Journal of Experimental Psychology: Learning, Memory, and Cognition

Distinguishing Between Temporary and Permanent Removal in Verbal Working Memory

Miriam Tortajada, Víctor Martínez-Pérez, Lucía B. Palmero, Luis J. Fuentes, and Guillermo Campoy

Online First Publication, April 7, 2025. https://dx.doi.org/10.1037/xlm0001481

AMERICAN PSYCHOLOGICAL ASSOCIATION

Journal of Experimental Psychology: Learning, Memory, and Cognition

ISSN: 0278-7393

https://doi.org/10.1037/xlm0001481

Distinguishing Between Temporary and Permanent Removal in Verbal Working Memory

Miriam Tortajada[1], Víctor Martínez-Pérez[1], Lucía B. Palmero[2], Luis J. Fuentes[1], and Guillermo Campoy[1]

[1] Department of Basic Psychology and Methodology, Faculty of Psychology and Speech Therapy, University of Murcia

[2] Department of Psychology, University of Castilla-La Mancha

We employed the retro-cue paradigm to examine performance improvements resulting from permanent versus temporary removal in verbal working memory. Permanent removal entails discarding a subset of working memory representations marked as definitively irrelevant, while temporary removal involves momentarily setting aside the uncued subset of representations from the attentional focus, preserving accessibility for later refocusing. We observed that both permanent and temporary removal led to marked progressive reductions in reaction time and errors across cue-target intervals (200, 400, 800, and 1,600 ms), reflecting the gradual simplification of the search set following informative cues. Although removal conditions did not differ in accuracy, responses were slower in the temporary removal condition, especially at the longest interval. A key finding was that performance in the temporary removal condition, but not in the permanent removal condition, was modulated by the presentation order of the target's memory set. This order effect was also observed in a nonremoval control condition where double retro-cues marked all presented information as relevant. We suggest that order effects depend on maintaining the integrity of the retrieval framework (all the contextual cues) needed to guide attentional access to specific representations, including those provisionally set aside in the temporary removal condition. We conclude that the primary distinction between permanent and temporary removal processes is that only permanent removal simplifies the retrieval framework by removing unnecessary contextual cues, resulting in a greater reduction in the complexity of the search set compared to temporary removal.

Keywords: verbal working memory, retro-cue paradigm, removal, attentional focus, working memory updating

Working memory (WM) is the cognitive system that enables a limited set of mental representations to be readily available for ongoing cognitive tasks. Traditional models posited the existence of specialized stores (e.g., the phonological store) dedicated to holding WM representations (Atkinson & Shiffrin, 1968; Baddeley & Hitch, 1974). The prevailing view today, however, is that WM and declarative long-term memory share a common representational substrate, with WM representations being in a transitory state that allows them to be more immediately available than long-term memory representations (Cowan, 1995; Oberauer, 2002, 2009; Ruchkin et al., 2003). This second view usually comes with the additional assumption that, within WM, representations may differ in the degree to which they can be accessed and manipulated. The most crucial distinction is between representations currently attended (or currently included in an attentional refreshing loop) and those that have been temporarily left aside but remain in a state of privileged accessibility (Mallett & Lewis-Peacock, 2018; Oberauer, 2002; Oberauer & Awh, 2022; Oberauer & Hein, 2012; Olivers et al., 2011). These two levels of accessibility of WM representations may correspond to two different underlying neural mechanisms, persistent neural firing and some form of short-term synaptic plasticity (Masse et al., 2020; Miller et al., 2018; but see Stokes et al., 2020, for alternatives). Congruently with this view,

Eddy J. Davelaar served as action editor.

Miriam Tortajada https://orcid.org/0000-0002-3871-8283

Víctor Martínez-Pérez https://orcid.org/0000-0003-0358-346X

Lucía B. Palmero https://orcid.org/0000-0001-5693-6500

Luis J. Fuentes https://orcid.org/0000-0002-3203-9976

Guillermo Campoy https://orcid.org/0000-0002-3532-9178

Data are available at https://doi.org/10.5281/zenodo.12085678 (Tortajada, Martínez-Pérez, et al., 2024). This study was not preregistered.

The authors have no known conflicts of interest to disclose. This research was funded in whole, or in part, by the European Commission (Grant PID2021-125408NB-I00). For the purpose of open access, the author has applied a CC BY public copyright license to any Author Accepted Manuscript version arising from this submission.

Miriam Tortajada played a lead role in conceptualization, data curation, formal analysis, investigation, software, visualization, writing–original draft, and writing–review and editing. Víctor Martínez-Pérez played a supporting role in conceptualization, formal analysis, investigation, methodology, and writing–review and editing. Lucía B. Palmero played a supporting role in conceptualization, formal analysis, investigation, methodology, and writing–review and editing. Luis J. Fuentes played a lead role in funding acquisition, project administration, and resources and a supporting role in conceptualization, formal analysis, methodology, and writing–review and editing. Guillermo Campoy played a lead role in conceptualization, data curation, formal analysis, investigation, methodology, software, supervision, writing–original draft, and writing–review and editing.

Correspondence concerning this article should be addressed to Guillermo Campoy, Department of Basic Psychology and Methodology, Faculty of Psychology and Speech Therapy, University of Murcia, Campus de Espinardo, Murcia 30100, Spain. Email: gcampoy@um.es

some studies trying to decode WM representations from functional magnetic resonance imaging and electrophysiological neural signals have found that only attended representations can be effectively decoded (at least with the current technical means), while non-attended WM contents can transition from an undecodable state to a decodable one as it shifts from irrelevant to relevant for the ongoing mental operation (LaRocque et al., 2013, 2017; Lewis-Peacock et al., 2012; Rose et al., 2016; Sprague et al., 2016; Wolff et al., 2017; but see Christophel et al., 2017, 2018). These findings reinforce the pertinency of distinguishing between attended (neurally active) and nonattended (dormant but still privileged) WM representations.

In real life, there are many situations in which a subset of WM representations must be temporarily set aside to minimize interference with the current mental operation, but in a way that allows these contents to be maintained in WM for later attentional refocusing. Consider, for example, situations such as mentally solving a reasoning problem, comprehending an intricate sentence we have just heard, or mentally performing an arithmetic operation. Typically, these tasks are segmented into steps that require focusing on a different portion of the information held in WM. Therefore, as one progresses through these steps, different subsets of representations are dynamically transferred in and out of the attentional focus. We will use the term "temporary removal" to refer to the operation of disregarding from the attentional focus WM representations that are currently unnecessary but that will need to be refocused in a forthcoming step of the current task (Kim et al., 2020; Lewis-Peacock et al., 2018). We assumed that these temporarily unattended representations remain within WM in a dormant but privileged state of easy accessibility.

In contrast to temporary removal, there are also many instances during the execution of WM tasks where a portion of the attended information ceases to be relevant for good. In a mental calculation task, for example, once a partial operation is completed and its result is maintained in WM, information about that partial operation becomes unnecessary and can be permanently removed from WM. Due to the limited capacity of WM (Cowan, 2010), having a mechanism dedicated to eliminating contents that have become definitively irrelevant seems crucial to maintaining the system's proper functioning (Lewis-Peacock et al., 2018). Some evidence for such a beneficial effect of permanent removal comes from studies employing the retro-cue paradigm (Griffin & Nobre, 2003) with 100% valid cues. The procedure in these studies involved the supply, after the initial encoding, of a cue pointing out a set of the presented items as the only relevant for the imminent memory test. The assumption is that, following cue presentation, attention focuses on the relevant information while a removal mechanism operates on the uncued WM representations. With this procedure, it has been observed that the performance cost associated with the irrelevant set progressively diminished during the first seconds immediately following the cue, which has been interpreted as reflecting the time course of the removal of the uncued contents from WM (Oberauer, 2001, 2002, 2018; Souza et al., 2014). Since irrelevant sets in these situations are marked as definitively unnecessary, we term the type of removal involved as "permanent removal" (Lewis-Peacock et al., 2018).

