24. Auditory Working Memory

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This chapter reviews behavioral and neuroimaging findings on:

1. The comparison between verbal and tonal working memory (WM)
2. The impact of musical training
3. The role of sound mimicry for auditory memory
4. The influence of long-term memory (LTM) on auditory WM performance, i. e., the effect of strategy use on auditory WM.

Whereas the core structures, namely Broca's area, the premotor cortex, and the inferior parietal lobule, show a substantial overlap, results in musicians suggest that there are also different subcomponents involved during verbal and tonal WM. If confirmed, these results indicate that musicians develop either independent tonal and phonological loops or unique processing strategies that allow novel interactive use of the WM systems. We furthermore present and discuss data that provide substantial support for the hypothesis that motor-related processes assist auditory WM, and as a result we propose a strong link between sound mimicry and auditory WM.

24.1 The Baddeley and Hitch WM Model: Theoretical Considerations and Empirical Support

Working memory (WM) describes a brain system that is thought to be responsible for the temporary storage and simultaneous manipulation of information [24.1–4]. This system underpins higher cognitive functions like planning, problem solving, comprehension and reasoning, and is critical for understanding or appreciating speech and music.

There are many theories and models of short-term memory (STM) or WM (for an overview see [24.5–11]). Our chapter, however, is theoretically embedded in the highly influential *Baddeley* and *Hitch* [24.3] WM model due to the fact that studies that have examined WM for music and language have overwhelmingly focused on this framework [24.3, 12–18]. In addition, although parts of this model are still debated, no other verbal memory model is as well investigated, developed, or corroborated by research results [24.4].

There is little consensus in the literature regarding use of the terms STM and WM [24.19]. In some publications the term STM is used to describe the temporary storage of information, while WM refers to the maintenance and manipulation of information [24.6, 19]. Often, however, it is difficult to know whether a task needs further processing and/or manipulation in addition to the passive storage of information, e.g., if one tone has to be compared with several tones played in a sequence. Therefore, in this chapter no distinction is made between STM and WM; we refer only to WM. In

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addition, the term *auditory WM* will be used to describe WM processes for stimuli that were presented auditorily. Finally, it should be noted that whereas verbal WM has been investigated using both recall and recognition tasks, WM for tonal material has primarily been studied within recognition paradigms (but see [24.18] for a recall task for musical stimuli).

As mentioned, the present review is based on the *Baddeley* and *Hitch* WM model, the first version of which was described almost 40 years ago [24.3]. This initial WM model was developed from earlier frameworks such as the *Atkinson* and *Shiffrin* model [24.20], which assumed that:

1. Successful conversion to long-term storage required information to be held in the short-term store.
2. The short-term store was essential for access to long-term memory (LTM).
3. The short-term store was a seat of intellectual ability.

These assumptions were challenged by evidence that long-term memory (LTM) was dissociable from STM, as seen in neurological patients [24.21], and that complex encoding strategies, as opposed to simple rehearsal, predicted recall success [24.22].

Baddeley and *Hitch* [24.3] conducted their own series of dual task studies where they demonstrated that people could manage a concurrent task while holding items in memory for later recall with just a small decrement in processing speed, something that should not have been possible according to previous memory models. The concept of a unitary, passive short-term store was consigned to history and replaced with the WM model, which separated out attentional control from storage processes in memory. The original WM model proposed an attentional control system (the *central executive*) that operated in conjunction with two subsidiary systems: the visuospatial sketchpad and the phonological loop. Each of the subsidiary systems contained tightly coupled storage and rehearsal elements.

The central executive component was underresearched for many years, leaving the *homunculus* of the WM system poorly understood. After a decade, *Baddeley* [24.23] drew on a new theory proposed by *Norman* and *Shallice* [24.24] to suggest that the executive comprised a supervisory attentional system that allocated limited resources between the storage systems depending on task demands. More recent studies have confirmed the central executive's role in complex processes such as focusing and dividing attention, and task switching [24.6]. The true extent of the central executive's role in higher cognition however remains a highly contentious issue [24.25].

The *phonological loop* represents speech-based or verbal materials in WM. The loop comprises a short-term store and an articulatory rehearsal mechanism, both of which are described in more detail below. Theory regarding the development of the phonological loop framework was directly informed by behavioral research, which demonstrated that:

1. Storage within the loop is phonological as opposed to visual (the phonological similarity effect [24.26]).
2. Spoken material gains obligatory access to the storage component (the articulatory suppression effect [24.27]).
3. Subvocal rehearsal is likely to occur in real time (the word length effect [24.28]).

