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Zu Inhaltsverzeichnis

Visuo-spatial Working Memory as a Limited Resource of Cognitive Processing

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1 The Concept of a Resource-Limited Working Memory

Working memory is considered a cognitive component that mainly serves two functions. It *temporarily maintains* information that was either perceived but is no longer present in the environment, or that was internally generated, and it supplies a *work space* for transforming and manipulating elements of perception and thinking. Both functions are relevant for a successful interaction with the environment and it is therefore not surprising that WM is a central topic of research in the field of general psychology. This interest is further increased by the fact that WM is seen as a limited resource that constrains cognitive performances. Understanding working memory capacity (WMC) therefore promises gainful training methods to surmount these capacity limitations. In this chapter, we want to discuss aspects of WM that are relevant when we are talking about WM as a limited resource of cognitive processing. Our focus will be on VSWM although many principles can be applied also to other types of inputs.

Historically, WM research has its origin in research on short-term memory (STM). In 1887 already, Jacobs [47] introduced the so-called digit span to measure the capacity of STM. He presented a random series of digits and participants were required to repeat them in their correct serial order. The longest sequence that was correctly repeated was defined as digit span. It is usually limited to six or seven items and this figure was therefore given as the capacity of STM [76]. Until today, span measures remain the gold standard for estimating WM capacity [18], although nowadays different types of spans are distinguished and a limit of four items is discussed as we will show later. The reason for this differentiation was the observation that STM is not a unitary compartment. Patients with a verbal STM deficit, for example, have a digit span as short as two items, but they have a normal visuo-spatial span [120].

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Those who most clearly made this point and whose model had a strong impact on memory research were Baddeley and Hitch [7]. Because they considered memory as active, they suggested using the term working memory instead of short-term memory. They distinguished three components: a central executive (CE) and two domain-specific independent slave systems – the phonological loop (PL) and the visuo-spatial scratchpad (VSSP) for verbal and visual materials, respectively. According to this model, the CE is associated to attention and it controls the slave systems. The PL stores verbal surface information and it maintains this information by inner speech. In contrast, the VSSP stores visuo-spatial information and a kind of mental inspection was the presumed maintenance mechanism. Additionally, each system has its own limited capacity and therefore selective interference was postulated if two tasks tapping the same system were performed concurrently. If two tasks use the same part system, they compete for resources and dual-task performance is impaired, for example, verbal short-term memory and verbal articulation. If the two tasks are processed in different part systems, performances are similar to a single-task condition, for example, verbal short-term memory and movement tracking [65]. A practical consequence hereof is that one should avoid loading the same system to accomplish two tasks at the same time. Due to the assumed three components, this model is called the tripartite model. It is the only one that features an independent visual working memory. Extended by assumptions on the characteristics of the rehearsal processes, it explains temporary memory for verbal items quite well and it also explains domain-specific differences between memories of verbal and pictorial materials (see [100] for a review). However, it is less successful when dealing with differences *within* the visual domain as we will see in the next section. More recently, the episodic buffer was added as a fourth component of WM [5]. The episodic buffer represents integrated multi-modal information from different systems and modalities including semantic information.

Besides the tripartite model, a number of other suggestions were put forward for explaining WM performances – see the contributions in Miyake and Shah [79]. Some researchers consider (long-term) memory as a network of knowledge entries that can be in a passive or active state, and WM is simply the active part of long-term memory [66]. Capacity limits are also assumed in these models but they are attributed to attention.[1] The number of memory entries that can be in the focus of attention is limited to about four items (e.g. Cowan [20]). Oberauer [80] made an even finer distinction within this set of items. He also assumes that among the active nodes a small set of items is in direct access – this was the formerly mentioned set of four items – but only one item of this set is in the focus of attention. Focused is the item that is selected for a cognitive action, and only this item has a clear processing advantage. The smaller number of only four items compared to the higher digit span of about seven items is due to methodological differences. Complex span measures are enhanced by chunking phenomena – elements can be conjoined – so that a more

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[1] A further limitation is given by structural interference. For example, if the items in WM are perceptually similar to each other, memory is worse than if they are different [123].

efficient rehearsal is possible. Four items can be very different things. An item can be a “simple” feature like colour but also a complex unit (a chunk) made of many parts [41]. Hence, if items can be recoded into larger units, more information can be held in WM than if this recoding is not possible. Therefore, training the ability to chunk items is one way to enhance the capacity of working memory [122].

According to the unitary models, WM is not an additional part system or store, but a state of mental processing units, and the main function of WM is providing information for action control. Memory is only a by-product of using information in these processes [27]. Similarly, attention mainly serves this function and the one-element focus of attention is the selection of information for an overt or covert (cognitive) action. These assumptions, however, do not yet explain why only four items are in direct access. This number is empirically well substantiated (see [20]), although there is some variability over individuals and types of to-be-remembered material (see below). The reason for this capacity limit may be found at the neural level. It is very likely that information is represented by synchronised oscillations of cell assemblies. Cell assemblies representing features of the same object oscillate in a synchronous manner, and this synchronicity codes that these features belong to the same object. Simulations of these neural networks showed that only about four items can be stored by this mechanism because neural activities representing more items are not sufficiently separated in time [95]. Limitations due to domain-specific processes are not a main topic in unitary models, although domain-specific storage is conceded and recently its contribution to WM was acknowledged [15, 21]. Hence, WM capacity is probably limited by a domain-general storage mechanism – only a limited number of distinguishable cell assemblies can be simultaneously active – and by domain-specific characteristics of the represented content.