An intriguing question regarding temporary and permanent removal revolves around the similarities and differences between these two mechanisms. Both mechanisms appear to involve removing the information deemed unnecessary for the ongoing mental operation from the attentional focus while attention focuses on the relevant content. Differences, therefore, might concentrate on operations related to the accessibility level of the unattended information and how easily representations left aside can be refocused by attention when necessary. In this regard, it has been proposed that permanent removal operates by gradually disrupting the binding of items and their context through Hebbian antilearning (Lewis-Peacock et al., 2018; Oberauer, 2018). Unattended representations, therefore, are not obliterated but merely disconnected from their associated context. This would explain why irrelevant items, including those belonging to previous trials, generate strong interference when presented as negative probes in Sternberg-like tasks, even after long intervals since that information was flagged as irrelevant (Berman et al., 2009; Campoy, 2011, 2012; Oberauer, 2001, 2018). Although the irrelevant representations were not obliterated during permanent removal, the fact that they were unbinding from the current context simplifies search processes and facilitates the encoding of new items by reducing cue overload (Dames & Oberauer, 2022; Festini & Reuter-Lorenz, 2014; Souza et al., 2014). From this perspective, the main difference between permanent and temporary removal would be that context-content bindings should remain intact after temporary removal to enable the subsequent retrieval of this information for the attentional focus (Koch et al., 2013; Lewis-Peacock et al., 2018). Considering that the enhancement in performance associated with permanent removal partially arises from the unbinding of items from their context, a process absent in temporary removal, it logically follows that temporary removal would likely lead to a smaller improvement in performance compared to permanent removal. This represents a simple prediction that aligns seamlessly with intuition. However, as far as we know, it has not been experimentally tested. The main purpose of this study is to address this gap.

We rely on the retro-cue paradigm with 100% valid cues outlined above. The condition designed to evaluate permanent removal mimics previous studies. Two sets of items were sequentially presented, followed by a cue marking one of the sets as the one relevant for the upcoming memory test, which was applied after a variable brief interval (the cue-target interval [CTI]). Based on previous findings, performance was anticipated to improve as the CTI increased, reflecting the time course of uncued-set removal (Oberauer, 2018). The temporary removal condition was created by adding, immediately following the response, a second memory test on the other set, the one initially marked as irrelevant. The existence of this second test forced participants to maintain the irrelevant set in an accessible state during the first interval. Introducing a second response regarding previously irrelevant information is not new (LaRocque et al., 2013; Oberauer, 2005). What is novel is incorporating both single-response and double-response trials within the same experiment in a fully predictable manner (allowing participants to apply the most suitable removal mechanism in each case) and keeping all other experimental parameters equal to enable direct comparison. Since there were different CTIs, we could compare not only the global effect of permanent and temporary removal but also their temporal course.

In addition to these key conditions, we introduced two single-response control conditions to provide baseline comparisons. One had double retro-cues, so the two memory sets were marked as relevant. This control condition was needed to verify that removing the irrelevant set, either permanently or temporarily, enhances performance. In the other control condition, only one memory set was presented at encoding, followed by a cue redundantly marking that set as relevant (to keep the trial structure consistent). We anticipated observing a progressive convergence of performance in conditions with removal toward the performance in this second control condition as the amount of WM representations in the attentional focus became equated across CTIs.

Besides comparing the beneficial effect of permanent and temporary removal and their temporal courses, we aimed to investigate two additional issues. The first of these was not initially considered but gained prominence through the results of two pilot studies conducted before the one described here. In these pilots, we found that performance in the temporary removal condition, but not in the permanent removal condition, significantly depended on whether the cued set was the one presented first or second during initial encoding. Hence, we decided to design the present experiment considering this factor, which ultimately proved crucial for interpreting the results (as we elaborate in the Discussion section).

The second additional issue we aimed to address pertains to the second response in the temporary removal condition (the only one with two tests per trial). Specifically, we were interested in whether the length of the CTI preceding the first response would influence performance on the second test. If performance on the first test improves with longer CTIs due to participants having more time to complete the removal of the uncued set, then a prediction arises that the positive effect of CTI length on the first response may be accompanied by a negative mirror effect on the second response, when the removed set must be attentionally retrieved. We also tested this prediction.

A final methodological consideration concerns the memory set size, which was four items. This specific set size was chosen to ensure that participants were not compelled to focus on a subset of the information due to a limitation in the capacity of the attentional focus. This approach allowed us to attribute the observed results to the strategic decision of focusing on the cued subset, rather than being forced by capacity limitations. A limited set size enables us to study removal as an outcome of strategic processes guided by task goals, without the confounding influence of processes more related to unintentional forgetting.

Method

Participants

Fifty-six undergraduate students (43 females and 13 males; $M_{\text{age}} = 20.57$ years; $SD_{\text{age}} = 2.31$) from the University of Murcia participated for course credit. The number of participants was determined after conducting a simulated power analysis using the Superpower R package (Lakens & Caldwell, 2021). The mean reaction time (RT) values for each condition were based on pilot data and aligned with patterns observed in previous research (Oberauer, 2018; Tortajada, Fahrenfort, et al., 2024). This analysis estimated a sample size of 52 to achieve a power of 0.80 for the three-way interaction of our $4 \times 4 \times 2$ within-participants design, assuming a medium partial eta-squared effect size (0.053). The final number was 56 because we needed a multiple of eight (see the Procedure section). Three participants initially included in the sample were replaced due to poor performance (see the Results section).

All participants reported normal-to-corrected vision. This study was approved by the University of Murcia Ethics Committee and was conducted according to the ethical standards of the 1964 Declaration of Helsinki.

Materials

The experiment was controlled by a computer program written with E-Prime 3.0 (*Psychology Software Tools*, 2016). Stimuli were presented on a 22″ monitor while responses were collected via Chronos devices. Participants were tested individually in sound-attenuated booths.