The *visuospatial sketchpad* is responsible for processing and storing both visual and spatial information. There is a degree of dissociation between visual and spatial memory within this WM component as evidenced from findings of behavioral dual task paradigms, [24.29] and the neuroimaging literature [24.30].

The *episodic buffer* was introduced as a fourth component to the WM model to acknowledge the mutual interaction between LTM and WM [24.31]. As a limited capacity system, the episodic buffer is thought to:

1. Bind information from the subsidiary systems
2. Store information in a multimodal code
3. Enable the interaction of resources between the WM and LTM systems [24.6, 32].

24.2 WM: Behavioral Data

24.2.1 Verbal Information

Baddeley and *Hitch's* [24.3] multicomponent WM model predicts that verbal information is processed by the phonological loop. As described above, this component can be further subdivided into (i) the *phonological store*, a passive storage component and (ii) the *articulatory loop*, an active rehearsal mechanism. The store can maintain speech-based information only for a few seconds [24.2, 5]. If longer maintenance is required, then the articulatory loop can rehearse the information, a process comparable to subvocal speech [24.1].

The phonological loop component of the WM model continues to provide a parsimonious account of a number of verbal memory phenomena. Firstly, the phonological similarity effect describes how memory span is lower for lists of visually presented acoustically similar verbal items compared to lists of dissimilar sounding verbal items (B, V, P, T, G versus X, R, J, Y, S). Furthermore, errors made in this task are typically phonological rather than visual (i. e., recalling a C instead of a T). As a result of this finding, *Conrad* [24.33] argued that short-term storage of verbal materials must rely on recoding visual letters into subvocal auditory codes. (Note that such subvocal processing presumably involves sensorimotor-related codes, i. e., codes related to vocalization. This issue will become important when we discuss the *tonal loop*.) This argument has remained a principle of the WM model ever since. Phonological similarity is disruptive to memory as the phonological codes become confused either during the storage or retrieval phases of recall [24.34, 35].

A second, well-established finding in verbal memory research is that maintenance and rehearsal of stored material in the articulatory loop can be interrupted by articulatory suppression [24.1, 2], and overt or covert movement of the articulators including the jaw, tongue and throat musculature [24.28, 34, 36–39]. According to theory, articulatory suppression gains obligatory control over at least part of the articulatory loop within WM, which then reduces the overall functionality of the phonological loop by preventing the basic recoding of visually presented materials into (sensorimotor-related) phonological codes and/or disrupting the rehearsal process [24.27, 40].

Finally, the word length effect demonstrates that subvocal rehearsal within the articulatory loop is likely to occur in real time. People achieve greater memory spans [24.28] and superior recognition accuracy [24.36] for lists of short words compared to lists of long words. Although the word length effect has proved to be one of the most contentious aspects of the WM model [24.41], both the effects of articulatory suppression and of word length suggest that verbal material is maintained within WM in a manner comparable to subvocal speech [24.1, 2, 6].

24.2.2 Tonal Information

Because the *Baddeley* and *Hitch* WM model [24.1, 3] was developed to explain mainly verbal and visual-spatial information, the framework does not specify whether nonphonological information is processed by the phonological loop, or whether, in addition to the phonological loop, different subsystems exist for other materials such as tones [24.12, 15]. We have seen above that verbal material is maintained in WM by internal articulatory rehearsal; can tonal pitch also be maintained in this way?

Studies have found that internal rehearsal improved WM performance for tones [24.14–16]. Other studies, however, report that internal rehearsal only leads to a small improvement of WM performance or no improvement at all [24.42–44]. These conflicting results could be explained by the fact that the experimental stimuli used across these studies differed to the degree to which participants can imitate them. Studies that found a small or no beneficial effect of internal rehearsal used auditory stimuli that were difficult to sing or repeat, because:

1. The pitches of the tones did not correspond to the Western chromatic scale [24.43, 44].
2. The pitch difference between the tones was smaller than one semitone [24.43, 44].
3. Chords were used, which consisted of several simultaneously played sine wave tones [24.42].

By comparison, studies that found a benefit of rehearsal used auditory stimuli with (i) pitches that corresponded to the Western chromatic scale [24.15, 16] and/or (ii) pitch differences larger than one semitone [24.14–16], and are thus easy to sing/repeat. Overall therefore, the data support the assumption that internal rehearsal mechanisms underlie WM for tones.

