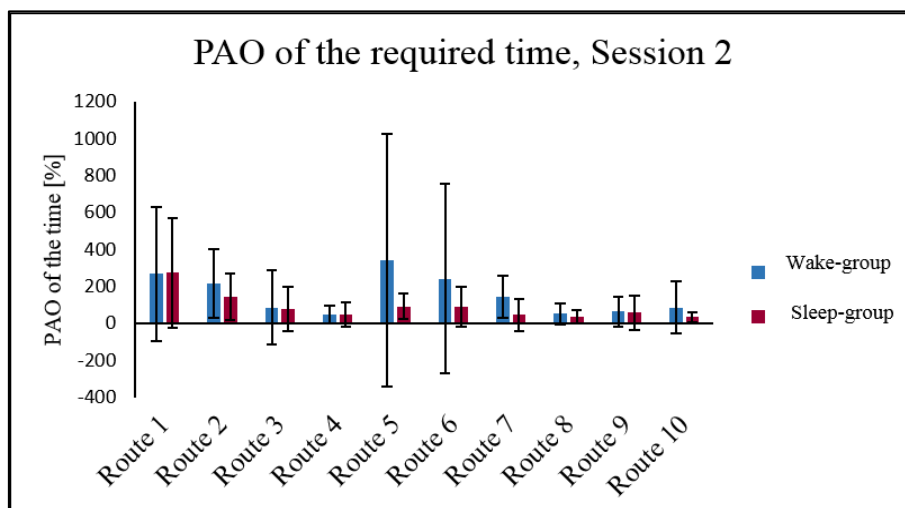


Figure 8: Required time (PAO), shown per group and per session.

Again, there was a positive correlation between subjects' performance in the first and in the second session: subjects who completed the tasks fast in the first session also did so in the second one, and the Sleep group covered shorter distances than the Wake group (Spearman-Correlation: $r(18) = 0.734$; $p < 0.05$; Fig. 9).

There were no interactions between the factors Sleep and Group, neither for the covered distance ($F = 0.65$; $p = 0.225$; $\eta^2 = 0.081$) nor for the required time ($F = 1.046$; $p = 0.235$; $\eta^2 = 0.077$).

Both groups showed an improvement regarding the time and the travelled distances in the second session, but only for the Sleep group did this become significant.

We also considered a possible influence of the daytime of the test sessions, as the time of the day and circadian rhythms influence cognitive performance (Pomplun et al, 2012). The Sleep group passed the first session in the evening, the Wake group in the morning.

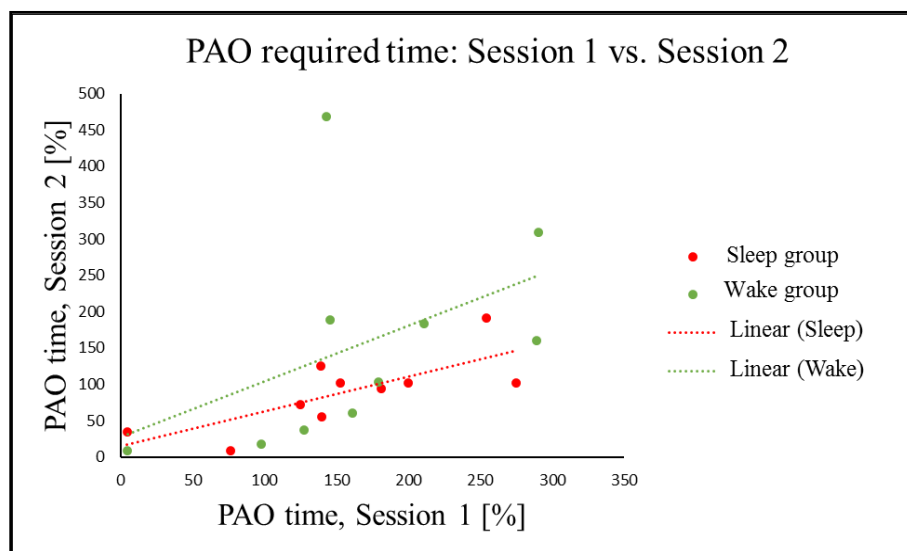


Figure 9: Required time (PAO), Session 1 vs. Session 2 per subject, incl. regression lines.

We did not find an effect of the daytime, neither for the distance (t-test: $p = 0.465$) nor for the required time (t-test: $p = 0.381$).

A gender effect was not found either (distance: $F = 4.001$; $p = 0.061$; $\eta^2 = 0.182$; time: $F = 1.846$; $p = 0.191$; $\eta^2 = 0.093$).

Sketch score

After the second session, subjects were asked to draw a sketchmap of the experimental environment. It may be the case that people with a better visual memory draw better maps, as they remember more features of the environment, which also facilitates the completion of navigation tasks.

The drawing of an accurate sketch requires both the recognition of the environmental layout as well as the recall of places and the routes connecting them. For each of these features – number of recalled places, position of the places, connecting routes – one point could be reached, resulting in a maximum score of 3 points. We considered the sketch map as a measurement for both, and were interested in the correlation with the direct behavioral navigational variables, distance and time. The evaluation of the sketches drawn after the second session showed a correlation between high-quality sketches and navigational performance (correlation with the distance: $r(18) = -0.508$; $p = 0.022$; Fig. 10):