Procedure

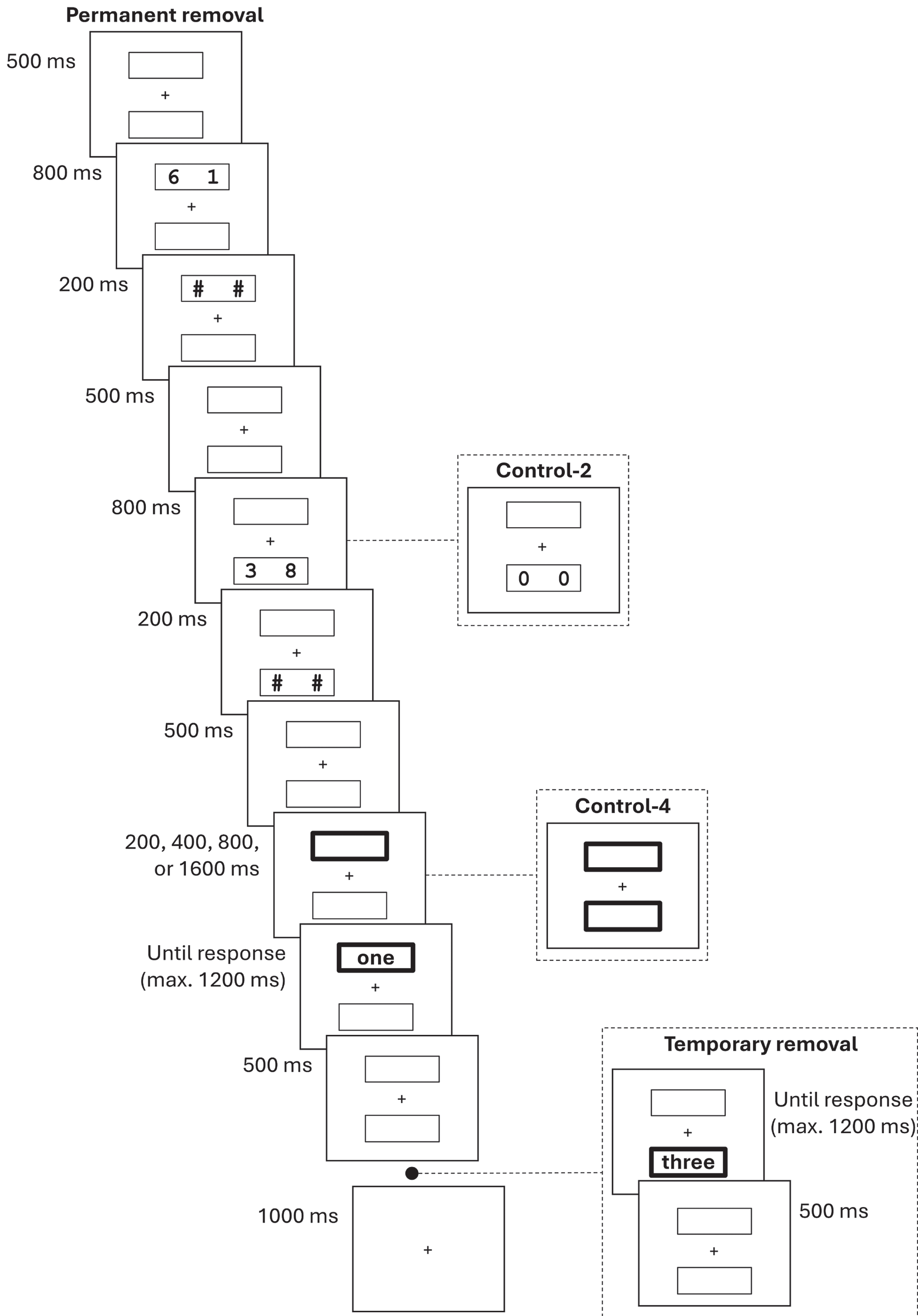
The participants completed 192 experimental trials divided into four blocks of 48 trials. These blocks corresponded to the four experimental conditions: permanent removal, temporary removal, Control 4, and Control 2, implying that all trials of the same type were presented consecutively. Preceding each block, participants received instructions and completed 16 practice trials.

We will begin by describing the procedure used in the permanent removal condition. Afterward, the differences between this condition and the other three conditions will be outlined. Following the same strategy, Figure 1 depicts the procedure for the permanent removal condition as a complete example, highlighting only the differences for the other three conditions.

Trials began with two empty rectangular frames with a narrow black border displayed against a white background (Figure 1). These frames appeared symmetrically above and below a centrally located fixation point. After 500 ms, two digits were simultaneously presented within one of the frames (the presentation Frame 1) for 800 ms, followed by a 200-ms mask (two "#" signs). After an interval of 500 ms, two different digits were presented in the other frame (the presentation Frame 2) following the same procedure. The four digits in each trial were randomly selected from 1 to 9 with the following restrictions: (a) All four digits had to be different; (b) no two consecutive numbers were allowed within a frame; (c) no digit could appear in the same position (left or right) as in the previous trial, regardless of whether it appeared in the same frame or not; and (d) the two digits in a frame were not allowed to be the same as the two numbers presented in a frame from the previous trial, regardless of whether it was the same frame or not. After 500 ms, the border of one of the presentation frames thickened (by a factor of 10), cueing participants that only the items that appeared in that frame were relevant for the upcoming memory test. Finally, after a CTI of 200, 400, 800, or 1,600 ms, one of the two numbers that had appeared in the cued frame was displayed within the same frame in its alphabetical form. Participants were instructed to indicate, as fast and accurately as possible, the location (left or right) where that target number had previously appeared by pressing the left or right bottom of the Chronos device, respectively. Targets remained visible until response or until a maximum of 1,200 ms elapsed. As feedback, the screen briefly flashed red (50 ms) following incorrect responses or failures to respond within the 1,200-ms time window. The next trial commenced after a 1,500-ms interval (subsuming the 50-ms feedback if provided).

Trials in the other three conditions differed only in the following aspects. In the temporary removal condition, 500 ms after the first

Figure 1
Schematic Representation of the Experimental Procedure



Note. max. = maximum.

response, the border of the uncued frame thickened, and one of the numbers previously presented within that frame appeared in alphabetic form. Participants then provided a second response following the same procedure as in the initial one. In the Control 4 condition, the two presentation frames were cued, marking the four digits as relevant for the upcoming test. In the Control 2 condition, digits from the frame assigned to be the uncued one were replaced by zeros at the initial presentation, so only two digits had to be encoded and maintained. Note that retro-cues were noninformative in the Control 4 condition and valid in the other three conditions. Invalid retro-cues were not used because the goal was to examine how the opportunity to discard irrelevant information improves performance on tests on the relevant subset. A retro-cue reliability of 100% facilitated that participants trust the retro-cue and use it to focus on the relevant subset.

The 48 trials of each block were designed to ensure equal representation of all the combinations of target presentation frame (1 or 2), target location (left or right), and CTI (200, 400, 800, or 1,600 ms). At least one participant was randomly assigned to each of the 4! × 2 = 48 arrangements resulting from combining the administration order of the four blocks and the location of the presentation Frame 1 (above or below the fixation point; note that the set appearing in the presentation Frame 1 is the one presented first at initial encoding). Across participants and Frame 1 locations, each of the four block types was administered the same number of times in each position.

The average duration of the experimental session, including instructions, practice trials, and rest breaks between blocks, was 34 min.

Table 1
Post Hoc Comparisons Between Conditions Across CTIs

Comparison	Interval	*M* difference	Cohen's *d*	*t*	*p*
PR–TR	200 ms	−23 ms	−0.25	−2.430	.064
	400 ms	−12 ms	−0.14	−1.286	.597
	800 ms	−27 ms	−0.29	−2.771	.030
	1,600 ms	−43 ms	−0.46	−4.415	<.001
	Total	−26 ms	−0.29	−3.624	<.001
PR–C2	200 ms	76 ms	0.82	7.872	<.001
	400 ms	34 ms	0.37	3.574	<.001
	800 ms	1 ms	0.02	0.143	.886
	1,600 ms	2 ms	0.03	0.249	1.000
	Total	29 ms	0.31	3.935	<.001
PR–C4	200 ms	−51 ms	−0.56	−5.310	<.001
	400 ms	−99 ms	−1.08	−10.273	<.001
	800 ms	−136 ms	−1.48	−14.139	<.001
	1,600 ms	−163 ms	−1.76	−16.857	<.001
	Total	−112 ms	−1.22	−15.483	<.001
TR–C2	200 ms	99 ms	1.08	10.302	<.001
	400 ms	47 ms	0.51	4.861	<.001
	800 ms	28 ms	0.31	2.913	.028
	1,600 ms	45 ms	0.49	4.663	<.001
	Total	55 ms	0.60	7.559	<.001
TR–C4	200 ms	−28 ms	−0.30	−2.880	.024
	400 ms	−87 ms	−0.94	−8.987	<.001
	800 ms	−110 ms	−1.19	−11.369	<.001
	1,600 ms	−120 ms	−1.30	−12.442	<.001
	Total	−86 ms	−0,93	−11.859	<.001
C2–C4	200 ms	−127 ms	−1.38	−13.182	<.001
	400 ms	−134 ms	−1.45	−13.847	<.001
	800 ms	−138 ms	−1.50	−14.282	<.001
	1,600 ms	−165 ms	−1.79	−17.106	<.001
	Total	−141 ms	−1.53	−19.418	<.001

Note. *p* values were corrected for multiple comparisons (30) using the Holm–Bonferroni method. CTI = cue-target interval; PR = permanent removal; TR = temporary removal; C2 = Control 2; C4 = Control 4.

Results

Data from three participants were excluded from the reported results because their proportion of trials with correct responses (0.58, 0.62, and 0.64) deviated from the mean by more than 3 *SD* (the next lowest proportion was 0.83). In applying this same criterion to the second response of the temporary removal condition, no additional participant's data were excluded.