24.2.3 Comparison Between Verbal and Tonal WM

The majority of auditory WM studies to date have used verbal materials (phonemes, syllables, and words) to explore both storage and rehearsal processes. By contrast, research on WM for pitch, or research comparing verbal and tonal WM, is rather scant and to date provides an inconsistent picture.

Deutsch [24.45] was among the first to conduct an auditory WM experiment and reported that intervening tones interfered more strongly with memory for a single tone compared to intervening phonemes. Deutsch interpreted this result as evidence for a specialized tonal WM system, at least when it comes to the storage of single tones. Furthermore, *Salame* and *Baddeley* [24.46] observed that vocal music interfered more with verbal WM than instrumental music, again supporting the assumption of two independent WM systems for verbal and tonal stimuli.

Semal et al. [24.47], however, criticized the lack of control of the pitch relations between the standard tones and the intervening verbal material in *Deutsch*'s [24.45] study, and argued that this could explain the missing interference between the to-be-remembered tones and the intervening verbal material. In their experiment, pitch similarity of the intervening stimuli, which were either words or tones, modified WM performance to a greater degree than the nature of their modality, suggesting that pitch for both verbal and tonal material was processed in the same WM system. This result was replicated by *Ueda* [24.48] using different stimuli. Furthermore, *Chan* et al. [24.49] showed that better verbal WM performance was associated with musical training, a result also pointing towards overlapping mechanisms underlying verbal and tonal WM.

Few behavioral studies have attempted to compare WM storage using sequences of verbal and tonal materials. Whilst it seems difficult to recreate classic WM storage effects such as phonological similarity in the musical domain, some studies have drawn close parallels in order to compare verbal and tonal WM. *Williamson* et al. [24.18] argued that the phonological similarity effect was based on acoustic confusion at the point of memory storage, an effect that could be represented in music by pitch proximity [24.47]. In *Williamson* et al. [24.18] nonmusician participants recalled sequences of phonologically similar (B, D, G) or dissimilar (M, Q, R) letters and pitch proximal (C4, D4, E4) or distant tones (C4, G4, B4), the notes being balanced according to theory of tonal hierarchy [24.50]. The results replicated the traditional phonological similarity effect with verbal items and saw in parallel a smaller effect of pitch proximity with tonal stimuli. Participants were pretested for their ability to perceive the difference between the tones, meaning that acoustic confusion within memory storage was the most likely explanation for the observed effect. This study supports the theory that storage of both verbal and tonal material in WM is based on acoustic representations of sound. Whilst this finding argues for similar processing constraints in verbal and tonal WM storage it does not, in of itself, support storage system overlap; the principles of storage may be similar for verbal and tonal materials but storage could still be separable, based on the individual codes of speech (phonological store) and tones (tonal store) [24.51].

Studies of rehearsal activity in WM for verbal and tonal material more clearly show support for overlap than is necessarily justified for storage processes. *Schendel* and *Palmer* [24.16] demonstrated that when musicians carry out music suppression (singing *la*) there was decreased recognition accuracy for both digit and tone sequences, in the same manner as with verbal suppression (producing the word *the*), indicating that musical or verbal suppression does not selectively impair verbal or tonal WM. (To our knowledge, there is lack of studies investigating effects of nonphonological sensorimotor suppression, such as moving the fingers of the left hand in string players during a pitch WM task.) *Williamson* [24.52] required nonmusician participants to carry out whispered articulatory suppression while encoding and recalling sequences of letters and tones. She reported that both verbal and tonal WM tasks showed a decrement under articulatory suppression, a finding that could not be accounted for by the dual-task nature of the experiment. This result suggests that subvocal rehearsal of verbal and tonal material may take place in a similar way within the articulatory loop.

24.3 Neural Correlates Underlying WM

24.3.1 Verbal Information

As with behavioral work, most neuroimaging studies that have explored the functional neuroarchitecture underlying auditory WM utilize verbal material. The internal rehearsal of verbal material has been found to be supported by a functional network comprised mainly of Broca's area and premotor areas (as well as the supplementary motor area (SMA) and pre-SMA) [24.53–57]. In addition, data indicates that both the insular cortex [24.54, 58, 59] and the cerebellum [24.57, 60, 61] are involved during the internal rehearsal of verbal information.