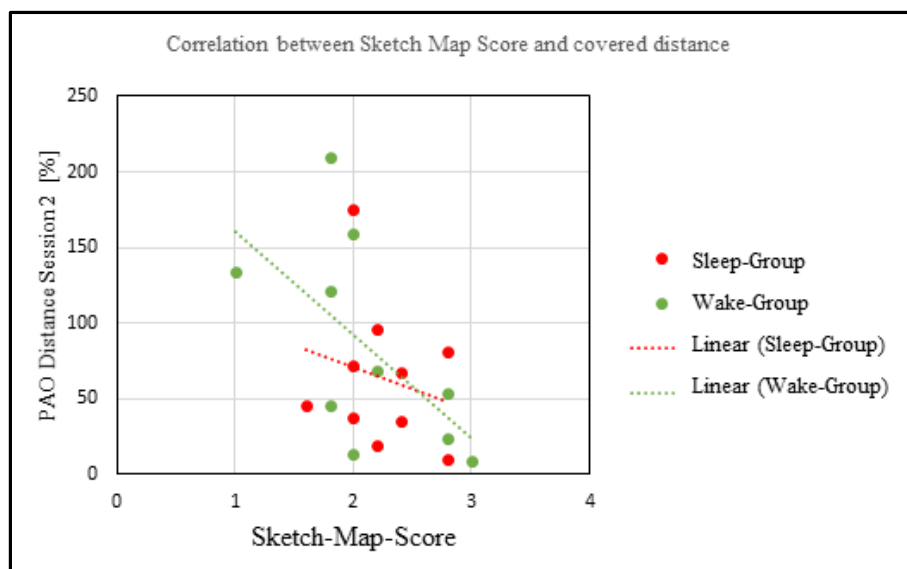


Figure 10: PAO of the time, Session 1 vs. Session 2, per subject, with regression lines).

The sketch map can also show whether some environmental features that are more likely to be used as landmarks than others (Fig. 11 + 12).

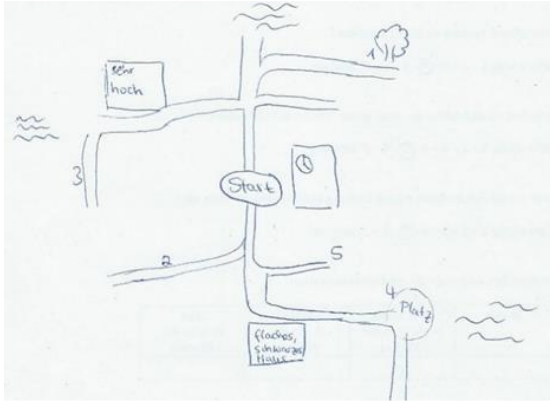


Figure 11: Sketch map, Wake Group,
Score: 1.8

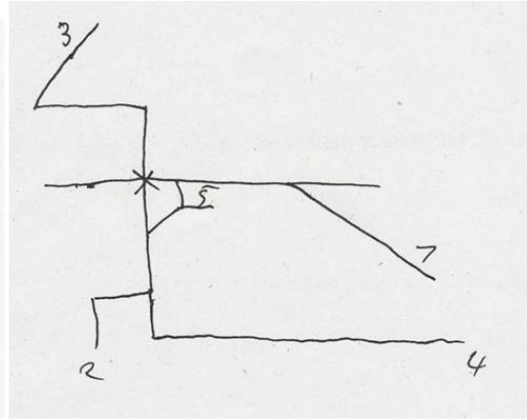


Figure 12: Sketch map, Sleep Group,
Score: 2.4

4.5. Discussion

It was the aim of this experiment to detect possible beneficial effects of sleep on spatial memory, namely on the integration of cues on landmark and route level into a more abstract, generalized survey representation. During sleep, brain areas active during navigation are reactivated, namely the hippocampus, a structure that is important for memory consolidation and spatial information processing (Ekstrom et al., 2003). A consolidating effect on spatial knowledge has been reported (Ferrara et al., 2008), also, an improving effect on explicit route knowledge (Noack et al., 2017).

Here, subjects performed 2 sessions of navigation tasks within 12 hours, and were assigned to one of two groups: the Wake group and the Sleep group.

The subjects of the Sleep group solved the navigational tasks of the second session – combining familiar route segments in an unfamiliar way and thus creating a shortcut to the target point – both faster and more precisely than the subjects of the Wake Group. The learning effect was stronger, though we did not find a statistically significant effect with the ANOVA. The better quality of the sketches of the Sleep group also suggests a beneficial effect on memory consolidation.

Several factors are likely to have contributed to the big variance concerning the detection and use of novel shortcuts:

First, there were substantial differences concerning the familiarity with the Head-Mounted Display and the navigation by joystick. Subjects who were not at ease with the handling of the display and the setup, could focus less on the environment and the places than subjects familiar with such gear. Humans use different navigational strategies (Wolbers & Hegarty, 2010) and landmarks and regions are features in the environment that are encoded very early during exploration of an unfamiliar environment (Wiener, Schnee, Mallot, 2004). The content of spatial memory is not one homogeneous whole but an assembly of hierarchically structured subdivisions (e.g. Wiener & Mallot, 2003). In a following experiment, we would test more subjects, and separate them in accordance to the time spent with computational games.

Second, personal preferences for navigational strategy also complicate the attribution of navigational success completely to the existence of a generalized mental representation. Due to the number of different strategies, e.g. landmark-based-navigation, navigation based on left-right-choices, as well as the differences in preferences between subjects, it is hard to judge whether and to what extent the subjects had formed a generalized survey representation, if they just took a wrong turn, or if they had no concept of the virtual environment at all. Some subjects did not use novel shortcuts at all but just combined the previously learned routes, some routes were quite simple and could be performed solely with path integration.

In future studies, both an assessment of the preferred navigational strategy as well as of general orientation skills (e.g. Santa Barbara Sense of Direction Questionnaire) would be means to eliminate confounding factors.

4.6. Conclusions

We found that the subjects in the Sleep group navigated better and recalled more features of the experimental environment, which indicates a supportive effect of sleep both on the formation and recall of survey-knowledge.