The primary statistical tests were repeated measures analyses of variance (ANOVA). When Mauchly's sphericity test reached statistical significance, the Greenhouse–Geisser correction was applied. Post hoc analyses were corrected for multiple comparisons using the Holm–Bonferroni method. A significance level of 0.05 was adopted for all analyses.

We began analyzing RTs in the four conditions (in the temporary removal condition, only RTs from the first response). Trials with no response (1.03%), with RTs shorter than 250 ms (0.11%), or with incorrect responses (5.11%) were excluded from the analysis. A 4 (Condition) × 4 (CTI) × 2 (Target Frame) repeated measures ANOVA revealed an effect of condition, $F(3, 165) = 140.523$, $p < .001$, $\eta_p^2 = 0.719$, with post hoc comparisons (Table 1) indicating differences among the four conditions (Control 4 > temporary removal > permanent removal > Control 2). There was also a Condition × CTI interaction, $F(9, 495) = 20.604$, $p < .001$, $\eta_p^2 = 0.273$. While independent ANOVAs for each condition showed statistically significant effects of CTI in all the conditions (Table 2), inspection of Figure 2 and effect sizes in Table 2 suggests that the interaction resulted from a stronger effect of CTI on the removal conditions compared to the control conditions. Congruently, the four possible independent ANOVAs involving one removal condition and one control condition showed a Condition × CTI interaction, all Fs$(3, 165) \geq 18.994$, ps $< .001$. Importantly, the Condition × CTI interaction reached statistical significance in an independent ANOVA that included only the two removal conditions, $F(3, 165) = 2.938$, $p = .035$, $\eta_p^2 = 0.051$. This interaction emerged because the difference between the two conditions became more pronounced at the longest CTI (Table 1). Finally, the global ANOVA revealed a Condition × Target Frame interaction, $F(2.6, 145.0) = 11.546$, $p < .001$, $\eta_p^2 = 0.164$. As illustrated in Figure 3 and Table 3, and confirmed by individual ANOVAs for each condition (Table 2), this interaction resulted from the frame modulating RTs only on the temporary removal and Control 4 conditions, with faster responses when the target appeared in Frame 1 (i.e., when the target belonged to the set presented first) than when presented in Frame 2 (i.e., when the target belonged to the set presented second). The triple interaction in the global ANOVA did not reach conventional levels of statistical significance, but the p value ($p = .083$) falls within the range often interpreted as marginally significant, $F(9, 495) = 1.714$, $\eta_p^2 = 0.030$. Inspection of Figure 3 suggests that this marginal significance arises from the fact that, in the two conditions where there is a frame effect, the advantage of Frame 1 diminished at the longer CTI. However, as

Table 2
Independent ANOVA Results for RT in Each Condition

Condition	Effect	*F*	*df*	*p*	η_p^2
PR	CTI	148.946	3, 165	<.001	0.730
	Frame	0.020	1, 55	.888	0.000
	CTI × Frame	0.214	3, 165	.886	0.004
TR	CTI	110.796	3, 165	<.001	0.668
	Frame	47.757	1, 55	<.001	0.465
	CTI × Frame	6.569	2.5, 138.1	<.001	0.107
C2	CTI	42.173	3, 165	<.001	0.434
	Frame	1.483	1, 55	.228	0.026
	CTI × Frame	0.340	2.7, 147.7	.774	0.006
C4	CTI	8.371	2.6, 147.3	<.001	0.132
	Frame	14.889	1, 55	<.001	0.213
	CTI × Frame	2.311	3, 165	.078	0.040

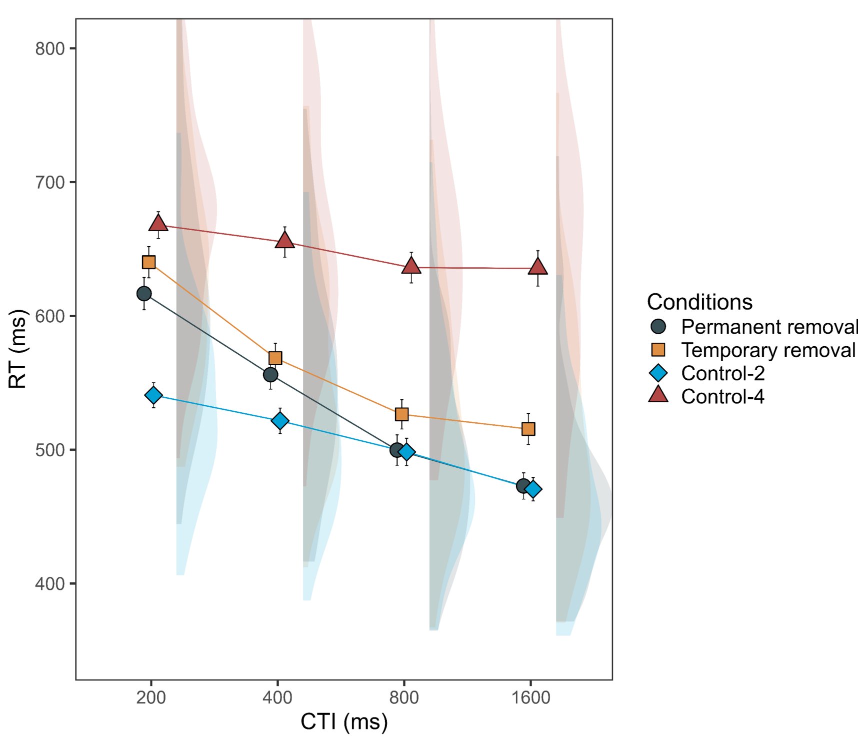
Note. ANOVA = analysis of variance; RT = reaction time; *df* = degrees of freedom; PR = permanent removal; CTI = cue-target interval; TR = temporary removal; C2 = Control 2; C4 = Control 4.

the interaction does not reach statistical significance and the effect was not anticipated, these observations should be considered with caution.

An equivalent ANOVA on the proportion of correct responses (Figure 4) revealed statistically significant main effects of CTI, $F(3, 165) = 3.850, p = .011, \eta_p^2 = 0.065$, and condition, $F(2.6, 142.0) = 20.350$, $p < .001$, $\eta_p^2 = 0.270$. Post hoc tests revealed poorer performance in the Control 4 condition than in the other three conditions, all *t*s ≥ 5.375, *p*s < .001. There was a tendency for better performance in the Control 2 condition than in the two removal conditions, but differences did not reach the statistical significance level after correcting for multiple comparisons, both *t*s ≥ 1.708, $p \geq .145$. Importantly, the proportion of correct responses in the two conditions with removal was equivalent, $t < 1$, and not even a numerical advantage was found in favor of the condition with permanent removal over the temporary removal condition (Table 3). There was also a Condition × Frame interaction, $F(3, 165) = 3.134$, $p = .027$, $\eta_p^2 = 0.054$. Congruently with RT results, there was a tendency for better performance when the target appeared in Frame 1 in the temporary removal and the Control 4 conditions (Table 3), although, in this case, the post hoc test did not reach the statistical significance level after correcting for multiple comparisons, both *t*s ≥ 2.011, *p*s ≥ .136. No other main effect or interaction reached statistical significance.

