The visual world around us is rich in detail but we are able to only represent a very small subset of that information. For adaptive behavior it is therefore critical that we limit our neural processing machines to information that is directly relevant rather than focusing on every single bit of information that hits the retinae. Mechanisms of selective attention and its dynamic interplay with the content of VWM allow us to selectively process the most relevant information in a visual scene. VWM and attention to a large extent recruit the same machinery, which not only has the advantage that attention can be shifted in a similar fashion between perceptual and memory representations, but at the same time allows the content of VWM to interact with perceptual selection. In the preceding chapters I have discussed several aspects of this bi-directional interaction between VWM and attention. Here, I will summarize the most important findings and try to integrate them into existing frameworks of VWM.

The opening example of this dissertation, where I asked you to locate a green car in the red section of the airport’s parking lot, illustrates that VWM not only holds visual information online, it also needs to prioritize this information during sequential moments in time. Whereas one memory representation is directly relevant, (e.g. red section), other information is stored for later use and therefore temporarily irrelevant to the current cognitive operations (e.g. green car). To prevent interference from such irrelevant memory representations VWM needs to continuously monitor which of multiple representations is most relevant for the task at hand and adjust priority settings accordingly. In this dissertation, I have used two different approaches to impose such a temporal dissociation, one where already at encoding it was clear when a memory would become relevant and one where only after encoding it became clear when each memory representation needed to be prioritized. The results of these two approaches converge to a single conclusion, namely that VWM is a very flexible system in which information can be represented via different representational states, one active state that guides attention to matching perceptual input and a more passive state that nevertheless supports accurate memory. Moreover this dissociation
within VWM is not static, as retro-active shifts of attention can raise the status of previously deprioritized memories, and vice versa.

Contemporary models of VWM conceptualize information being held in memory as existing in several states of activation – states that are determined by the allocation of attention. The results of Chapter 8 are directly in line with such a theoretical framework. We were able to reconstruct the specific location held in memory via the topographic distribution of alpha-power, but only when covert attention could exclusively be focused on the internal memory representation. Instead, when the task required observers to shift covert attention to another location during the delay period, reconstruction of the memorized location temporarily deteriorated, while a reliable reconstruction of the attended location emerged. The loss of location specificity for the memorized location in alpha-band topography, however, was not irreversible, as a second shift of attention reinvigorated the memory reconstruction. A similar pattern was observed in a recent study by Sprague et al. (2016) who demonstrated that a degraded memory representation, as indexed with an image reconstruction technique, could be restored when prioritized by a retro-cue. Together, these studies suggest that changes in priority settings are accompanied by a switch in storage mechanisms.

Although speculative, one idea is that the prioritized information is brought to (or kept in) the focus of attention, whereas the deprioritized information is maintained in a more an activity silent format. Indeed, recent work theorizes that information can also be maintained in the absence of sustained neural firing, possibly via transient elevations of calcium levels in presynaptic neurons (Mongillo et al., 2008) or via subthreshold membrane potential depolarization (Erickson et al., 2010). Consistent with such a view, it has been shown that when one of two memory representations is retrospectively cued as being temporarily irrelevant, multivariate decoding accuracy for the uncued memory drops to chance (LaRocque et al., 2013; LaRocque et al., 2016; Lewis-Peacock et al., 2012).
In Chapter 8 the temporal sequence of events was fixed such that observers knew beforehand at what moment in time the memory representation was irrelevant and when it would become relevant again. One possibility therefore is that the VWM representation was strategically deprioritized such that it did not interfere with the ongoing task, but nevertheless could be restored when deemed relevant again. In Chapter 7 we aimed to get a better understanding of the fate of the deprioritized information in VWM. For this purpose we included a second retro-cue on a subset of trials to examine whether information that was retroactively assigned as irrelevant for subsequent behavior could still be recalled when attention was shifted back again. It was found that the retro-cue benefit was accompanied by a cost for the uncued information in VWM, indicating that shifting attention goes at the expense of the non-selected information in memory. Importantly this retro-cue cost could only partly be restored by a second cue such that performance was back to the same level as on no-cue trials.

The results of Chapter 7 indicate that the status of VWM is not static but can be adjusted to new priority settings by internal shifts of attention. These shifts of attention between representations inevitably create different levels of robustness within VWM. Whereas the deprioritized information is maintained in a format that is sensitive to degradation processes, the prioritized information is maintained in a privileged, protected state. The results of Chapter 6 demonstrate that it takes about 400 ms to fully implement these new priority settings as from that moment on prioritized information was no longer susceptible to the deteriorating effects of irrelevant visual input.