Attention plays also a central role in a third family of WM models of which Engle is one of the leading proponents. According to these models, WMC is related to the ability of controlling central attention [33, 49] and especially to the ability of inhibiting irrelevant information. In support of this assumption, mainly two results are cited. One is the observation that WM capacity correlates with general intelligence and with performances in tasks that have high demands on attentional control (see [32] for a review). The other one is that participants with a low memory span are less efficient in filtering irrelevant background information than those with a high span [17, 31]. In these experiments, span is often defined as “operation span” [116]. In a typical task, participants are sequentially presented with a series of arithmetic equations (e.g. $7 - 3 = 5$) each followed by a word. Participants are required to evaluate the correctness of each equation and to remember the words. After the list, participants have to report the verbal items in their correct order. Hence, a serial verbal memory task is intermixed with arithmetic calculations. This task has high demands on storage and control. It therefore does not surprise that controlled attention is the critical variable that causes the correlation with general intelligence as structural equation models have revealed [34]. More specifically it is executive control, i.e. the ability to allocate attention to the critical task and to resolve task conflicts which distinguish between high-span and low-span participants [99]. In contrast to the control component, the storage component is rather domain-specific with separate contributions of visual and verbal abilities [50]. A similar picture emerges when visual and verbal mental tests are systematically compared with each other in tasks that have different demands on storage, supervision, and coordination [81, 82].

The many tasks used to investigate WM obviously measure different aspects of working memory and their respective demands determine which component limits memory performances. Therefore, it depends on the used memory paradigm what is considered as WMC. Three independent types of limitations have been identified: (1) memory overload caused by additional perceptual input that enters the same part system and competes for representation (interference), (2) the maximal size of the set of items that can be in direct access, and (3) the efficiency of controlled attention (inhibition of irrelevant items and conflict resolution). Controlled attention seems to be a domain-general ability, whereas as soon as a storage component is involved domain-specific capacities come into play.

2 Components and Capacities of Visual Working Memory

As we have explicated, a domain-specific component contributes to WM and its characteristics depend on the stored content. Two questions therefore arise. What types of information are stored in VSWM and what are the operating characteristics of VSWM? In the model of Baddeley and Hitch, it was assumed that the VSSP represents *spatial* information. This component was not specifically bound to the visual modality because a visuo-spatial main task was impaired by an auditory-spatial secondary task [8]. This view changed some years later when it was observed that presenting irrelevant pictures during maintenance impaired a WM task that makes use of a visual imagery mnemonic [63]. Based on this so-called irrelevant picture effect, Logie concluded that perceived visual information enters the VSSP and interferes with the stored content. More recently, Quinn and colleagues demonstrated that even dynamic visual noise (DVN) – a fast-changing checkerboard randomly filled with black and white dots – interferes with visual imagery [72, 93]. This DVN effect demonstrates that the interference is really a visual effect and not a semantic one. Hence, VSWM should store both types of information and additional spatial as well as visual inputs should impair visuo-spatial memory tasks.

However, the relationships are more complicated. First, the type of the assigned spatial memory task has to be considered. Baddeley and others often used the *Brooks matrix task*. In this task, a spatial sequence of locations within a matrix has to be memorised in correct order (an imaginary path through an empty matrix). The *Corsi task*, which is also frequently used, is structurally very similar. In this task, a sequence of temporarily marked items that are only distinguishable by their spatial location has to be remembered. Active spatial movements impaired the Corsi task [94], as did auditory spatial information [110], and even decision making [51]. It is therefore unlikely that an overload of spatial information in WM by additionally processed spatial information caused the interference. It is more likely that a disruption of (spatial) attention is critical. In order to maintain a temporal sequence within a set of homogenous elements, spatial marking is necessary, and for that purpose attention is serially directed to locations during the retention interval (spatial rehearsal). Therefore, any process that prevents the allocation of spatial attention during rehearsal should impair spatial memory. We could show that additional spatial processing during maintenance did not interfere with a spatial task if only spatial and not temporal information was relevant [133]. We required our participants to remember the spatial layout of objects. Neither additional visual material nor a spatial suppressor task (spatial tapping) impaired object relocation which of course needs spatial memory. In contrast, performances in a spatio-temporal main task (Corsi) were reduced by spatial but not visual interference. We assumed that directing spatial attention to target locations constitutes spatial rehearsal within VSWM if a spatial sequence in a homogenous field of objects has to be remembered – as in a Corsi task. This rehearsal process is impaired by spatial distraction tasks. In contrast, it seems to be possible to maintain the spatial location of objects by other mechanisms that do not rely on spatial rehearsal as we will discuss later.