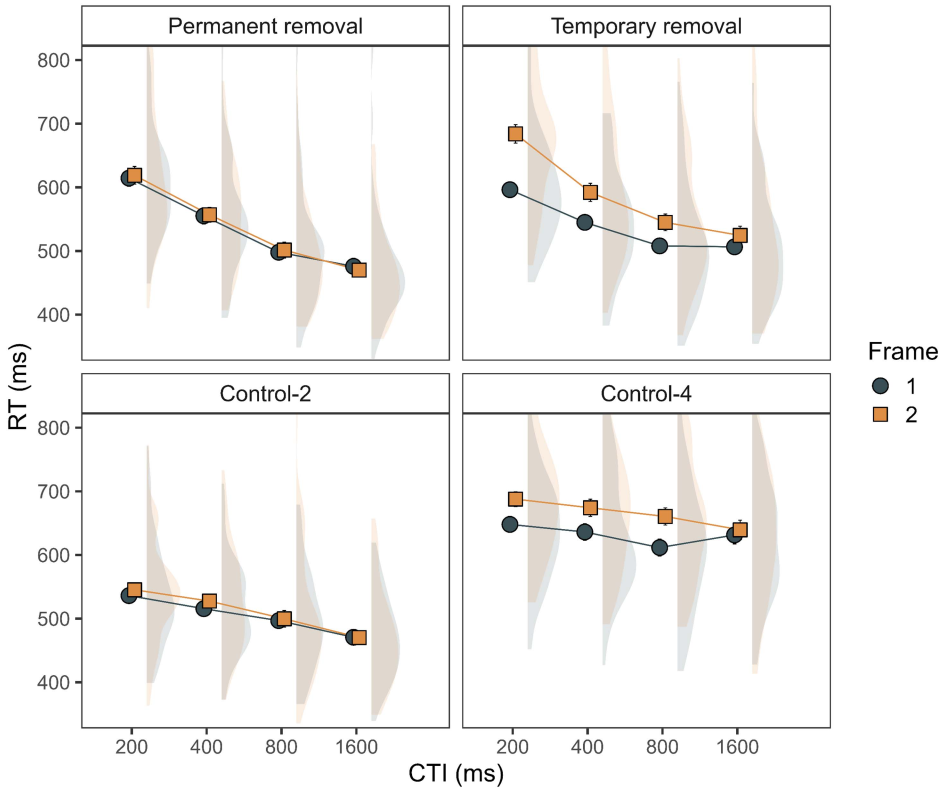
The last set of analyses focused on the second response in the temporary removal condition (Figure 5). The aim of these analyses was to examine how the CTI preceding the first response influences the second response. Moreover, we investigated whether an order-of-presentation effect also emerges for this second response by including the factor presentation frame. Notice that the presentation frame now refers to the frame in which the information relevant to

Figure 2
Mean RT Across Conditions and CTIs



Note. Error bars represent ±1 standard error of the mean. RT = reaction time; CTI = cue-target interval. See the online article for the color version of this figure.

Figure 3
Mean RTs Across Presentation Frames and Conditions



Note. Error bars represent ±1 standard error of the mean. RT = reaction time; CTI = cue-target interval. See the online article for the color version of this figure.

the second response was presented at initial encoding (Frame 1 corresponds to information presented first, and Frame 2 corresponds to information presented second).

For the RT analysis, trials with no response (1.23%), with RTs shorter than 250 ms (0.04%), or with incorrect responses (6.81%) were excluded. A 4 (CTI) × 2 (Target Frame) repeated measures ANOVA showed a main effect of CTI, $F(3, 165) = 12.466$, $p < .001$, $\eta_p^2 = 0.185$. Post hoc tests revealed that the effect of CTI was the consequence of slower responses when the CTI preceding the first response was the longest, all $ts \geq 3.708$, $ps < .001$. There was also a main effect of frame, $F(1, 55) = 19.497$, $p < .001$, $\eta_p^2 = 0.262$, indicating that RTs were faster when targets appeared in Frame 2 (i.e., when the cued set for the first response was the one presented first at initial encoding, and thus, the current target belonged to the set presented second). The CTI × Frame interaction did not reach the statistical significance level, $F < 1$.

An equivalent ANOVA on the proportion of correct responses revealed statistically significant effects of CTI, $F(1, 165) = 3.825$, $p = .011$, $\eta_p^2 = 0.065$, and frame, $F(1, 55) = 7.135$, $p = .010$, $\eta_p^2 = 0.115$. Congruently with the RT analysis just described, this main effect resulted from lower error rates for targets presented in Frame 2 and poorer accuracy when the CTI preceding the previous response was the longest.

Table 3
Mean RT (in ms) and Proportion of Correct Responses (Accuracy) as a Function of Condition and Presentation Frame

		Frame 1		Frame 2		Difference	
Measure	Condition	*M*	*SD*	*M*	*SD*	*M*	*SD*
RT	PR	534	79	536	76	3	47
	TR	534	73	582	88	48	52
	C2	498	61	504	71	6	35
	C4	626	84	664	87	38	66
Accuracy	PR	0.95	0.06	0.96	0.04	−0.01	0.06
	TR	0.97	0.05	0.95	0.07	0.02	0.06
	C2	0.97	0.04	0.97	0.04	0.00	0.06
	C4	0.92	0.07	0.91	0.08	0.02	0.08

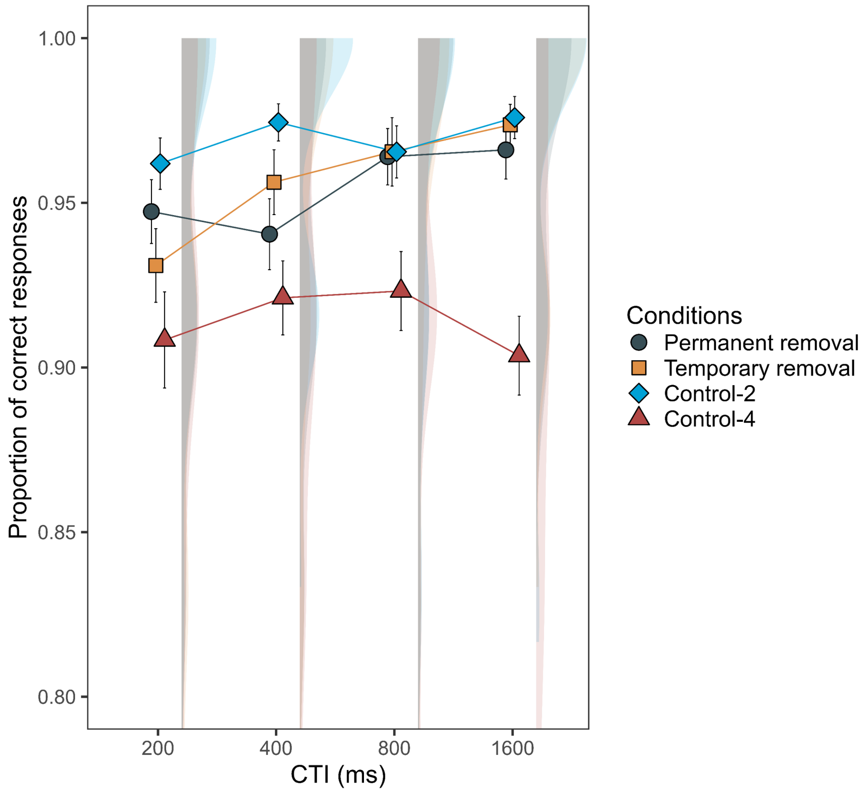
Note. RT = reaction time; PR = permanent removal; TR = temporary removal; C2 = Control 2; C4 = Control 4.