4.3. Visual priming and the formation of regionalized representations of space

Abstract

This experiment was inspired by the findings from Wiener & Mallot (2003), who found perception of regional subdivision induced through landmarks belonging to different semantic categories, as well as the study from Schick, Halfmann and Mallot, (2015) who found that this effect can also be induced through verbal cues. They used nouns, in the current study, the cues were adjectives and the subjects were primed with a picture-sorting task beforehand. The question was whether the associations between the adjectives in the priming pictures would be transferred and integrated into subjects' perception of the environment. If this happens, a similar bias on the route choice as well as reference to the regionalization in the questionnaire after the experiment, the sketch-map, or both should be found.

Methods

Subjects were assigned to one of two priming groups and had to assort the pictures (from open-source picture libraries) to categories they had to define themselves beforehand. The pictures showed natural scenes in which the qualities described by the adjectives were contained. (See Fig. 1 and Table 1).

Then, an exploration and a training phase in the virtual environment followed. Each of the places was characterized by a name displayed on three signs.

In the test phase, subjects had to find the shortest route connecting the three places that were the targets. The test routes allowed for two equidistant solutions that only differed in the number of the - invisible - regional boundaries to be transgressed.

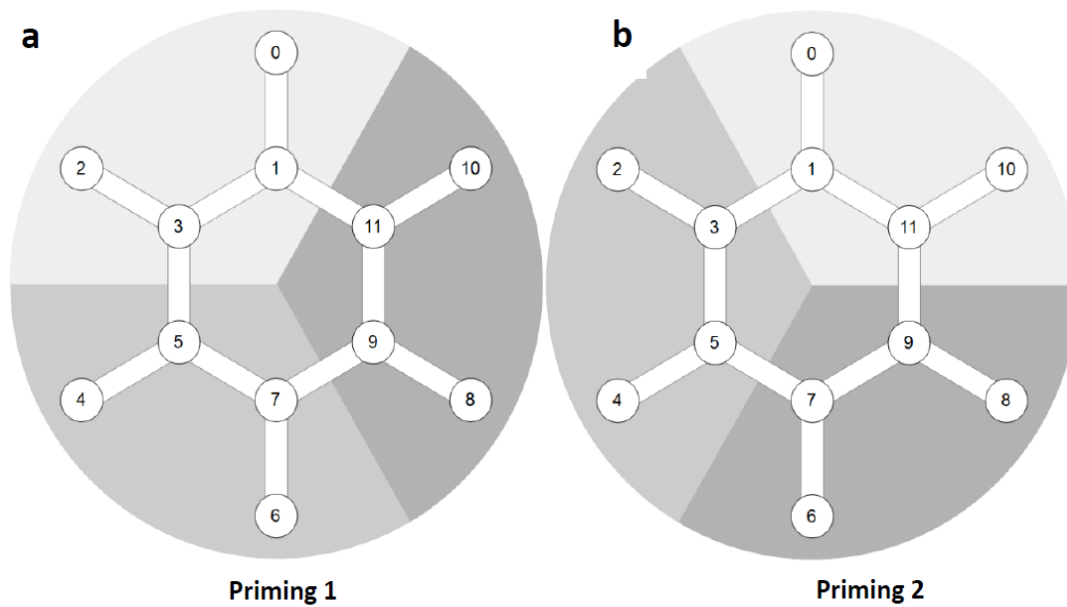


Figure 1: Regional subdivision for both priming conditions

<i>Scenes Priming 1</i>	<i>Adjectives</i>
Misty lake	dark, grey, misty, wet
Snowy landscape	bare, cold, powdery, white
Sunny beach	glistening, light, sandy, warm
<i>Scenes Priming 2</i>	<i>Adjectives</i>
Autumn mist	bare, cold, dark, misty
Winter impressions	glistening, light, powdery, white
Grey beach	Grey, sandy, warm, wet

Table 1: Place cues and the corresponding priming scenes

Participants

14 subjects were tested (8 m, 6 f, mean age: 27,25 years). All of them spoke German as maternal language or on a comparable level. Two of them did not complete the experiment, their data is not considered in the analysis.

Results

A two-sample t-test did not show differences in the navigation performance between the priming groups. A preference for one of the equidistant route types was not found either. There was a correlation between the quality of the sketch map and the navigation: good navigators drew better sketches. Also, some of the sketches included regional boundaries.

Conclusions

The priming did not influence route choice, but the intended grouping was found in some of the questionnaires. Possibly, the degree of abstraction was too high. Ideas for further studies would be the usage of nouns instead of adjectives, as well as choosing scenes in which the attribution to one of the three intended categories is very clear and obvious.

5. REFERENCES

- Acredolo, L., & Boulter, L. (1984). Effects of hierarchical organization on children's judgments of distance and direction. *Journal of Experimental Child Psychology*, 37, 409–425.
- Allen, G. (1981). A developmental perspective on the effect of “subdividing” macrospatial experience. *Journal of Experimental Psychology: Human Learning and Development*, 7, 120–132.
- Appleyard, D. (1969). Why buildings are known. A predictive tool for architects and planners. *Environment and behaviour*, 1(2), 131-156.
- Aschenbrenner, S., Tucha, O., Lange, K.W. (2000). *Regensburger Wortflüssigkeits-Test: RWT*. Verlag für Psychologie.
- Avraamides, M. N., Loomis, J. M., Klatzky, R., & Golledge, R. C. (2004). Function equivalence of spatial representations derived from vision and language: evidence from allocentric judgements. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 30, 801 - 814.
- Bahrack, H. P. (1983). The cognitive map of a city: Fifty years of learning and memory. *Psychology of Learning and Motivation*, 17, 125 - 163.
- Bailenson, J., Shum, M., & Uttal, D. (1998). Road climbing: Principles governing asymmetric route choices on maps. *Journal of Environmental Psychology*, 18, 251–264.
- Bailenson, J. N., Shum, M., & Uttal, D. (2000). The initial segment strategy: A heuristic for route selection. *Memory & Cognition*, 28, 306–318.
- Bailey, S. M. (2008). *Content assessment in intelligent computer-aided language learning: Meaning error diagnosis for English as a second language* (Unpublished doctoral dissertation). The Ohio State University.
- Bakeman R. (2005). Recommended effect size statistics for repeated measures designs. *Behavior Research Methods* 37 (3), 379-384.
- Balaguer J., Spiers H., Hassabis D., Summerfield C. (2016). Neural Mechanisms of