The crucial role of Broca's area and the premotor cortex for internal rehearsal has been corroborated by numerous studies (for an overview see [24.1]). Findings regarding the phonological store, however, are much less conclusive. It has been suggested that parietal areas, particularly the inferior parietal lobule [24.53, 54, 56, 60–64], but also the superior parietal lobule [24.53, 60], serve as the underlying neural correlate of the phonological store. However, pinpointing the phonological store in the parietal lobe is controversial. Firstly, neural activity in the parietal lobe has been associated with attention, and therefore activation in this area might also reflect increased engagement of attentional resources [24.65, 66]. Secondly, the coordinates of the reported activation during tasks requiring storage of verbal material differ greatly between studies [24.4]. And finally, passive listening does not activate the inferior parietal lobule (IPL) [24.4, 67], a finding predicted by the WM model [24.3, 4] if this structure is involved in automatically storing incoming auditory information.

As a consequence of these theoretical and empirical inconsistencies, area Spt (Sylvian-parietal-temporal, i. e., left posterior planum temporale), has been suggested as an alternative neural structure underlying the temporary storage of verbal information during WM tasks [24.4] based on the following observations. First, activation in the left Spt was (i) enhanced during the delay period of a WM task [24.13, 68] and (ii) not influenced by the modality of the presented stimuli (auditory or visual [24.68]). In addition, area Spt is involved during the perception and production of speech. Based on these findings it has been suggested that area Spt acts as an auditory-motor interface for WM [24.4, 13, 68], meaning that perception, production and WM are more closely linked than previously believed. This proposition is corroborated by the dual-stream model of speech processing [24.69–72]. This model assumes a ventral stream that supports speech comprehension via lexical access and a left dominant dorsal stream comprising also area Spt, which enables humans to map perceived speech signals onto articulatory representations, and therefore supports sensory–motor integration.

24.3.2 Tonal Information

Far fewer neuroimaging studies have investigated WM for tones than have investigated the phonological loop. *Gaab* et al. [24.73] showed the involvement of the supramarginal gyrus (SMG), the intraparietal sulcus (IPS), the planum temporale, premotor regions encroaching on Broca's area, and cerebellar regions during a pitch memory task in participants that were not selected for musical expertise. The neural network observed in this study is surprisingly similar to the network supporting the phonological loop described above. Another group had previously observed activation of a similar network during a WM task for tones, including the inferior frontal and insular cortex, the planum temporale, and the SMG [24.74].

24.3.3 Comparison Between Verbal and Tonal WM

To our knowledge, only three neuroimaging studies have compared the neuroarchitecture of auditory WM for sequential tonal and verbal material [24.13, 14, 17]. In a functional magnetic resonance imaging (fMRI) experiment, *Hickok* et al. [24.13] studied nonmusicians and compared the neural correlates underlying verbal and tonal WM. The authors presented piano melodies during a tonal condition and pseudoword sentences during a verbal condition. The internal rehearsal of the verbal and tonal materials involved activation of area Spt and premotor regions encroaching on Broca's area [24.13]. A similar functional network was uncovered in a WM recognition study by *Koelsch* et al. [24.14] in which neural similarities between WM for verbal (syllables) and tonal (pitch) material were explored, again in nonmusicians. The functional network observed during verbal rehearsal included the premotor cortex, the anterior insula, the SMG/IPS, the planum temporale, the inferior frontal gyrus, pre-SMA and the cerebellum. Importantly, internal rehearsal of the tonal stimuli relied on a virtually identical network to that activated during verbal rehearsal.

In a follow-up study, *Schulze* et al. [24.17] employed a recognition task to compare the neuroarchitecture supporting the internal rehearsal of verbal and tonal WM. In a replication of the above-described experiment [24.14], both verbal and tonal WM tasks activated structures previously reported during either verbal [24.1, 53, 54, 56] or tonal [24.13, 73, 74] WM processes in nonmusicians, namely Broca's area, the left premotor cortex, (pre-)SMA, left insular cortex, and left IPL. This finding corroborates data from previous experiments, which have reported considerable overlap of the functional networks subserving verbal and tonal WM [24.13, 14]. Importantly, all these core structures activated during tonal WM were also activated during verbal WM in nonmusicians. By contrast, verbal but not tonal WM relied on additional structures, including the right ventrolateral premotor cortex, right IPL, right cerebellum and the left mid-dorsolateral prefrontal cortex (mid-DLPFC). These structures have previously been associated with verbal WM tasks [24.1, 75, 76]. This activation difference between verbal and tonal WM was also expressed in the behavioral data: nonmusicians showed superior performance during verbal than during tonal WM.