Discussion

We employed the retro-cue paradigm to investigate the following main question: Does permanently discarding a subset of WM contents marked as irrelevant offer additional benefit for WM performance compared to just temporarily putting them aside? Answering this apparently straightforward question requires careful examination of nuanced patterns. The first relevant observation is that performance in the permanent and temporary removal conditions

Figure 4

Proportion of Correct Responses Across Conditions and CTIs



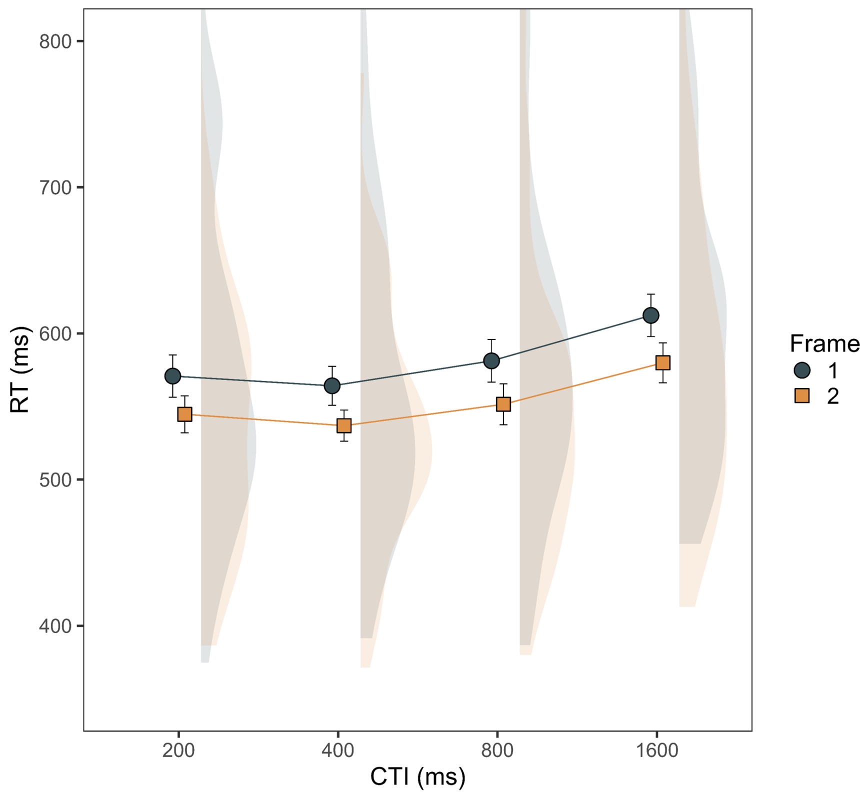
Note. Error bars represent ±1 standard error of the mean. CTI = cue-target interval. See the online article for the color version of this figure.

did not differ in terms of accuracy. This fact suggests an equivalent quality of WM representations for the relevant set, including items, contextual cues, and the binding between them, as well as an equal precision in the process of searching for the required information. In contrast to accuracy, differences between the two removal conditions did appear in RT terms, with slower responses in the temporary removal condition. To interpret this, we must consider two additional observations: the evolution of RTs across CTIs and the modulatory effect of the order of presentation of the cued set. We will explore these issues in turn.

Consistently with previous studies (Oberauer, 2018; Tortajada, Fahrenfort, et al., 2024), RTs in the permanent removal condition decreased across CTIs, progressively diverging from the Control 4 condition, in which the irrelevant set could not be discarded in advance, and ultimately converging with the Control 2 condition, in which only the relevant set was presented at initial encoding. This pattern suggests that participants used the CTI to focus attention on the relevant set and remove the irrelevant contents, progressively reducing the complexity of the search set and, consequently, the time required to locate the required information. Importantly, although responses were generally slower in the temporary removal condition compared to the permanent removal condition, the progression of both conditions was similar during the first three intervals, with a slight increase in the advantage of permanent removal at the longer interval. This observation seems to rule out some potential explanations for the longer RTs in the temporary removal condition. For example, it could be argued that participants in the temporary removal condition delayed the onset of the removal operation to strengthen the representation of the irrelevant set before removing it, thereby facilitating its later retrieval. However, this interpretation would predict a reduction of the difference between the two removal conditions at the longer intervals once RT in the permanent removal condition reached the minimum level informed by the Control 2 condition, which is the opposite pattern to what was found.

Regarding the effect of the order of presentation of the cued set, we found that, in the conditions in which the two memory sets should be maintained in an accessible state (i.e., in temporary removal and Control 4 conditions), performance was better when the target belonged to the set presented first; in contrast, when only one set should be maintained available (i.e., in the permanent removal and Control 2 conditions), performance was not modulated by the order of presentation of the relevant information. A related observation is that the permanent removal condition showed better performance than the temporary removal condition only when the tested set was the one presented second; when the target belonged to the set presented first, the two removal conditions yielded equivalent RTs. In our opinion, this modulatory effect of the order of presentation is key to understanding the underlying differences between the temporary and permanent removal conditions.

Figure 5
Mean RTs on the Second Response of the Temporary Removal Condition



Note. Error bars represent ±1 standard error of the mean. RT = reaction time; CTI = cue-target interval. See the online article for the color version of this figure.

We will articulate our interpretation as follows: (a) RTs in the present task were mainly determined by the complexity of the search set. We posit that the complexity of the search set is directly related to both the size of the retrieval framework (the number of contextual cues) that participants maintain to guide attentional access to a specific representation or representation set and the number of active representations bound to this retrieval framework. (b) In the two removal conditions, the complexity of the search set diminished progressively during the CTI, whereas it remained constant in the two control conditions. That is why RTs decreased more markedly across intervals in the removal conditions. (c) Simplifying the search set in the permanent removal condition included reducing the retrieval framework. We could conceive, for instance, that item representations are bound to two contextual cues representing the two memory sets (or the two presentation frames), which, in turn, are connected to a global trial-level context. The permanent removal process would entail unbinding the set-level contextual cue from the global context, eventually equalizing the complexity of the search set to that in the Control 2 condition, in which only one set-level contextual cue was established at initial encoding. (d) Simplification of the search set in the temporary removal condition was achieved by withdrawing attention from the irrelevant representations and, consequently, reducing the number of active representations bound to the retrieval framework. However, no reduction in the size of the retrieval framework is possible because the initially unneeded contextual cues are required later to retrieve the uncued set for the second test. (e) Whenever the whole retrieval framework was maintained (i.e., in the temporary removal and Control 4 conditions), an order effect appeared because of the well-known tendency in verbal WM to scan the contents sequentially (Kessler & Oberauer, 2015). In summary, therefore, our proposal posits that, compared to temporary removal, permanent removal enables superior WM performance by simplifying the context utilized for accessing item representations via context-content associations.

The observation that, when contents are accessed through the whole retrieval framework, there is an advantage for the information presented first is congruent with the common assumption that verbal information in WM is encoded, maintained, and scanned in a serial-ordered way (Kessler & Oberauer, 2015; Majerus, 2019). Early evidence revealed that when participants must respond to whether a probe stimulus belonged to a list presented right before, RTs increase with the list length, suggesting that representations are scanned sequentially (Sternberg, 1966). From a neurophysiology point of view, it has been proposed that the serial organization of representations in WM responds to a neural substrate in which individual items are presented in gamma cycles sequentially coupled in theta cycles (Lisman & Jensen, 2013). In this regard, Ideriha and Ushiyama (2024) found that recall of sequential information from WM follows a theta rhythm. Bahramisharif et al. (2018) used intracranial recording to show that item-specific gamma activation was coupled to theta in a position-dependent manner. Moreover, the benefit of testing in the same order in which the information was encoded is also well-known. For instance, recall is more accurate when it is done in the same order as encoding (Oberauer, 2003), and recognition is faster when items are tested in the forward order, as compared to random or backward order (Lange et al., 2010, 2011). There is also a trend to free recall in the same order as information was encoded even when it is not explicitly requested (Klein et al., 2005). These findings have been accounted for by models that include a chaining effect (Ebbinghaus, 1885; Logan & Cox, 2021). These models propose that representations are encoded in WM tightly linked to a context, being the previously encoded items part of this context. This causes the previous item to serve as a cue for retrieving the present item, but not vice versa (Kahana & Caplan, 2002; Nairne et al., 2007). This latter suggestion is pivotal for interpreting the pattern of results observed in the second response of the temporary removal condition, where participants were required to respond to the set initially marked as irrelevant (see below). An observation for which we have no clear explanation is that in the two conditions with an effect associated with the presentation frame (temporary removal and Control 4 conditions), this effect disappears at the longest interval. Tentatively, we can speculate that increasing time may have allowed participants to better organize the information and plan their retrieval strategies in such a way that the order of presentation no longer influenced their performance. In any case, the fact that the same pattern emerged in both conditions is consistent with our proposal that the temporary removal and Control 4 conditions share the necessity to maintain the retrieval framework intact, leading to the emergence of an equivalent pattern associated with the presentation frame in both conditions.