- Hierarchical Planning in a Virtual Subway Network. *Neuron* 90, 893-903. doi:10.1016/j.neuron.2016.03.037.
- Baroni, M., Bernardini, S., Ferraresi, A., & Zanchetta, E. (2009). The WaCky wide web: a collection of very large linguistically processed web-crawled corpora. *Language Resources & Evaluation*, 43 , 209 - 226.
- Barsalou, L. W. (2008). Grounded cognition. *Annual Review of Psychology*, 59 , 617 - 645.
- Basten K., Meilinger T., Mallot H.A. (2012). Mental travel primes place orientation in spatial recall. Lecture Notes in Artificial Intelligence. Stachniss C., Schill K., & Uttal D. (Ed.) *Spatial Cognition*, 7 (463), 378-385.
- Baumann O., Skilleter A.J., & Mattingley J.B. (2011). Short-Term Memory Maintenance of Object Locations during Active Navigation: Which Working Memory Subsystem Is Essential? *PLoS one* 6(5). doi.org/10.1371/journal.pone.0019707
- Binder, J., Westbury, C., McKiernan, K., Possing, E., & Medler, D. (2005). Distinct brain systems for processing concrete and abstract concepts. *Journal of Cognitive Neuroscience* 17(6), 905-917.
- Borghi, A. M., Binkofski, F., Castelfranchi, C., Cimatti, F., Scorolli, C., & Tummolini, L. (2017). The challenge of abstract concepts. *Psychological Bulletin*, 143 , 263 - 292.
- Bower, G. H., & Morrow, D. G. (1990). Mental models in narrative comprehension. *Science*, 247 , 44 - 48.
- Carbon C.C., Leder H. (2005). The wall inside the brain: overestimation of distances crossing the former Iron Curtain. *Psychonomic Bulletin & Review*, 12(4), 746-750.
- Carruthers, P. (2002). The cognitive functions of language. *Behavioral and Brain Sciences*, 2(:6), 657 – 726.
- Cohen, R., Baldwin, L., & Sherman, R. C. (1978). Cognitive maps of naturalistic setting. *Child Development*, 49, 1216–1218.
- Couclelis, H., Golledge, R. G., Gale, N., & Tobler, W. (1987). Exploring the anchorpoint hypothesis of spatial cognition. *Journal of Environmental*

Psychology, 7, 99–122.

- Denis, M., Mores, C., Gras, D. et al. (2014). Is Memory for Routes Enhanced by an Environments' Richness in Visual Landmarks? *Spatial Cognition & Computation* 14(4), 284-305.
- Diba, K. & Buzsaki, G. (2007). Forward and reverse hippocampal place-cell sequences during ripples. *Nature Neuroscience* 10(10), 1241-1242.
- Diekelmann S., Born J. (2010). The memory function of sleep. *Nature Reviews Neuroscience*, 114-126. doi:10.1038/nrn2762.
- Diekelmann S., Born J., Wagner U. (2010). Sleep enhances false memories depending on general memory performance. *Behavioural Brain research* 208(2), 425-429. doi:10.1016/j.bbr.2009.12.021.
- Dinges, D.F., Powell, J.W. (1985). Microcomputer analyses of performance on a portable, simple visual RT task during sustained operations. *Behavior Research Methods, Instruments, & Computers*, 17 (6), 652-655.
- Dudai Y., Karni A., Born J. (2015). The Consolidation and Transformation of Memory. *Neuron* 88, 20-32. doi:10.1016/j.neuron.2015.09.004.
- Durrant S.J., Cairney S.A., Lewis P.A. (2013). Overnight consolidation aids the transfer of statistical knowledge from the medial temporal lobe to the striatum. *Cerebral Cortex* 23, 2467-2478. doi:10.1093/cercor/bhs244.
- Durrant S.J., Taylor C., Cairney S., Lewis P.A. (2011). Sleep-dependent consolidation of statistical learning. *Neuropsychologia* 49, 1322 -1331. doi:10.1016/j.neuropsychologia.2011.02.015.
- Eichenbaum, H. (2000). Hippocampus: Mapping or memory? *Current biology* 10(21), 785-787.
- Eichenbaum, H. (2017). The role of the hippocampus in navigation is memory. *Journal of Neurophysiology*, 117(4), 1785-1796.
- Ekstrom, A. D., et al. (2003). Cellular networks underlying human spatial navigation. *Nature* 425.6954, 184-188.
- Ferrara M., Iaria G., Tempesta, D., Curcio, G., Moroni, F., Marzano, C., De Gennaro, L., Pacitty, C. (2008). Sleep to find your way: The role of sleep in the consolidation of memory for navigation in humans. *Hippocampus* 18(8), 844-

851. doi:10.1002/hipo.20444.