The chapters discussed so far provide corroborating evidence for the idea that the mechanics of VWM allow for a rapid reorganization of the representational content. A striking aspect of these results is that following new priority settings attentional resources are redistributed, even when the information within VWM is well within the traditional capacity limits of about 4 items (Zhang & Luck, 2008). In Chapter 7 we observed reliable retro-cue costs at load 2 and in Chapter 8 we showed that alpha-band reconstruction deteriorated, even though the memorized location was the sole representation in memory. Apparently, already at
load 2 it is advantageous to represent information via different states, even when the deprioritized information is known to become relevant again at a later stage. This raises the question how information in VWM is represented before the temporal order in which representations become relevant is established. One possibility is that the privileged state (i.e. the focus of attention) can only represent a single representation at a time such that it needs to stay vacant until it is clear which representation is most relevant for the upcoming task. Or there is a rapid resampling such that memory representation in turn are maintained within the focus of attention. Alternatively, initially multiple representations are held within the focus of attention, but as soon as one of these is prioritized, the other representations are put at a low ebb to prevent inter-item interference (Pertzov et al., 2013).

Chapters 2-4 were set out to dissociate between these two alternatives. The idea here was that information in VWM will interact with perceptual selection, but only if that information is maintained within the focus of attention and therefore adopts the status of attentional template (Olivers et al., 2011). In Chapters 2 and 3 the content of VWM interfered with a visual attention task, but only when VWM was filled with a single item. When memory was loaded with two colors VWM-based attentional capture completely disappeared, unless one of these colors was retroactively prioritized. In Chapter 4 we replaced the attentional capture paradigm with a b-CFS paradigm, which we argued would be more sensitive to VWM-based biases at higher loads. Here, we again observed a clear load constraint, but now at load 2 VWM-based facilitation was still reliable. Overall, the results of these chapters provide somewhat of a puzzle. Whereas the data of the first two chapters suggests that the mutual inhibition between multiple VWM representations prevents any of them to take on the status of attentional template, the data of Chapter 4 argues against such an interpretation. In Chapter 4 there was clear evidence for an interaction between VWM and perceptual selection at load 2, although it remains speculative whether this interaction was driven by a single template or by multiple representations simultaneously.
The discrepancy in our first three chapters is also reflected within the literature that shows supporting evidence for both a single and a multiple-item template account (Beck et al., 2012; Hollingworth & Beck, 2016; Olivers et al., 2011). The experiments presented in this dissertation do not resolve this discrepancy. However, they do provide new important insights that might help us understand why in some cases multiple VWM representations bias perception, but in other cases this happens only weakly or not at all. A notable difference between chapters that observed no evidence whatsoever for VWM-based biases at load 2 and the chapter that did, is that in the latter the memory match not only facilitated target selection, but it also took longer to detect the target. Consequently, observers may not only have had an incentive to use the memory content, the larger time window also created more opportunity for memory representations to bias selection. One possibility thus is that the level of VWM driven activation at load 2 is generally insufficient to interact with perception, unless the threshold for this interaction is lowered by specific manipulations. Consistent with this hypothesis, Hollingworth and Beck (2016) only found evidence for VWM-based attentional capture at load 2 when they included distractors matching both colors in memory or when they replaced the singleton-shape task by a more inefficient search task. In this respect it is interesting that in Chapter 3 retrospective cues almost instantaneously changed the attentional status of memory representations that were otherwise shielded from perception, as if the level of activation before the cue was only marginally below threshold. Future experiments are needed to establish whether such a variable threshold account can explain the discrepancy in results.

Regardless whether VWM can contain multiple or only a single item in the focus of attention, our results demonstrate that the status of a memory representation and not the quality of that representation determines whether or not it will interact with perception. When we limited our analysis to those trials where observers had a relatively poor representation of the only item in memory and a relatively precise representation of both items in memory, we still only observed VWM-based attentional capture at load 1 (Chapter 2, see also Hollingworth &
Hwang, 2013). Finally, the findings of Chapter 5 extend this idea to LTM. Here, we found that with repetition of the prospective memory, which was assumed to transfer the memory representation from VWM to LTM, its effect on attention rapidly diminished, while memory continued to improve. This stands in contrast to repetition of the target, which has been shown to result in increased attentional guidance by the target representation (e.g. Maljkovic & Nakayama, 1994). Taken together, this demonstrates that as a whole memory is a very flexible system, that dependent on the task context can either interact with or be shielded from perceptual input.