In other experiments, the Loci method or the Peg word techniques were used as main tasks. These tasks are imagery mnemonics and they require the generation of a visual image, e.g. imagining a named object at a specific location with the Loci method. Both tasks are impaired by additional visual input [63, 93] and one therefore may assume that imagery mnemonics are generated within VSWM. Considering these differences, Logie [62] suggested to distinguish two components within WM: a visual cache and an inner scribe. The inner scribe operates on the visual cache, it stores dynamic information (processing trajectories of movements and motor actions), and it serves spatial rehearsal. The Corsi task measures the capacity of the inner scribe. The visual cache provides visual information, e.g. shape and colour. Its capacity is measured by the *visual pattern span*. In that task, participants have to remember a pattern of black cells randomly distributed in a matrix for a short time and the number of cells increases from trial to trial [64]. Many results suggest the distinction of different types of visual information (see [62]). However, it remains unclear what type of information is represented in the inner scribe and in the visual cache. For example, spatial information is sometimes investigated as dynamic information and sometimes as configuration of objects (see [133] for a discussion).

We could show that the dynamic characteristic of a visual stimulus is not the critical component for processing of information in the true spatial component (the inner scribe) as it was originally suggested. We investigated WM for biological information (point-light walkers) – a dynamic stimulus – in an S1–S2 task with visual and spatial interference [131]. In the visual interference condition, we presented colour patches during maintenance that should load the visual cache. In the spatial interference condition, spatial tapping was performed during maintenance. Even though in the main task dynamic stimuli were used, we observed visual interference, and this was a function of the similarity between the stimuli of the main and the interference tasks. Irrelevant point-light walkers impaired memory more than irrelevant colours. Spatial tapping also caused interference but this effect was not due to spatial information because also non-spatial tapping interfered. We therefore assume that the distinction between visual information (appearance) and spatial information – where objects are located – is a critical dimension in VSWM and less the distinction between static and dynamic information. Recently this position was also supported by other studies [25].

This separation between object and location information in WM follows the separation of these two features in perception (e.g. [119]). It has been demonstrated both in behavioural and neurocognitive studies which we will discuss later. With this definition, however, spatial information is no longer confined to visual input because also other objects, e.g. sound objects, are perceived at specific locations. We tested the idea of common spatial coding in WM in a series of experiments on auditory spatial and visuo-spatial location memory. Our data clearly speak in favour of a common coding in spatial WM (SWM) independent of modality (Fig. 1).

We presented lists composed of only visual or of visual and auditory material in a spatial working memory task. If modality-specific SWMs exist each should have its own capacity. Because the capacity of each system limits the amount of remembered items, memory performance should be higher if the available capacity is higher. Hence, performance should be higher if memory load can be distributed over two memories (mixed-modality list) than if the complete list has to be hold within one component (uni-modality list). In contrast, if all spatial information is stored within one system, performances should be a function of list length independent of the modality of the items. We therefore presented uni- and mixed-modality

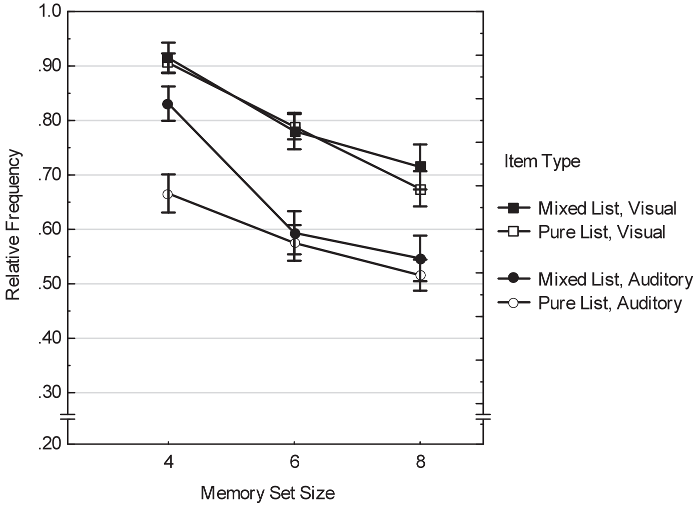

Fig. 1 Memory performances in a visuo-spatial working memory task as a function of modality (visual, auditory) and list type (pure, mixed), data from [60]. Note that the advantage for auditory material in a four-item mixed list is not a memory advantage. It is due to an advantage in auditory spatial perception caused by reduced spatial uncertainty (see the additional data presented in the original work)

lists of visual and auditory objects within a S1–S2 matching task framework [60]. Memory load was a function of the number of items and it was not dependent on input modality. Auditory-spatial and visuo-spatial tasks seem to be processed within the same working memory system.

We ran comparable experiments as electrophysiological studies and these data supported the same conclusion. Event-related potentials during encoding were influenced by modality of the stimuli, but slow potentials during maintenance were a function of load but not of modality [61]. We therefore concluded that spatial information of visual and auditory input is processed and maintained by the same SWM. The spatial system probably represents object locations in egocentric coordinates relative to the coordinates of the observer's head.[2] In contrast, object-specific information is represented in separate domain-specific components according to its content, e.g. visual or auditory representations within a visual WM (VWM) and an auditory WM (AWM), respectively [3, 96].