- Firth, J. R. (1957). *Papers in linguistics, 1934 - 1951*. Oxford University Press.
- Fischer S., Drosopoulos S., Tsen J., Born J. (2006). Implicit learning - explicit knowing: a role for sleep in memory system interaction. *Journal of Cognitive Neuroscience* 18(3), 311-319.
- Friedman, A., Kerkman, D. D., Brown, N. R., Stea, D., & Cappello, H. M. (2005). Cross-cultural similarities and differences in North Americans' geographic location judgments. *Psychonomic Bulletin & Review*, 12, 1054-1060.
- Friedman, A., & Montello, D. (2006). Global - scale location and distance estimates: Common representations and strategies in absolute and relative judgments. *Journal of Experimental Psychology: Learning, Memory and Cognition*, 32, 333 - 346.
- Friedrich M., Wilhelm I., Born J., Friederici A.D. (2015). Generalization of word meanings during infant sleep. *Nature Communications*, 6. doi:10.1038/ncomms7004.
- Fyhn, M., Molden, S., Witter, M.P., Moser, E.I., Moser, M.B. (2004). Spatial representation in the entorhinal cortex. *Science* 305(5688), 1258-1264.
- Gallese, V., Keysers, C., & Rizzolatti, G. (2004). A unifying view of the basis of social cognition. *Trends in Cognitive Sciences*, 8, 396 - 403.
- Garden, S., Cornoldi, C., & Logie, R. H. (2002). Visuo-spatial working memory in navigation. *Applied cognitive psychology*, 16(1), 35-50.
- Giesbrecht, B., Camblin, C. C., & Swaab, T. Y. (2004). Separable effects of semantic priming and imageability on word processing in human cortex. *Cerebral Cortex*, 14(5), 521-529.
- Gillner, S., Mallot, H.A. (1998). Navigation and acquisition of spatial knowledge in a virtual maze. *Journal of Cognitive Neuroscience*, 10, 445-463.
- Gillner S., Weiss A.M., Mallot H.A. (2008): Visual Homing in the Absence of Feature-Based Landmark Information. *Cognition* 109:105-122.
- Goldberg, R. F., Perfetti, C. A., & Schneider, W. (2006). Distinct and common cortical activations for multimodal semantic categories. *Cognitive, Affective & Behavioral Neuroscience*, 6(3), 214-222.

- Golledge, R. G. (1999). Human wayfinding and cognitive maps. In Golledge, R.G., (Ed.), *Wayfinding behavior: Cognitive mapping and other spatial processes*. Johns Hopkins University Press, 5–45.
- Görtelmeyer, R. (1981). *Schlaffragebogen SF-A und SF-B. Internationale Skalen für Psychiatrie*. Beltz, Weinheim.
- Görtelmeyer R. (2011). *SF-A/R und SF-B/R: Schlaffragebogen A und B*. Hogrefe.
- Hardiess G., Basten K., Mallot H.A. (2011). Acquisition vs. memorization trade-offs are modulated by walking distance and pattern complexity in a large scale copying paradigm. *PLoS ONE*, 6(4). doi.org/10.1371/journal.pone.0018494.
- Hardiess, G., Halfmann, M., & Mallot, H.A. (2014). Explicit place-labeling supports spatial knowledge in survey, but not in route navigation. In: *Cognitive Processing*, 15 (Suppl.1), 44.
- Hartley T., Lever C., Burgess N., O'Keefe J. (2014). Space in the brain: how the hippocampal formation supports spatial cognition. *Philosophical Transactions of the Royal Society*, 369, 20120510. doi:10.1098/rstb.2012.0510.
- Hartley T., Maguire E.A., Spiers H.J., Burgess N. (2003). The well-worn route and the path less traveled: distinct neural bases of route following and wayfinding in humans. *Neuron*, 37, 877-888.
- Hauser, M. D., Chomsky, N., & Fitch, W. T. (2002). The faculty of language: what is it, who has it, and how did it evolve? *Science*, 298 , 1569 - 1579.
- Hearst, M. A. (1997). TextTiling: Segmenting text into multi-paragraph subtopic passages. *Computational Linguistics*, 23 , 33 - 64.
- Hegarty M., Richardson A.E., Montello D.R., Lovelace K., Subbiah I. (2002). Development of a self-report measure of environmental spatial ability. *Intelligence*, 30, 425-447. doi:10.1016/S0160-2896(02)00116-2.
- Henrich, A. (2008). *Information retrieval 1. Grundlagen, Modelle und Anwendungen*. Lehrstuhl für Medieninformatik, University of Bamberg, Germany. Retrieved from <https://www.uni-bamberg.de/minf/ir1-buch/>
- Hirtle SC, Jonides J. (1985). Evidence of hierarchies in cognitive maps. *Memory & Cognition*, 13(3) , 208-217. doi:10.3758/BF03197683.
- Hoddes E., Zarcone V., Dement W. (1972). Development and use of Stanford

- Sleepiness scale (SSS). *Psychophysiology*, 9, 150.
- Holcomb, P. J., Kounios, J., Anderson, J. E., & West, W. C. (1999). Dual-coding, context-availability, and concreteness effects in sentence comprehension: an electrophysiological investigation. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 25(3), 721 -742.
- Horne J.A. (1988). Sleep loss and "divergent" thinking ability. *Sleep*, 11, 528-536.
- Huttenlocher, J., Hedges, L. V., & Duncan, S. (1991). Categories and particulars: Prototype effects in estimating spatial location. *Psychological Review*, 98, 352-376.
- Iaria G., Petrides M., Dagher, A., Pike, B., Bohbot, V.D. (2003). Cognitive strategies dependent on the hippocampus and caudate nucleus in human navigation: variability and change with practice. *Journal of Neuroscience*, 23, 5945-5952.
- Inostroza M., Born J. (2013). Sleep for preserving and transforming episodic memory. *Annual Review of Neuroscience*, 36, 79-102. doi:10.1146/annurev-neuro-062012-170429.
- Javadi A.H., Tolat A., Spiers H.J. (2015). Sleep enhances a spatially mediated generalization of learned values. *Learning & Memory*, 22, 532-536. doi:10.1101/lm.038828.115.
- Janzen, G., Hermann, T., Katz, S., Schweizer, K. (2000). Oblique angled intersections and barriers: Navigating through a virtual maze. *Spatial Cognition II, Volume 1849*, 277-294.
- Janzen, G., & Weststeijn, C. G. (2007). Neural representation of object location and route direction: an event-related fMRI study. *Brain Research*, 1165, 116-125.
- Janzen, G., Wagensveld, B., & van Turenout, M. (2007). Neural representation of navigational relevance is rapidly induced and long-lasting. *Cerebral cortex*, 17(4), 975-981.
- Juliani, A. W., Bies, A. J., Boydston, C. R., Taylor, R. P., & Sereno, M. E. (2016). Navigation performance in virtual environments varies with fractal dimension of landscape. *Journal of Environmental Psychology*, 47, 155 - 165.
- Kosslyn S.M., Pick H.L., Jr., Fariello G.R. (1974). Cognitive maps in children and men. *Child Development* 45, 707-716.