This study focuses on the verbal domain, and we are unable to predict how the findings might change with the use of visual materials. While serial order processing is a fundamental aspect of WM, it is unclear whether the maintenance of serial order differs between verbal and visual materials. Some research suggests that verbal and visual information rely on different, domain-specific mechanisms (Gmeindl et al., 2011; Tian et al., 2022). Specifically, serial order may be more strongly tied to verbal information than to visuospatial representations (e.g., Gmeindl et al., 2011), which could weaken the frame effect observed in the present results if visual materials were used instead. On the other hand, other studies propose that the same mechanisms may influence serial order across both domains (Ginsburg et al., 2017; Hurlstone & Hitch, 2018). Future research should explore these differences between the domains.

The last aspect to consider is our prediction regarding the second response in the temporary removal condition. This prediction was that longer intervals preceding the first response would result in slower responses in the second test. The logic behind this prediction is that longer intervals entail deeper removal of the irrelevant set prior to response one, consequently leading to a worse starting point for the subsequent reactivation of that set. The results confirmed this prediction but also revealed an order of presentation effect characterized by shorter RTs when the evaluated set was the one presented second during the initial encoding. This observation is consistent with the notion that the set presented first acted as a retrieval cue for the set presented second but not the other way around, as posited by chain models. Therefore, the complete pattern in the temporary removal condition is clear: Optimal performance was achieved when the two memory sets were evaluated in their presentation order.

To summarize, our study showed that both permanent and temporary removal led to a marked progressive improvement in performance in terms of both RTs and accuracy. This improvement presumably results from the gradual reduction of the search set's complexity following the presentation of informative retro-cues. In temporary removal situations, irrelevant representations are deactivated, but the entire retrieval framework is preserved because contextual cues bound to the irrelevant set will be necessary later to guide attentional refocusing. In the permanent removal condition, however, the retrieval framework can be simplified by removing or unbinding unnecessary contextual cues. We suggest that this simplification in the retrieval framework with permanent removal accounts for the absence of order effects and leads to shorter RTs, representing the main difference between permanent and temporary removal processes.

References

Atkinson, R. C., & Shiffrin, R. M. (1968). Human memory: A proposed system and its control processes. In K. W. Spence & J. T. Spence (Eds.), *Psychology of learning and motivation* (Vol. 2, pp. 89–195). Academic Press. https://doi.org/10.1016/S0079-7421(08)60422-3

Baddeley, A. D., & Hitch, G. (1974). Working memory. In G. H. Bower (Ed.), *Psychology of learning and motivation* (Vol. 8, pp. 47–89). Elsevier. https://doi.org/10.1016/S0079-7421(08)60452-1

Bahramisharif, A., Jensen, O., Jacobs, J., & Lisman, J. (2018). Serial representation of items during working memory maintenance at letter-selective cortical sites. *PLOS Biology*, *16*(8), Article e2003805. https://doi.org/10.1371/journal.pbio.2003805

Berman, M. G., Jonides, J., & Lewis, R. L. (2009). In search of decay in verbal short-term memory. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *35*(2), 317–333. https://doi.org/10.1037/a0014873

Campoy, G. (2011). Retroactive interference in short-term memory and the word-length effect. *Acta Psychologica*, *138*(1), 135–142. https://doi.org/10.1016/j.actpsy.2011.05.016

Campoy, G. (2012). Evidence for decay in verbal short-term memory: A commentary on Berman, Jonides, and Lewis (2009). *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *38*(4), 1129–1136. https://doi.org/10.1037/a0026934

Christophel, T. B., Iamshchinina, P., Yan, C., Allefeld, C., & Haynes, J.-D. (2018). Cortical specialization for attended versus unattended working memory. *Nature Neuroscience*, *21*(4), 494–496. https://doi.org/10.1038/s41593-018-0094-4

Christophel, T. B., Klink, P. C., Spitzer, B., Roelfsema, P. R., & Haynes, J.-D. (2017). The distributed nature of working memory. *Trends in Cognitive Sciences*, *21*(2), 111–124. https://doi.org/10.1016/j.tics.2016.12.007

Cowan, N. (1995). *Attention and memory: An integrated framework*. Oxford University Press.

Cowan, N. (2010). The magical mystery four: How is working memory capacity limited, and why? *Current Directions in Psychological Science*, *19*(1), 51–57. https://doi.org/10.1177/0963721409359277

Dames, H., & Oberauer, K. (2022). Directed forgetting in working memory. *Journal of Experimental Psychology: General*, *151*(12), 2990–3008. https://doi.org/10.1037/xge0001256

Ebbinghaus, H. (1885). *Über das Gedächtnis: Untersuchungen zur experimentellen Psychologie* [On memory: Investigations into experimental psychology]. Duncker & Humblot.

Festini, S. B., & Reuter-Lorenz, P. A. (2014). Cognitive control of familiarity: Directed forgetting reduces proactive interference in working memory. *Cognitive, Affective, & Behavioral Neuroscience*, *14*(1), 78–89. https://doi.org/10.3758/s13415-013-0231-1

Ginsburg, V., Archambeau, K., van Dijck, J.-P., Chetail, F., & Gevers, W. (2017). Coding of serial order in verbal, visual and spatial working memory. *Journal of Experimental Psychology: General*, *146*(5), 632–650. https://doi.org/10.1037/xge0000278

Gmeindl, L., Walsh, M., & Courtney, S. M. (2011). Binding serial order to representations in working memory: A spatial/verbal dissociation. *Memory & Cognition*, *39*(1), 37–46. https://doi.org/10.3758/s13421-010-0012-9

Griffin, I. C., & Nobre, A. C. (2003). Orienting attention to locations in internal representations. *Journal of Cognitive Neuroscience*, *15*(8), 1176–1194. https://doi.org/10.1162/089892903322598139

Hurlstone, M. J., & Hitch, G. J. (2018). How is the serial order of a visual sequence represented? Insights from transposition latencies. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *44*(2), 167–192. https://doi.org/10.1037/xlm0000440

Ideriha, T., & Ushiyama, J. (2024). Behavioral fluctuation reflecting theta-rhythmic activation of sequential working memory. *Scientific Reports*, *14*(1), Article 550. https://doi.org/10.1038/s41598-023-51128-7

Kahana, M. J., & Caplan, J. B. (2002). Associative asymmetry in probed recall of serial lists. *Memory & Cognition*, *30*(6), 841–849. https://doi.org/10.3758/BF03195770

Kessler, Y., & Oberauer, K. (2015). Forward scanning in verbal working memory updating. *Psychonomic Bulletin & Review*, *22*(6), 1770–1776. https://doi.org/10.3758/s13423-015-0853-0

Kim, H., Smolker, H. R., Smith, L. L., Banich, M. T., & Lewis-Peacock, J. A. (2020). Changes to information in working memory depend on distinct removal operations. *Nature Communications*, *11*(1), Article 6239. https://doi.org/10.1038/s41467-020-20085-4

Klein, K. A., Addis, K. M., & Kahana, M. J. (2005). A comparative analysis of serial and free recall. *Memory & Cognition*, *33*(5), 833–839. https://doi.org/10.3758/BF03193078

Koch, G., Ponzo, V., Di Lorenzo, F., Caltagirone, C., & Veniero, D. (2013). Hebbian and anti-Hebbian spike-timing-dependent plasticity of human cortico-cortical connections. *The Journal of Neuroscience*, *33*(23), 9725–9733. https://doi.org/10.1523/JNEUROSCI.4988-12.2013

Lakens, D., & Caldwell, A. R. (2021). Simulation-based power analysis for factorial analysis of variance designs. *Advances in Methods and Practices in Psychological Science*, *4*(1), 1–14. https://doi.org/10.1177/2515245920951503