These domain-specific components have their own constraints. The VWM can represent only a limited number of objects simultaneously. Luck and Vogel [67, 123] estimated the capacity of VSWM as about three to four items – they made no distinction between visual and spatial information. They presented their participants objects (e.g. colour patches or conjunctions of colours and shapes) and after a short delay a test picture was presented. The number of objects was varied. In all conditions, memory was nearly perfect up to four objects (features or conjunctions of features) and then it declined. The authors concluded that VWM can hold four objects and that each object can represent an arbitrary number of features without any additional costs. Hence, VWM is limited in the number of objects not in the number of features. The capacity limit of VWM was therefore set to four objects. Meanwhile, however, we know that feature conjunctions cause additional processing effort [114] and that the capacity also depends on physical characteristics of the "objects". Figures have to be spatially coherent to define an object [126], and the more visually complex items are (e.g. Chinese letters vs. colour squares) the less items that can be remembered [1]. Visual working memory is therefore not only limited by the number of items of the same type, but also by the structural qualities of these items.

However, even the assumption that VSWM consists of two independent part systems – representing visual appearance and spatial information – has to be further differentiated. A frequently used WM task is the S1–S2 matching task. A to-be-remembered stimulus is presented and shortly afterwards either the same or a changed stimulus is presented for comparison. In a dual-task condition, additional material has to be processed in as secondary task. If the second task loads the same WM component as the main task, performances are reduced compared to the single-task condition. It is assumed that both tasks together exceed the capacity of WM

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[2] We will not go into details of spatial representations. A closer look would reveal different types of spatial relations, for example, ego-centric and allocentric spatial representations with different reference systems [126].

and therefore performances collapse. However, when the additional information is exclusively presented during maintenance, often no interference was observed [2, 4, 91, 132]. Even demanding secondary tasks during maintenance did not influence visuo-spatial memory in a S1–S2 working memory task [130]. This should not happen if the additionally perceived material automatically enters WM and competes with the material of the main task. Logie [62] explained the absence of interference by the assumption that visual input does not automatically and directly enter WM but it does so only after some kind of higher cognitive processing that filters visual input. Consequently, only relevant information would enter WM, whereas irrelevant information would be inhibited although it is perceived. However, this explanation does not work either because other working memory conditions that are impaired by additional (irrelevant) input during maintenance do exist. For example, dynamic visual noise during maintenance impaired a visual, just noticeable difference size task [71] – in this task the size of a circle has to be compared with another one presented a few seconds before. Similarly, we observed that temporary visual memory for movements (point-light walkers) was impaired by additional visual input (colour patches or other walkers to be ignored) [131]. Quinn and colleagues therefore argued to distinguish between passively hold visual material and material that is held in an active visual buffer [90, 91]. According to their view, visual input has direct access to a visual store [70, 92], but this visual store is not the passive visual cache but an active visual buffer [90, 91]. This buffer holds conscious visual representations of perceived stimuli as well as of mentally generated ones (visual images).

Within the visual working memory framework, a separate buffer was already postulated by Pearson [84]. This buffer should hold a conscious visual image, and it should therefore be closely tied to central executive and conscious awareness. The idea of a *visual buffer* that is used for image generation was originally put forward by Kosslyn and a lot of research in the context of the so-called imagery debate was devoted to this structure and its characteristics [55–57]. The controversy was about the quasi-pictorial quality of representations within this buffer. Kosslyn assumed that the buffer represents visual information in a depictional manner, preserving distance between represented objects, and all processes on this buffer are analogous to processes in physical space. Mental rotation for example is a stepwise process passing intermediate positions between the start and the target orientation [107], and mental scanning follows a trajectory in a two-dimensional space with Euclidean characteristics [58]. However, until today it is controversial whether these characteristics are caused by constraints of the mental (or neural) representation or they are only simulations of the real world [89]. Nevertheless, many results have shown that imagery processes, for whatever reason, behave as if they were performed in physical reality. For example, visual images "have" a specific resolution, size, include angles and distances between objects, etc. and these features follow the same processing characteristics as their physical counterparts [55]. One can therefore consider these features as quasi-physical constraints of visual imaginal processing. They come into effect when information is processed within the visual buffer.

In summary, the conception of VSWM is more differentiated than in its beginning. WM for spatial information is distinguished from WM for objects. SWM is closely related to spatial attention and rehearsal is provided by shifts of spatial attention. Objects are represented in domain-specific WM in the case of visually perceived objects, very likely as distributed representations of visual features (see below). The maximal number of objects is limited to about four items. Additionally, however, the complexity of stimulus material restricts the number of successfully remembered items. It may be that both limitations are caused by different mechanisms. Furthermore, we have to distinguish passive and active temporary memories of visual information. The former is not actively maintained, whereas the latter one is held active in a visual buffer and is closely related to attention.

3 Working Memory and Higher Cognitive Performances

In the classical, structural view on WM, domain-specific storage components and executive functioning – which can be seen as higher cognitive processes – are viewed as separate mechanisms, or resources, and consequently, they are measured separately [6]. For instance, the storage capacity of verbal WM was measured with simple span tasks (e.g. with classical digit span in the verbal domain) and the capacity of VSWM with the Corsi blocks task [77]. Another example is the arrow span task that requires remembering a series of directions successively indicated by an arrow. Examples for measurements of the central executive function are random number generation (asking a participant to generate a sequence of numbers that have a random order) and the Tower of Hanoi problem (minimising the number of moves, participants have to rebuild a tower of discs considering several constraints).