- Lakoff, G. (1987). *Women, fire, and dangerous things. What categories reveal about the mind*. Chicago and London: The University of Chicago Press.
- Lewis P.A., Durrant S.J. (2011). Overlapping memory replay during sleep builds cognitive schemata. *Trends in cognitive sciences*, 15(8), 343-351. doi:10.1016/j.tics.2011.06.004.
- Louwerse, M. M. (2008). Embodied relations are encoded in language. *Psychonomic Bulletin & Review*, 15(4), 838-844.
- Louwerse, M. M., & Jeuniaux, P. (2008). Language comprehension is both embodied and symbolic. *Symbols and embodiment: Debates on meaning and cognition*, 309-326.
- Louwerse, M.M., Jeuniaux, P. (2010). The linguistic and embodied nature of conceptual processing. *Cognition*, 114, 96-104.
- Louwerse, M. M. (2011a). Symbol interdependency in symbolic and embodied cognition. *Topics in Cognitive Science*, 3, 273–302.
- Louwerse, M., & Connell, L. (2011b). A taste of words: Linguistic context and perceptual simulation predict the modality of words. *Cognitive Science*, 35(2), 381-398.
- Louwerse, M. M., & Benesh, N. (2012). Representing spatial structure through maps and language: Lord of the Rings encodes the spatial structure of Middle Earth. *Cognitive science*, 36(8), 1556-1569.
- Maguire, E., Woollet, K., Spiers, H.J. (2006). London taxi drivers and bus drivers: A structural MRI and neuropsychological analysis. *Hippocampus*, 16(12), 617-629.
- Majid, A., Bowerman, M., Kita, S., Haun, D. & Levinson, S.C. (2004). Can language restructure cognition? The case for space. *TRENDS in Cognitive Science*, 8(3), 108-114.
- Maki, R. (1981). Categorization and distance effects with spatial linear orders. *Journal of Experimental Psychology: Human Learning and Memory*, 1, 15–32.
- Manning, C., & Schütze, H. (1999). *Foundations of statistical natural language processing*. Cambridge, MIT press.
- Marshall, L., Born, J. (2007). The contribution of sleep to hippocampus-dependent

- memory consolidation. *Trends in Cognitive Sciences*, 11(10), 442-450.
- McNamara T.P. (1986). Mental representations of spatial relations. *Cognitive Psychology* 18, 87-121.
- McNamara, T.P., Hardy, J.K. & Hirtle S.C. (1989). Subjective Hierarchies in Spatial Memory. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 15(2), 211-227.
- Meilinger, T. (2008). The network of reference frames theory: a synthesis of graphs and cognitive maps. *Lecture Notes in Artificial Intelligence*, 5248 , 344 - 360.
- Meilinger, T., Knauff, M., & Bühlhoff, H. H. (2008). Working memory in wayfinding - a dualtask experiment in a virtual city. *Cognitive Science*, 32, 755 - 770.
- Mellet, E., Bricogne, S., Crivello, F., Mazoyer, B., Denis, M., & Tzourio-Mazoyer, N. (2002). Neural basis of mental scanning of a topographic representation built from a text. *Cerebral Cortex*, 12 , 1322 - 1330.
- Mellet, E., Tzourio, N., Denis, M., and Mazoyer, B. (1998). Cortical anatomy of mental imagery of concrete nouns based on their dictionary definition. *Neuroreport* 9, 803-808.
- Miller, J., Neufang, M., Solway, A., Brandt, A., Trippel, M., Mader, I., Hefft, S., Merkow, M., Polyn, S.M., Jacobs, J., Kahana, M.J., & Schulze-Bonhage, A. (2013). Neural Activity in Human Hippocampal Formation Reveals the Spatial Context of Retrieved Memories. *Science*, 342, 1111- 1114.
- Moeser, S. D. (1988). Cognitive mapping in a complex building. *Environment and Behavior*, 20(1), 21-49.
- Montello, D. R. (1993). Scale and multiple psychologies of space. *Lecture Notes in ComputerScience*, 716, 312 - 321.
- Montello, D. R., Goodchild, M. F., Gottsegen, J., & Fohl, P. (2003). Where's downtown? Behavioral methods for determining referents of vague spatial queries. *Spatial Cognition & Computation*, 3(2-3), 185-204.
- Mormann, F., Ison, M. J., Quiroga, R. Q., Koch, C., Fried, I., & Kreiman, G. (2014). Visual Cognitive Adventures of Single Neurons in the Human Medial Temporal Lobe. *Single Neuron Studies of the Human Brain: Probing Cognition*. MIT Press, 121-151.