Lange, E. B., Cerella, J., & Verhaeghen, P. (2011). Ease of access to list items in short-term memory depends on the order of the recognition probes. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *37*(3), 608–620. https://doi.org/10.1037/a0022220

Lange, E. B., Verhaeghen, P., & Cerella, J. (2010). Dual representation of item positions in verbal short-term memory: Evidence for two access modes. *European Journal of Cognitive Psychology*, *22*(3), 463–479. https://doi.org/10.1080/09541440903155658

LaRocque, J. J., Lewis-Peacock, J. A., Drysdale, A. T., Oberauer, K., & Postle, B. R. (2013). Decoding attended information in short-term memory: An EEG study. *Journal of Cognitive Neuroscience*, *25*(1), 127–142. https://doi.org/10.1162/jocn_a_00305

LaRocque, J. J., Riggall, A. C., Emrich, S. M., & Postle, B. R. (2017). Within-category decoding of information in different attentional states in short-term memory. *Cerebral Cortex*, *27*(10), 4881–4890. https://doi.org/10.1093/cercor/bhw283

Lewis-Peacock, J. A., Drysdale, A. T., Oberauer, K., & Postle, B. R. (2012). Neural evidence for a distinction between short-term memory and the focus of attention. *Journal of Cognitive Neuroscience*, *24*(1), 61–79. https://doi.org/10.1162/jocn_a_00140

Lewis-Peacock, J. A., Kessler, Y., & Oberauer, K. (2018). The removal of information from working memory. *Annals of the New York Academy of Sciences*, *1424*(1), 33–44. https://doi.org/10.1111/nyas.13714

Lisman, J. E., & Jensen, O. (2013). The theta-gamma neural code. *Neuron*, *77*(6), 1002–1016. https://doi.org/10.1016/j.neuron.2013.03.007

Logan, G. D., & Cox, G. E. (2021). Serial memory: Putting chains and position codes in context. *Psychological Review*, *128*(6), 1197–1205. https://doi.org/10.1037/rev0000327

Majerus, S. (2019). Verbal working memory and the phonological buffer: The question of serial order. *Cortex*, *112*, 122–133. https://doi.org/10.1016/j.cortex.2018.04.016

Mallett, R., & Lewis-Peacock, J. A. (2018). Behavioral decoding of working memory items inside and outside the focus of attention. *Annals of the New York Academy of Sciences*, *1424*(1), 256–267. https://doi.org/10.1111/nyas.13647

Masse, N. Y., Rosen, M. C., & Freedman, D. J. (2020). Reevaluating the role of persistent neural activity in short-term memory. *Trends in Cognitive Sciences*, *24*(3), 242–258. https://doi.org/10.1016/j.tics.2019.12.014

Miller, E. K., Lundqvist, M., & Bastos, A. M. (2018). Working memory 2.0. *Neuron*, *100*(2), 463–475. https://doi.org/10.1016/j.neuron.2018.09.023

Nairne, J. S., Ceo, D. A., & Reysen, M. B. (2007). The mnemonic effects of recall on immediate retention. *Memory & Cognition*, *35*(1), 191–199. https://doi.org/10.3758/BF03195954

Oberauer, K. (2001). Removing irrelevant information from working memory: A cognitive aging study with the modified Sternberg task. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *27*(4), 948–957. https://doi.org/10.1037/0278-7393.27.4.948

Oberauer, K. (2002). Access to information in working memory: Exploring the focus of attention. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *28*(3), 411–421. https://doi.org/10.1037/0278-7393.28.3.411

Oberauer, K. (2003). Understanding serial position curves in short-term recognition and recall. *Journal of Memory and Language*, *49*(4), 469–483. https://doi.org/10.1016/S0749-596X(03)00080-9

Oberauer, K. (2005). Control of the contents of working memory—A comparison of two paradigms and two age groups. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *31*(4), 714–728. https://doi.org/10.1037/0278-7393.31.4.714

Oberauer, K. (2009). Design for a working memory. In B. H. Ross (Ed.), *The psychology of learning and motivation* (Vol. 51, pp. 45–100). Academic Press. https://doi.org/10.1016/S0079-7421(09)51002-X

Oberauer, K. (2018). Removal of irrelevant information from working memory: Sometimes fast, sometimes slow, and sometimes not at all. *Annals of the New York Academy of Sciences*, *1424*(1), 239–255. https://doi.org/10.1111/nyas.13603

Oberauer, K., & Awh, E. (2022). Is there an activity-silent working memory? *Journal of Cognitive Neuroscience*, *34*(12), 2360–2374. https://doi.org/10.1162/jocn_a_01917

Oberauer, K., & Hein, L. (2012). Attention to information in working memory. *Current Directions in Psychological Science*, *21*(3), 164–169. https://doi.org/10.1177/0963721412444727

Olivers, C. N. L., Peters, J., Houtkamp, R., & Roelfsema, P. R. (2011). Different states in visual working memory: When it guides attention and when it does not. *Trends in Cognitive Sciences*, *15*(7), 327–334. https://doi.org/10.1016/j.tics.2011.05.004

Psychology software tools [E-Prime 3.0]. (2016). https://support.pstnet.com/

Rose, N. S., LaRocque, J. J., Riggall, A. C., Gosseries, O., Starrett, M. J., Meyering, E. E., & Postle, B. R. (2016). Reactivation of latent working memories with transcranial magnetic stimulation. *Science*, *354*(6316), 1136–1139. https://doi.org/10.1126/science.aah7011

Ruchkin, D. S., Grafman, J., Cameron, K., & Berndt, R. S. (2003). Working memory retention systems: A state of activated long-term memory. *Behavioral and Brain Sciences*, *26*(6), 709–728. https://doi.org/10.1017/S0140525X03000165

Souza, A. S., Rerko, L., & Oberauer, K. (2014). Unloading and reloading working memory: Attending to one item frees capacity. *Journal of Experimental Psychology: Human Perception and Performance*, *40*(3), 1237–1256. https://doi.org/10.1037/a0036331

Sprague, T. C., Ester, E. F., & Serences, J. T. (2016). Restoring latent visual working memory representations in human cortex. *Neuron*, *91*(3), 694–707. https://doi.org/10.1016/j.neuron.2016.07.006

Sternberg, S. (1966). High-speed scanning in human memory. *Science*, *153*(3736), 652–654. https://doi.org/10.1126/science.153.3736.652

Stokes, M. G., Muhle-Karbe, P. S., & Myers, N. E. (2020). Theoretical distinction between functional states in working memory and their corresponding neural states. *Visual Cognition*, *28*(5–8), 420–432. https://doi.org/10.1080/13506285.2020.1825141

Tian, Y., Beier, M. E., & Fischer-Baum, S. (2022). The domain-specificity of serial order working memory. *Memory & Cognition*, *50*(5), 941–961. https://doi.org/10.3758/s13421-021-01260-4

Tortajada, M., Fahrenfort, J. J., Sandoval-Lentisco, A., Martínez-Pérez, V., Palmero, L. B., Castillo, A., Fuentes, L. J., Campoy, G., & Olivers, C. N. L. (2024). Decoding load or selection in visuospatial working memory? *Psychophysiology*, *61*(10), Article e14636. https://doi.org/10.1111/psyp.14636

Tortajada, M., Martínez-Pérez, V., Palmero, L. B., Fuentes, L. J., & Campoy, G. (2024). *Dataset for "distinguishing between temporary and permanent removal in verbal working memory"* [Data set]. Zenodo. https://doi.org/10.5281/zenodo.12085679

Wolff, M. J., Jochim, J., Akyürek, E. G., & Stokes, M. G. (2017). Dynamic hidden states underlying working-memory-guided behavior. *Nature Neuroscience*, *20*(6), 864–871. https://doi.org/10.1038/nn.4546

Received June 21, 2024
Revision received January 31, 2025
Accepted February 2, 2025 ■