Other scientists focused on simultaneous storage-and-processing tasks to measure the capacity of working memory (e.g. [23]). According to this approach, WM performance is measured as the number of elements that can be remembered in the face of ongoing processing. A typical task requires a participant to process some information (e.g. to read a sentence aloud or to evaluate whether a simple mathematical equation is correct) and simultaneously store some information besides processing (e.g. remember the last words of the preceding sentences or remember the results of the preceding equations). The number of to-be-remembered items that can be recalled after a list of such sentences or equations has been processed is the individual working memory span. Individuals differ reliably in such storage-and-processing tasks (see [18] for a review). Classical measures are reading span [23], operation span [116], and counting span [14]. In the visuo-spatial domain, similar processing-and-storage measures have been constructed. In the rotation letter span [106], a picture of a rotated letter is shown. This rotation is produced either with the original letter or with a mirrored version of the letter. Participants are asked to judge whether the letter is mirrored or not (processing component) while remembering the directions of the rotations of preceding letters, similar to the arrow span task (storage component).

These storage-and-processing parameters have become particularly important when one is interested in higher cognitive performances because they have a diagnostic value for higher cognitive tasks and intelligence. Studies investigating the relation of WM to cognitive performances in different domains and application fields (e.g. language comprehension, spatial ability, and environmental learning) typically utilise an individual differences approach. They relate the individual WM capacity measured by a specific span to performances in higher cognitive tasks. For example, Daneman and Merikle conducted a meta-analysis of 77 studies in which the association between WM capacity and language comprehension ability was investigated [24]. WMC as measured with storage-and-processing tasks was a good predictor of language comprehension. The predictive power of such tasks was higher than the predictive power of STM tasks that measure storage alone. Moreover, not only reading span (working memory and language processing) but also operation span (working memory and math processing) predicted language comprehension.

In the context of storage-and-processing tasks, the issue of whether there are domain-specific WMCs is controversial. Shah and Miyake [106] propose the idea that there are different domain-specific resource pools that fuel two domains of higher-level cognition: spatial thinking and language comprehension. In their study, they related visuo-spatial (letter rotation span and arrow span) and verbal WMC (reading span) to psychometric tests of spatial ability and to scores of language ability. Three spatial visualisation tests (Paper Form Board Test, Space Relations Test, and Clocks Test) and one perceptual speed test (Identical Pictures Test) were used. The Paper Form Board Test, for example, consists of several drawings of two-dimensional pieces that can be put together. A clear pattern was obtained. The visuo-spatial WMC measure (letter rotation span) was strongly related to a composite measure of the spatial visualisation tests, whereas it was not related to verbal ability. Vice versa, verbal WMC (reading span) was considerably related to verbal ability but not to spatial ability [106]. In another study, it was observed that performances in the Tower of Hanoi task were related to spatial span but not to verbal span measures, whereas conditional reasoning was related to the reading span task but not to the spatial span task [42]. Thus, not only storage functions as investigated in S1–S2 tasks, but also higher-level functions and problem-solving tasks involving the central executive appear separable with respect to domain-specificity and further to visual and verbal WM capacities.

Recently, attempts have been made to structure WM functions more theoretically, in order to clarify their role in cognitive performance and intelligence. As in models of intelligence, Oberauer and colleagues [81] have differentiated the working memory construct along the content dimension (verbal, spatial-figural, and numerical tasks) and the function dimension (storage-and-processing, supervision, and coordination). In order to test this, their participants performed a series of WM tasks with different cognitive demands according to these two dimensions. The studies however yielded mixed outcomes for the separation of different WM components. The results spoke predominantly in favour of the assumption that spatial components can be separated from verbal ones, but there was a less clear separation of processes.

Finally, visuo-spatial WMC was related to *visuo-spatial abilities* as measured in intelligence tests. Spatial abilities are traditionally measured by paper-and-pencil tests, and they represent the spatial dimension of intelligence. For example, these tests require to mentally rotate a three-dimensional object, to find an embedded figure, or to mentally fold and unfold a piece of paper. In their investigation of the relation between VSWM and spatial abilities, Miyake and colleagues, e.g. [78], have included storage-and-processing tasks (e.g. the letter rotation task), short-term storage tasks (e.g. the Corsi blocks task), and central executive tasks (e.g. the Tower of Hanoi). It has been found that different spatial ability tasks put different demands on WM. There are tasks of spatial visualisation which “reflect processes of apprehending, encoding, and mentally manipulating spatial forms” ([13], p. 309). These tests require to perform a series of transformations on mental representations of objects (such as mentally folding a piece of paper), and they appear closely related to central executive functioning. However, tests that require rather low mental manipulation (such as identifying a picture in a row of similar pictures, classified as perceptual speed) are more directly related to VSWM. Moreover, in the visuo-spatial domain, the storage-and-processing tasks and the storage tasks appear to measure the same construct [78]. This observation is to be expected when we consider the fact that the visual buffer as a work space for active maintenance and imaginal processing is closely tied to conscious awareness and the central executive.