- Mou, W. M., & McNamara, T. P. (2002). Intrinsic frames of reference in spatial memory. *Journal of Experimental Psychology: Learning, Memory and Cognition*, 28, 162 - 170.
- Moser E.I., Roudi, Y., Moser, M.B., (2014) Network mechanisms of grid cells. *Philosophical Transactions of the Royal Society B*, 369,1635.
- Nelson, T., & Chaiklin, S. (1980). Immediate memory for spatial location. *Journal of Experimental Psychology: Human Learning and Memory*, 6 (5), 529–545.
- Newcombe, N., & Liben, L. (1982). Barrier effects in the cognitive maps of children and adults. *Journal of Experimental Child Psychology*, 34, 46 - 58. doi:10.1016/0022-0965(82)90030-3.
- Nguyen N.D., Tucker M.A., Stickgold R., Wamsley E.J. (2013). Overnight Sleep Enhances Hippocampus-Dependent Aspects of Spatial Memory. *Sleep*, 36, 1051-1057. doi:10.5665/sleep.2808.
- Nieuwenhuis IL, Folia V., et al. (2013). Sleep promotes the extraction of grammatical rules. *PLoS ONE* 8, e65046. doi:10.1371/journal.pone.0065046.
- Noack, H., Schick, W., Mallot, H. A., & Born, J. (2017). Sleep enhances knowledge of routes and regions in spatial environments. *Learning and Memory*, 24, 140 - 144.
- Noppeney, U., & Price, C. J. (2004). Retrieval of abstract semantics. *Neuroimage*, 22, 164–170.
- O’Keefe, J. & Nadel, J. (1978). *The Hippocampus as a Cognitive Map*, Oxford University Press.
- Olejnik S., Algina J. (2003). Generalized eta and omega squared statistics: measures of effect size for some common research designs. *Psychological Methods*, 8, 434-447. doi:10.1037/1082-989X.8.4.434.
- Orban P., Rauchs G., Balteau E., Degueldre C., Luxen A., Maquet P., Peigneux P. (2006). Sleep after spatial learning promotes covert reorganization of brain activity. *Proceedings of the National Academy of Sciences of the United States of America*, 103(18), 7124-7129. doi:10.1073/pnas.0510198103.
- Paivio, A. (1978). Imagery, language, and semantic memory. *International Journal of Psycholinguistics*, 5, 31–47.

- Paivio, A. (1986). *Mental representations: A dual coding approach*. Oxford University Press.
- Pavlidis C., Winson J. (1989). Influences of hippocampal place cell firing in the awake state on the activity of these cells during subsequent sleep episodes. *Journal of Neuroscience*, *9*, 2907-2918.
- Payne J.D., Schacter D.L., Propper R.E., Huang L.W., Wamsley E.J., Tucker M.A., Walker M.P., Stickgold R. (2009). The role of sleep in false memory formation. *Neurobiology of Learning and Memory* *92*(3), 327-334. doi:10.1016/j.nlm.2009.03.007.
- Peigneux P., Laureys S., Fuchs, S., Collete, F., Perrin, F., Reggers, J., Phillips, C., Degueldre, C., Del Fiore, G., Aerts, J., Luxen, A., Maquet, P. (2004). Are spatial memories strengthened in the human hippocampus during slow wave sleep? *Neuron* *44*(3), 535-545. doi:10.1016/j.neuron.2004.10.007.
- Pomplun, M., et al. (2012). The effects of circadian phase, time awake, and imposed sleep restriction on performing complex visual tasks: Evidence from comparative visual search. *Journal of vision*, *12*(7), 1-19.
- Rasch, R., Born, J. (2013). About Sleep's Role in Memory. *Physiological Reviews*, *93*(2), 681-766.
- Rauchs, G., Orban P., Schmidt, C., Albouy, G., Balteau, E., Degueldre, C., Schnackers, C., Sterpenich, V., Tinguely, G, Luxen, A., Maquet, P., Peigneux, P. (2008). Sleep Modulates the Neural Substrates of Both Spatial and Contextual Memory Consolidation. *PloS ONE*, *3*. doi:10.1371/journal.pone.0002949.
- Richardson, A. E., Montello, D., & Hegarty, M. (1999). Spatial knowledge acquisition from maps, and from navigation in real and virtual environments. *Memory and Cognition*, *27*, 741–750.
- Robertson E.M., Pascual-Leone A., Press D.Z. (2004). Awareness modifies the skill-learning benefits of sleep. *Current Biology*, *14*(3), 208-212. doi:10.1007/s10339-015-0722-9.
- Röhrich, W., Hardiess, G., & Mallot, H. A. (2014). View-based organization and interplay of spatial working and longterm memories. *PlosONE*, *9* (11), e112793.

- Sabsevitz, D. S., Medler, D. A., Seidenberg, M., & Binder, J. R. (2005). Modulation of the semantic system by word imageability. *Neuroimage*, *27*(1), 188-200.
- Schick W., Halfmann M., Mallot H.A. (2015). How to construct a linguistic landmark: language cues in the formation of hierarchical representations of space. *Cognitive Processing*, *16*, 383-388. doi:10.1007/s10339-015-0722-9.
- Schölkopf, B. & Mallot, H.A. (1995). View-Based Cognitive Mapping and Path Planning. *Adaptive Behavior*, *3*, 311-348.
- Schwanenflugel, P. J., & Shoben, E. J. (1983). Differential context effects in the comprehension of abstract and concrete verbal materials. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *9*(1), 82-102.
- Siegel, A. W., & White, S. H. (1975). The development of spatial representations of large-scale environments. H. W. Reese (Ed.), *Advances in child development and behavior*, *10*, 9–55.
- Skaggs W.E., McNaughton B.L. (1996). Replay of neuronal firing sequences in rat hippocampus during sleep following spatial experience. *Science*, *271*, 1870-1873. doi:10.1126/Science.271.5257.1870.
- Stankiewicz, B., Kalia, A.A. (2007). Acquisition of structural versus object landmark knowledge. *Journal of experimental psychology – human perception and performance*, *33*(2), 378-390.
- Stevens, A., & Coupe, P. (1978). Distortions in judged spatial relations. *Cognitive Psychology*, *10*, 422 - 437.
- Strohecker, C. (2000). Cognitive zoom: From object to path and back again. In: Freksa, C., et al. (Eds.). *Spatial cognition II*. Springer, 1–15.
- Taylor, H. A., & Tversky, B. (1992). Descriptions and depictions of environments. *Memory & Cognition*, *20*, 483-496.
- Thorndyke, P. (1981). Distance estimation from cognitive maps. *Cognitive Psychology*, *13*, 526–550.
- Tom, A., & Denis, M. (2004). Language and spatial cognition: comparing the roles of landmarks and street names in route instructions. *Applied Cognitive Psychology*, *18*, 1213 - 1230.