In summary, the few neuroimaging studies that have directly compared the structures underlying verbal and tonal WM [24.13, 14, 17] have obtained data from nonmusicians that point towards a considerable overlap of neural resources underlying WM for verbal and tonal material. This common (core) network is mainly left-lateralized and includes fronto-parietal structures, that is premotor cortex, Broca's area, and in two of the three studies also the IPL [24.14, 17] and the cerebellum [24.14, 17], as well as the planum temporale/area Spt [24.13, 14]. (*Schulze* et al. [24.17] did not scan continuously like in the other fMRI studies [24.13, 14], but employed a sparse-temporal sampling scanning technique. Thus, participants did not have to separate scanner noise from the information they had to rehearse, possibly leading to less (or no) activation of area Spt. Another possibility is that the sparse temporal scanning method was not sensitive enough to capture the involvement of area Spt.)

24.3.4 Comparison Between Nonmusicians and Musicians

Speech is a fundamental human skill typically acquired during early childhood. Thus, while both musicians and nonmusicians are trained in processing and producing speech, nonmusicians' expertise in the music domain is comparatively far less developed. This begs the question of whether tonal WM would be different in musicians compared to nonmusicians, where a group difference in verbal WM would not be predicted. In support of this hypothesis *Williamson* et al. [24.18] found that nonmusicians showed effects of both phonological similarity and pitch proximity, whereas musicians showed the former but not the latter. It was suggested that musicians, thanks to their specialized training, develop systems and/or strategies for storing tones that negate the impact of pitch proximity. Nonmusicians, on the other hand, are more likely to store a basic acoustic representation of the tonal sounds that they hear, which are then more vulnerable to the impact of pitch proximity.

Schulze et al. [24.17] directly studied the neural underpinnings of verbal and tonal WM in highly trained musicians to see how they compared to the established WM network in nonmusicians. The aim was to determine if musicians had developed a specialized or alternative system for processing tones. Many of the structures (Broca's area, left premotor cortex, left insular cortex, (pre-)SMA, and left IPL) that were activated more strongly in nonmusicians during verbal WM showed an increased involvement in musicians compared to nonmusicians during tonal WM. That is, the functional network that supported verbal WM in nonmusicians was also used by musicians for tonal WM tasks. In addition, unlike nonmusicians, musicians recruited a number of structures exclusively for either verbal or tonal WM: the left cuneus, the right globus pallidus, the right caudate nucleus, and the left cerebellum supported WM for tonal material; the right insular cortex was exclusively involved in processing verbal information.

On top of these differences, activation distinctions between verbal and tonal WM tasks were reported for a number of structures in musicians, thus supporting the existence of two WM systems, potentially a phonological loop maintaining and processing phonological information and a tonal loop maintaining and processing tonal information. Both WM systems showed a considerable overlap in activation because the same WM core structures were activated. Differences, however, were also observed for both systems in that they relied on different neural subcomponents. Importantly, it is not possible to explain the observed functional differences between the verbal and tonal WM tasks in musicians by citing performance differences between both tasks, because several brain structures were recruited selectively for verbal or tonal WM [24.17, 77]. Instead, musical expertise might facilitate the development of a more extended network underlying tonal WM, which shows similarities to the functional network supporting verbal WM, but also substantial differences.

24.4 Sensorimotor Codes – Auditory WM and the Motor System

To acknowledge the interconnection of verbal WM with speech perception and production, the underlying representations of verbal WM have been named sensorimotor codes [24.78]. In the following we explain and discuss results that indicate internal WM rehearsal for verbal material shares characteristics with speech production.

The word length effect and the articulatory suppression effect, which were described above, support the assumption that verbal WM is similar to subvocal speech (for an overview see [24.1]). In addition, the phonological loop has been conceptualized as a memory system that involves internal articulatory speech actions implemented by motor-related areas such as Broca's area, premotor and insular cortices [24.1, 58], SMA [24.53, 54, 57], and the cerebellum [24.1, 57, 60]. As discussed above, results suggest that tonal WM can be improved by internal rehearsal only if participants are able to imitate and repeat these auditory stimuli [24.14–16, 42–44]. WM thus seems more closely linked to production (i. e., action-related) processes than previously believed. This assumption has been supported by data that compares the neural correlates of verbal and tonal WM between musicians and nonmusicians described above [24.17]. The better performance of nonmusicians for verbal compared to the tonal WM tasks, and the superior performance of musicians compared to nonmusicians for tonal WM tasks, was primarily associated with activation differences in neural structures that have been described to support planning, programming, executing and controlling actions, like Broca's area, premotor cortex, (pre-)SMA, left insular cortex, intraparietal sulcus and IPL, and the cerebellum.