4 Neural Structures Underlying Working Memory

The different WM functions are provided by a distributed network of active brain structures. Neurocognitive studies have shown that anterior and posterior cortical structures contribute to WM. These are mainly the dorsolateral and ventrolateral prefrontal cortex (referred to as DLPFC and VLPFC in the following) on the one hand and distributed regions in occipital, parietal, and temporal cortex on the other. Functionally, posterior structures have been ascribed the role of passive temporary buffers specialised for different representation formats. In contrast, anterior structures are assumed to be more active modules providing rehearsal and manipulation mechanisms for the contents of working memory as well as monitoring the posterior subsystems in a central executive manner.

The results of the first neuroimaging studies on WM indicated a hemispheric specialisation. Verbal WM seemed to rely primarily on a left-hemispheric network whereas visuo-spatial information in WM required mainly cortical structures in the right hemisphere [109]. While for verbal WM the specialisation of the left hemisphere has been repeatedly demonstrated and is therefore widely accepted, the right hemisphere’s dominance in short-term retention of visuo-spatial material has been questioned [124].

In contrast to the less stable right lateralisation of VWM, the specialisation of dorsal and ventral areas for processing of spatial and visual information respectively is empirically well supported. A major result from a range of neurocognitive studies is the dissociation of posterior brain structures contributing to visual object (e.g. shape, colour, and texture) and spatial processing, sometimes also called the “what” and “where” processing streams. Occipito-temporal regions showed more activation when object features of visual stimuli were to be retained whereas spatial features in WM led to stronger activations in occipito-parietal structures [9, 19, 73, 101, 121]. By transcranial magnetic stimulation (TMS) it was further demonstrated that these areas are in fact functional for WM tasks and their activity is not an epiphenomenon. In this paradigm, repetitive pulses through a coil (shaped as an eight) that is placed over the brain area of interest temporarily disturb processing in the respective structures. Ranganath and colleagues [98] identified regions in the fusiform face area and in parahippocampal place area that show category-specific activity. When these neural structures were temporarily interrupted by TMS, a stimulation of the temporal cortex slowed responses in object tasks, whereas stimulating the parietal cortex caused slower responses in spatial tasks [54].

If we look at posterior structures involved in WM retention at feature level, we can state that these processing structures can be further subdivided. In functional magnetic resonance imaging (fMRI) studies, feature-specific brain structures were found active dependent on the type of information that was maintained. During short-term retention of object categories, specific brain areas were preferentially active: fusiform, lingual, and inferior temporal cortex for shape information [88, 121], posterior parietal cortex including intraparietal sulcus for positions [22], fusiform face area for facial identity [29, 87], and parahippocampal place area for places and scenes [97, 98].

In a recent fMRI study from our lab, we directly compared movement, position, and colour information during retention in working memory [117]. Participants’ working memory for selective features of dynamic and static stimuli was tested within an S1-cue-S2 paradigm consisting of two coloured dots (S1 and S2). The cue indicated the feature that had to be compared and it was presented after S1 offset to focus on selective rehearsal and to circumvent effects of selective encoding. A retention interval of 6,000 ms followed, in that the respective information should be rehearsed. We contrasted brain activity during this maintenance interval as a function of the cued feature. For dynamic stimuli, either movement or end-position information and for static stimuli, either position or colour information had to be retained in working memory. Results indicate that regions that are also involved in movement perception (MT/V5, superior temporal sulcus, and premotor cortex) were differentially activated during short-term retention of movement information. Position WM (with static or dynamic stimuli) especially recruited parahippocampal regions and the lateral occipital complex (LOC), structures known to be involved with spatial representations of objects. Furthermore, left fusiform cortex (a structure belonging to the ventral processing stream) was significantly more activated when participants retained the coloured dot’s end position in working memory as compared to its movement. This result (together with parahippocampal and LOC activations) strengthens the perspective that a coloured dot’s position is remembered as an object at a specific location having specific features (e.g. colour). In contrast, movement information can be rehearsed in a more abstract way without the necessity to imagine the moving object with its features. Selective retention of colour information in WM yielded activations in the anterior portion of the right superior temporal gyrus and in early visual processing regions. This suggests that for short-term retention feature-selective posterior regions can be defined which in part comprise the same structures that are active during domain-specific perception (Fig. 2).

While posterior structures show a domain-specific organisation, the functional role and specificity of regions in the prefrontal cortex is controversial. Two main perspectives can be identified: the *domain-specific hypothesis* and the *process-specific hypothesis*. The first perspective assumes that the "what" and "where" dissociation equally holds for prefrontal cortex [118]. Short-term retention of spatial information involves DLPFC whereas VLPFC is mainly concerned with the retention of visual object information. An alternative view is the dissociation of prefrontal cortex as to the processes that are applied to information in WM [83, 85, 86]. According to this perspective, VLPFC is involved in active maintenance of to-be-remembered stimuli whereas DLPFC deals with the manipulation of working memory content. Although this controversy is not resolved, it is likely that the PFC is not the storage site of sensory information. These regions may function as pointers to posterior feature-specific areas and therefore they appear as if they represent domain-specific information. We assume that anterior and posterior areas are part of the network that provides VSWM [36, 103]. The anterior structures refer to posterior domain-specific representations and keep them active during maintenance. The domain-specific brain areas are widely the same that represent the visual features in perception and these structures also function as storage sites for both working and long-term memory processes [127].