- Trope, Y., & Liberman, N. (2010). Construal-level theory of psychological distance. *Psychological Review*, *117*, 440 - 463.
- Turney, P. (2001). Mining the web of synonyms: PMI-IR versus LSA on TOEFL. In De Raedt, L. & Flach, P. (Eds.), *European conference on Machine Learning 2001* (Vol. 2167, 491 - 502). Berlin, Heidelberg: Springer Verlag.
- Uttal, D. H., Friedman, A., Hand, L. L., & Warren, C. (2010). Learning fine-grained and category information in navigable real-world space. *Memory and Cognition*, *38*, 1026 - 1040.
- Wagner U., Gais S., Haider H., Verleger R., Born J. (2004). Sleep inspires insight. *Nature*, *427*, 352-355. doi:10.1038/nature02223.
- Wamsley, E. J., Tucker, M. A., Payne, J. D., & Stickgold, R. (2010). A brief nap is beneficial for human route-learning: The role of navigation experience and EEG spectral power. *Learning & Memory*, *17*(7), 332-336. doi:10.1101/lm.1828310.
- Wang, R. X. F., & Brockmole, J. R. (2003). Human navigation in nested environments. *Journal of Experimental Psychology: Learning, Memory and Cognition*, *29*, 398-404.
- Weber, F. D., Wang, J.Y., Born, J., Inostroza, M. (2014). Sleep benefits in parallel implicit and explicit measure of episodic memory. *Learning & Memory*, *21*(4), 190-198. doi:10.1101/lm.033530.113.
- Whorf, B. L. (1956). *Language, thought, and reality*. Cambridge, MA: MIT Press.
- Wiener, J. M., Ehbauer, N. N., & Mallot, H. A. (2009). Planning paths to multiple targets: Memory involvement and planning heuristics in spatial problem solving. *Psychological Research*, *73*, 644 - 658.
- Wiener, J. M., & Mallot, H. A. (2003). 'Fine-to-coarse' route planning and navigation in regionalized environments. *Spatial Cognition and Computation*, *3*, 331-358.
- Wiener, J.M., Schnee, A., Mallot, H. A. (2004). Use and interaction of navigation strategies in regionalized environments. *Journal of Environmental Psychology*, *24*, 475 - 493.
- Wiener, J. M., & Tenbrink, T. (2008). Traveling salesman problem: The human case. *Künstliche Intelligenz*, *22*, 18 - 22.
- Wilhelm I., Rose M., Imhof KI, Rasch B., Buchel C., Born J. (2013). The sleeping

- child outplays the adult's capacity to convert implicit into explicit knowledge. *Nature Neuroscience*, *16*, 391-U337. doi:10.1038/Nn.3343.
- Wilson M.A., McNaughton B.L. (1994). Reactivation of hippocampal ensemble memories during sleep. *Science*, *265*, 676-679. doi:10.1126/science.8036517.
- Wolbers, T., Wiener, J. M., Mallot, H. A., & Büchel, C. (2007). Differential recruitment of the hippocampus, medial prefrontal cortex, and the human motion complex during path integration in humans. *The Journal of Neuroscience*, *27*(35), 9408-9416.
- Wolbers, T. & Hegarty, M. (2010). What determines our navigational abilities? *Trends in cognitive sciences*, *14*(3), 138 – 146.
- Xu, Y., He, Y., & Bi, Y. (2017). A tri-network model of human semantic processing. *Frontiers in Psychology*, *8*, 1538.
- Zacks, J. M., Speer, N. K., Swallow, K. M., Braver, T. S., & Reynolds, J. R. (2007). Event perception: a mind/brain perspective. *Psychological Bulletin*, *133*, 273 - 293.
- Zacks, J. M., & Tversky, B. (2001). Event structure in perception and conception. *Psychological Review*, *127*, 3 - 21.
- Zander, T., Volz, K.G., Born, J., Diekelmann, S. (2017). Sleep increases explicit solutions and reduces intuitive judgments of semantic coherence. *Learning & Memory*, *24*, 641-645.

ACKNOWLEDGEMENTS

The work described in this paper was carried out at the Department of Biology of the University of Tübingen. The candidate received support from the Landesgraduiertenförderung Baden-Württemberg.

And finally, it's time for a big *thank you*

- to Professor Mallot, for being a great supervisor
- to Professor Hamm and Professor Karnath
- to Dr. Marc Halfmann, whose door was always open for me
- to Michaela Mohr and Martina Schmöee-Selich, who encouraged and supported me, and who were always there when I needed a second opinion
- to PD Dr. Heinz Bendele and PD Dr. Gregor Hardiess
- to Detmar Meurers and Stephanie Wolf from the Department of Computer Linguistics, for their help with the word-co-occurrence analysis
- to Hannes Noack, for approaching me with an idea for a sleep-study
- to all the students who were involved in the data collection: Matthias Baumann, Paula Hilsendegen, Julia Holzmann, and Svenja Zehender
- and to my parents, all the other members of my family and my friends who supported me!