Initially we interpreted these observed behavioral and neurophysiological differences between verbal and tonal WM in nonmusicians as a consequence of the extensive production and rehearsal of verbal material in their daily life, which for nonmusicians is not the case, or is to a lesser degree, for musical material. An alternative but related interpretation is that musical training could lead to a long-term learning of associations between pitch information and motor actions [24.79–83]. As a result of this process, musicians could have developed more elaborate sensorimotor codes supporting the internal rehearsal of tones compared to nonmusicians. Such codes probably include, e.g., finger representations, and codes of finger movements, in piano and string players.

To our knowledge no studies have investigated whether the ability to repeat an auditory stimulus might facilitate its internal rehearsal and therefore increase auditory WM capacity, but there is some indication that mimicry is important for auditory WM [24.84–86]. For example, WM processes for timbres, which are difficult or impossible to mimic, differ from those for tones and words, which are easy to mimic: Whereas WM for timbre seems to rely on a passive sensory trace, WM for verbal and tonal stimuli appears to be maintained by active internal rehearsal processes [24.85]. Furthermore, distractors that share features with hard-to-mimic auditory stimuli are likely to overwrite and degrade their memory trace [24.87, 88].

Interestingly, monkeys, who are not vocal learners and therefore cannot learn to mimic unfamiliar auditory stimuli, seem to rely only on a *passive form of auditory STM* (the authors [24.89] referred to a passive form of STM to explicitly distinguish it from WM, therefore this term has also been used here. Otherwise, as explained in the introduction, in the present chapter no distinction has been made between STM and WM): *Scott* et al. [24.89] used a small set of sounds from different categories (pure tones, environmental sounds, monkey calls, etc.) and observed that monkeys performed very poorly on an auditory serial delayed match-to-sample task. The authors observed an *overwriting* effect for auditory stimuli (including monkey vocalizations) that was far greater compared to that in the visual domain, indicating that the observed performance in monkeys depended on the passive form of STM and not on WM. Interestingly, when humans are tested on auditory stimuli that they cannot mimic, they too seem to rely on passive auditory STM [24.87, 88].

The idea that auditory WM relies on the assistance of the motor system is further supported by patient studies. Speech disorders such as speech apraxia, a disorder of speech planning and programming [24.90], are associated with decreased performance in a verbal WM task [24.91]. Another piece of evidence comes from the investigation of the three-generational KE family, half of whom suffer from a speech and language disorder caused by a mutation of the FOXP2 gene [24.92, 93]. Although the speech impairments of the affected KE (aKE) family members are widespread, their core deficit is in executing orofacial, especially articulatory, sequences. The structural and functional cortical abnormalities in the aKE also include the inferior frontal (Broca's) area and ventral premotor cortices [24.92, 94–96]. The first study to compare WM in aKE and controls used a test [24.97] based on the Baddeley and Hitch WM model and analyzed the different components of WM separately – the central executive, the phonological loop, and the visuospatial sketchpad [24.98]. Compared to controls (the control group was matched to the aKE for age and performance IQ), the aKE performed only worse for the tasks related to the phonological loop. Importantly, the aKE members were also impaired in the recognition-based subtest of the phonological loop *word list matching*, in which repetition (i. e., motor output) of speech-based material is not required. Results thus suggest that the aKE, who show both structural and functional abnormalities in Broca's area, a structure underlying phonological and auditory WM (see above), could be specifically impaired in phonological WM but not other domains of WM. This indicates an association between the speech difficulties of the aKE members and their representations underlying internal rehearsal of speech-based material in phonological WM [24.98].