Several of these brain areas found active during WM maintenance are also involved in visuo-spatial reasoning and in visual imagery tasks. In an fMRI study,

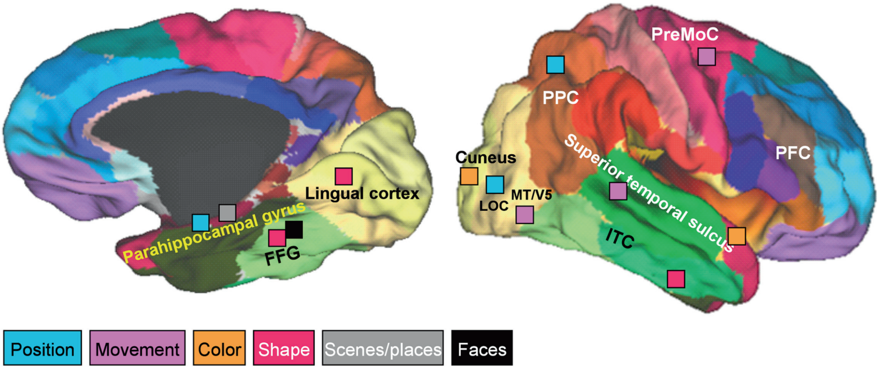

Fig. 2 An illustration of brain structures that were found active in different working memory tasks – *left*: medial view, *right*: lateral view on right hemisphere. *Coloured squares* indicate the type of feature that was relevant in the task. PFC, prefrontal cortex; PPC, posterior parietal cortex; PreMoC, premotor cortex; ITC, inferior temporal cortex; LOC, lateral occipital cortex; FFG fusiform gyrus

Todd and Marois [113] observed that activity in the intraparietal sulcus (IPS) and intraoccipital sulcus increased with the number of items in WM and the signal change correlated with the individual WM capacity [112]. Activity in the IPS was correlated to memory load and task difficulty [111]. Furthermore, the IPS was active in a mental scanning task [74] and in different types of spatial imagery tasks [69]. Also a spatial reasoning task showed enhanced activity in the IPS [115] and TMS of this structure impaired performances [105]. During mental rotation, negative slow potentials were observed at parietal electrodes [46] that increased with angular disparity [102]. Activity of the parietal cortex was also found in an fMRI study when figures, letters, or abstract shapes were rotated [48]. In contrast, object imagery tasks caused enhanced activity in the occipito-temporal and inferior-temporal cortex [28, 40, 75]. Kosslyn argued that even areas in the occipital cortex that are involved in early processing of visual input are activated if detailed visual images were generated [59]. Taken these and several other studies, it is likely that at the neural level the separation of visual and spatial processing also exists in imagery tasks and that occipito-temporal and parietal structures process these types of information, respectively. However, we only begin to understand the neural network that provides these imagery processes.

5 Visual Working Memory in an Applied Context

We have already presented a number of cognitive tasks that were influenced by VSWM efficiency but most of these tasks were artificial. They were designed to provide a relatively pure measure of VSWM in the laboratory. In this chapter we will have a look at visuo-spatial tasks that are relevant in applied settings.

Environmental learning. It appears that in the visuo-spatial domain specific task requirements constrain what resources are employed for cognitive performance. For instance, spatial abilities were related to spatial layout learning only if the learning experience was solely visual [43, 125]. In contrast, if the environment was studied by direct experience, then spatial abilities played a minor role. Hegarty and Waller [45] have therefore suggested that spatial abilities as measured in the laboratory – usually transformations of objects – should be distinguished from environmental spatial abilities. The latter, but not the former, require integrating different views of the environment over time to form a coherent mental representation. Moreover, the spatial reference frames differ. Navigational experience corresponds to the egocentric reference frame, which is view-based, depending on the current position and orientation in the environment. The orientation changes with one's own movements and spatial configurations are coded in relation to the body axes. Spatial ability tests, in contrast, require the comparison and/or mental manipulation of objects that can be apprehended in a single view. The reference frame here is allocentric, i.e. the spatial properties of the object are related to a fixed external coordinate system. Similarly, environmental survey knowledge (like on a map) corresponds to the allocentric reference frame, which is independent of the individual's position in the environment. However, a map is so complex that learning is based on fragments or regions that are put together mentally [128]. In support of this distinction, the relationship between spatial ability tasks and spatial performance tests in the environment was rather weak (see [45]). Bosco and colleagues related four different VSWM tasks to spatial orientation tasks measuring landmark knowledge, survey knowledge, and route knowledge [10]. VSWM spans explained only a limited percentage of the variance in the orientation tasks. However, all tasks were administered in the laboratory, i.e. they were solely visual.

When learning about the spatial configuration of an environment is based on direct experience, memory representations of different parts of the environment have to be maintained and integrated. Thus, WM may play an important role in spatial *environmental* learning [43]. Garden et al. [37] demonstrated that secondary tasks had detrimental effects on route learning in a real environment. Route learning was realised by following the experimenter through the centre of Padua. High-spatial ability participants appeared more affected by a spatial interference task, whereas low-spatial ability participants were more affected by a verbal interference task. Hegarty and colleagues have found considerable correlations between a VSWM measure (the arrow span) and learning from direct experience in the environment [43]. Similarly, in a series of experiments involving learning during navigation through a novel, real-world environment, we have found a substantial and robust relation between VSWM capacity and the acquisition of orientation knowledge in a real environment (see Zimmer et al., Visuo-Spatial Working Memory as a Limited Resource of Cognitive Processing of this volume).

In summary, the capacity of VSWM appears as a critical resource in real-world spatial orientation tasks. However, the functional role of VSWM in environmental learning has not been studied systematically yet.

Learning from diagrams and animations. When a static diagram of a mechanical system is studied, the movement of the system components has to be inferred by some mental processing. This mental processing has been characterised as involving "envisioning", "running a mental model", or "simulating the behaviour of a system in the mind's eye" (e.g. [38]). The term "mental model" refers to a mental representation that is dynamic and spatial. Such a representation allows to mentally simulate the system's operation. Dual-task studies with either verbal or visuo-spatial load while trying to understand the movement of the components of a simple mechanical system have shown that VSWM is involved [108]. Utilising an individual differences approach it was demonstrated that participants with low spatial visualisation ability (as measured with the Paper Folding Test, the Vandenberg Mental Rotation Test, the Guilford–Zimmerman Spatial Orientation Test, and the Bennett Mechanical Comprehension Test) performed worse on diagram comprehension and mental animation [44]. Thus the rather vague idea of "running a mental model" appears closely related to spatial visualisation and VSWM memory resources. It is likely that the efficiency of visual imagery causes this dependence.

These resources might also be critical if dynamic visual animations are presented in some multimedia learning material, that is, if mental animation is unnecessary because the movement of the system components is shown explicitly. Mayer and Sims [68] found that high-spatial ability subjects benefited from the concurrent presentation of an animation of a mechanical system with a narration as compared to a successive presentation (contiguity effect), while low-spatial ability subjects did not benefit from the concurrent presentation [68]. This result was explained with the ease with which high-spatial ability subjects could understand the explicit animation. Because of this superiority, more central WM resources could be devoted to building relations between the verbal narration and the visual animation. Low-spatial ability subjects, in contrast, had to devote central working memory resources to the understanding of the animation itself. In a task involving understanding of the spatial structure of a complex 3D-object, Cohen and Hegarty [16] provided subjects with interactive control over explicit animations. Large individual differences were found with respect to effectiveness of use of these interactive animations. High-spatial ability subjects were more likely to use the external animations. Thus, there was no evidence that low-spatial ability subjects used the external animations to compensate for poor mental animation. This result suggests that external multimodal support of learning needs additional assistance to enhance performances of users with low visuo-spatial abilities.

Spatial reasoning. Many of the WM tasks that we presented made spatial inferences necessary. Spatial reasoning can therefore be considered a prototypical task of SWM. However, many additional experiments exist that were specifically designed to investigate more complex spatial reasoning tasks. Already Brooks [11, 12] demonstrated that simultaneous processing of spatial relations and visually presented sentences interfered with each other and caused lower performances than auditory input. Similarly, Glass and Eddy reported better performances with auditory than with visual presentation of sentences if visual features were verified [30, 39]. They required their participants to ask questions on spatial relations between features of objects. These results can be explained by assuming that visually presented sentences and processing of visual features cause work load within the same WM component whereas auditory-verbal processing does not. Compatible with such an assumption we found evidence for visual processing if "inspection" of a visual image was needed in order to verify relations between stimuli but not if the answer could be retrieved from abstract propositional knowledge [129]. The fMRI studies reported above suggest that these tasks are processed in neural structures that are dedicated to visuo-spatial processing. A direct test of the involvement of the WM structures in reasoning was presented by Knauff and colleagues. While participants solved reasoning tasks with spatial relations, activity in the occipital parietal cortex was observed [52, 53, 104]. Interestingly, if visual imagery was used to solve these tasks the quasi-analogous features of visual images were also effective. Decision times in mental scanning were a function of Euclidean distance even if the mental map was constructed from texts [26]. Decision times were a function of the degree of mental rotation and they correlated with the hemodynamic response [35].

Obviously, solving visuo-spatial problems induces visual-imaginal processing. This type of processing is accompanied on the one hand with activations in specific neural structures and on the other hand with specific processing characteristics analogous to physical processes. Future research has to show whether the physical analogue characteristics are constraints of the neural structures or of the participants' experience with the physical world. However, independent of the answer to this question, the reported results at the behavioural and neural level already provide evidence for a separate VSWM processing resource. This part system processes a specific type of information, it has a specific capacity, it has specific processing characteristics, and it is provided by specific neural structures.

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