Interestingly, just as with auditory WM, auditory LTM appears to require the assistance of the (oro)motor system. *Schulze* et al. [24.99] tested whether a sound that can be neither mimicked nor labeled can be stored as a long-lasting representation for subsequent recognition by comparing participants' ability to recognize different auditory stimuli that varied widely in the degree to which they could be reproduced or labeled (words, pseudowords, nonverbal sounds, and reversed words, i. e., words played backwards, were presented auditorily). Participants listened to a list of 10 stimuli once for familiarization (study list), and then, after a 5 min interval filled with a counting task to block WM, were presented with these 10 items from the study list again in random order intermixed with 10 new items (recognition list), and had to make an old-new judgment for each of these items. The results were clear; participants showed recognition difficulty only for the reversed words, which were hard either to mimic or to label with an associate. Importantly, a control experiment demonstrated that recognition difficulty was not due to a perceptual failure. The participants' poor memory performance of the reversed words supports the proposal that a sound's pronounceability – its potential to activate subvocally the speech production system, potentially via an auditory mirror-neuron system [24.100, 101] – may be essential for generating a long-lasting representation of that sound.

In summary, sensorimotor processes are thought to be involved in the rehearsal and representation of information in auditory, verbal and tonal WM [24.13, 14, 17, 102, 103] and thus may play in important role during the representation and manipulation of auditory information. These action-related sensorimotor codes are assumed to rely on motor knowledge – how to produce the auditory stimulus (e.g., syllable, tone). The dual-stream model of speech processing [24.69, 71, 72] suggests that sensory–motor integration, i. e., mapping the perceived speech signals onto articulatory representations is one of the functions of the dorsal path of the auditory system. Results indicate that the superior longitudinal as well as the arcuate fasciculi [24.104] form the dorsal stream. Speech production requires motor speech representations as well as representations of sensory speech targets to compare between predicted and actual consequences of motor speech acts [24.70]. Sensorimotor integration also seems to play a role during singing [24.105, 106]. Therefore, we propose that internal rehearsal associated with auditory WM relies on sensorimotor representations, which also underlie singing and speaking.

24.5 The Influence of LTM on Auditory WM Performance

WM is a limited-capacity system in terms of how much information can be stored and for how long [24.1, 28, 107]. However, the use of a strategy based on information stored in LTM can improve WM performance, for example by chunking the to-be-remembered information [24.108, 109]. During chunking, items are organized into one unit or chunk [24.107], resulting in stronger associations between items within one chunk than between chunks [24.110]. This process is thought to be supported by the episodic buffer, which enables features from different sources to be bound [24.6]. Previously, the neural correlates underlying such strategy-based memorization were explored for the visual–spatial or verbal domain [24.111–114], but it was largely unknown whether a similar functional network was also involved during the strategy-based WM for tones.

By using structured (all tones belonged to one tonality) and unstructured (atonal) five-tone sequences, *Schulze* et al. [24.115] investigated: (i) whether musical structure influences performance on a nonverbal auditory WM task, and if so, (ii) how this is reflected in the brain of nonmusicians and musicians. Musicians, but not nonmusicians, performed better for the structured than for the unstructured sequences, indicating that musicians' knowledge about musical regularities helped them to maintain the structured sequences in WM [24.116–119]. In terms of brain responses, musicians showed stronger involvement of a lateral (pre)frontal–parietal network during the memorization of the structured sequences, including the right inferior precentral sulcus and the premotor cortex, as well as the left IPS. A similar network has been described previously to support strategy-based WM processing for visual and auditory–verbal stimuli [24.111, 113, 114]. The combined results point towards a modality-independent (pre)frontal–parietal network subserving strategy-based WM. A follow-up behavioral study by *Schulze* et al. [24.120] has confirmed the facilitating effect of tonality (structure) on tonal WM performance in both musicians and nonmusicians, but only during memory maintenance (forward task) and not complex memory manipulation (backward task).

24.6 Summary and Conclusion

This chapter reviewed and discussed research results demonstrating behavioral, structural, and functional differences and similarities between verbal and tonal WM. Whereas the core structures, namely Broca's area, premotor cortex, and IPL, show a substantial overlap, results in musicians suggest that there are also different subcomponents involved during verbal and tonal WM tasks. If confirmed, these results indicate that musicians develop either independent tonal and phonological loops or unique processing strategies that allow novel interactive use of the WM systems. In addition we discussed behavioral and neuroimaging results that provide substantial support for a strong link between sound mimicry and auditory

WM. Sensorimotor processes are thought to be involved in the rehearsal and representation of information in auditory WM. These action-related sensorimotor codes are assumed to rely on motor knowledge – how to produce the auditory stimulus (e.g., syllable, tone).

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