

Evidence for a single mechanism gating perceptual and long-term memory information into working memory

Sam Verschooren^{a,*}, Yoav Kessler^b, Tobias Egner^c

^a Ghent University, Ghent, Belgium

^b Ben-Gurion University of the Negev, Beer Sheva, Israel

^c Duke University, NC, USA

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ABSTRACT

An influential view of working memory (WM) holds that its contents are controlled by a selective gating mechanism that allows for relevant perceptual information to enter WM when opened, but shields WM contents from interference when closed. In support of this idea, prior studies using the reference-back paradigm have established behavioral costs for opening and closing the gate between perception and WM. WM also frequently requires input from long-term memory (LTM), but it is currently unknown whether a similar gate controls the selection of LTM representations into WM, and how WM gating of perceptual vs. LTM sources of information relate to each other. To address these key theoretical questions, we devised a novel version of the reference-back paradigm, where participants switched between gating perceptual and LTM information into WM. We observed clear evidence for gate opening and closing costs in both cases. Moreover, the pattern of costs associated with gating and input source-switching indicated that perceptual and LTM information is gated into WM via a single gate, and rely on a shared source-selection mechanism. These findings extend current models of WM gating to encompass LTM information, and outline a new functional WM architecture.

1. Introduction

Imagine you are teaching a class and need to bring to mind a student's name in order to call on her after an ongoing exercise is completed. You can either look at the class' name list (i.e., searching a *perceptual* source of information) or try to retrieve the name from memory (i.e., searching a *mnemonic* source of information). Once you found it, in either case you would need to first select and then maintain in mind the student's name, while discarding other students' names that you come across during the search process. Working memory (WM) is the cognitive system that allows us to select and temporarily maintain information in mind to guide ongoing behavior (Cowan, 2017; Oberauer, 2002, 2009). The above example illustrates two key characteristics of WM. First, the contents of WM are selected either from perceptual input or from long-term memory (LTM). Second, WM needs to grant selective access to task-relevant information, while remaining closed to potential intrusion from task-irrelevant information. Surprisingly, we currently lack an understanding of how the processes responsible for this type of selective updating of WM may differ and/or interact between input domains, that is, depending on whether information is selected

from perception or LTM. The goal of the present study was to examine the nature and relationship of WM updating from perception versus memory.

Previous research on how WM meets the demands of selective updating has primarily focused on how perceptual information is managed. Arguably the most influential neuro-cognitive model of WM regulation is the prefrontal basal ganglia working memory (PBWM) model, which proposes the existence of a dynamic gate between WM and perception (Frank, Loughry, & O'Reilly, 2001; O'Reilly & Frank, 2006). WM content is maintained, or shielded from irrelevant perceptual information when the gate is closed, but updated when the gate is opened, allowing new information to enter. The model separates the actual updating (thought to consist of changing active representations in prefrontal cortex) from the process that enables it, i.e. gate opening (proposed to be carried out by the basal ganglia).

The PBWM model's assumptions are supported by research using the reference-back paradigm (see Methods section), which has demonstrated separable response time (RT) performance costs for updating, gate-opening, and gate-closing (Rac-Lubashevsky & Kessler, 2016a, 2016b). In the reference-back task, participants are presented on each

* Corresponding author at: Department of Experimental Psychology, Ghent University, Ghent 9000, Belgium.

E-mail address: sam.verschooren@ugent.be (S. Verschooren).

trial with either the letter O or X (see Fig. 1). Each letter is surrounded by either a red or blue colored frame. On the first trial of the task, the participant encodes the letter they see into WM, and the letters shown on subsequent trials have to be compared to that reference stimulus, requiring a same/different response. Crucially, for subsequent blue-frame trials (“comparison” trials), the referent remains the same. Participants compare the WM stimulus with the on-screen stimulus, but WM content does not need to be updated, thus requiring a closed WM gate. By contrast, for red-frame trials (“reference” trials), the referent in WM has to be replaced with the stimulus shown in the red frame, thus requiring the gate to WM to be opened. When taking into account the nature of the current trial (n) and the preceding trial (n – 1), gate opening and closing costs can be isolated. That is, the gate opening cost is revealed by contrasting reference trials preceded by a comparison trial to those preceded by a reference trial, i.e., moving from a maintenance to an updating mode vs. staying in an updating mode. Similarly, the gate closing cost can be calculated by contrasting a comparison trial preceded by a reference trial to one preceded by a comparison trial, i.e., moving from an updating to a maintenance mode vs. staying in a maintenance mode. Previous work has shown dissociable individual-differences patterns (Rac-Lubashevsky & Kessler, 2016b) and neural correlates (Nir-Cohen, Kessler, & Egner, 2020; Rac-Lubashevsky & Kessler, 2018) involving the abovementioned processes.

Importantly, however, in addition to regulating the access of external, perceptual information to WM, we often need to do the same with internal information, that is, representations that originate in LTM. On the one hand, ongoing task performance can potentially be disrupted by internal information, for example, in the form of spontaneous thoughts that are unhelpful to the task at hand, or mind wandering (for a review, see Seli, Risko, Smilek, & Schacter, 2016). To preempt or mitigate such interruptions, the access of LTM representations to WM would have to be prevented. On the other hand, internal representations stored in LTM often need to be actively selected as task-relevant inputs to WM. For example, we may need to bring to mind an image of our car keys to use as a search template when trying to find our keys on a cluttered table. In other words, similar to perception, a gating mechanism is required that controls the content that is allowed to enter into WM from LTM.

While selective WM input-gating is clearly a requirement for dealing with both perceptual and LTM representations, very little research has asked whether and how gating mechanisms might differ between the two sources of information. While the PBWM model has not considered multiple gate, given that (attention to) perception and LTM are at least in part subserved by distinct neural systems (e.g., Chun, Golomb, & Turk-Browne, 2011), it is plausible that separate WM gating mechanisms may apply to these sources. One previous attempt at addressing this question is a study by Roth and Courtney (2007), who conducted an fMRI experiment to investigate whether a single neural mechanism may be responsible for WM updating with perceptual vs. memory information. Participants memorized different pairs of pictures of houses before the start of the main task. During the main task, they judged whether a picture presented on screen matched the one currently maintained in WM. For some trials, however, no judgment was required. Instead, based

on an auditory cue, they either updated WM with the picture presented on screen, updated WM with a memorized associate for the picture on screen, or maintained the current picture. The authors compared reaction time and error rates between both types of updating, but did not detect any differences. At the neural level, they found that the same fronto-parietal set of brain regions appeared to be involved in both types of updating, with additional activity in the precuneus observed during memory retrieval. This design, however, did not isolate the actual gate opening and closing processes that control WM content, as it did not allow for the relevant comparison to successive updating trials. As such, no conclusions about these gating processes and their underlying mechanism can be drawn. Nonetheless, this study provides preliminary evidence that a single mechanism might be responsible for WM updating with perceptual and LTM information.

1.1. The current study

Given the necessity of gating operations for both perceptual and LTM inputs to WM, a first, fundamental question addressed in the present study was whether we could detect gating costs for both sources of information. Gate opening and closing costs have been repeatedly observed for perceptual stimuli (Rac-Lubashevsky & Kessler, 2016a, 2016b). However, there currently exists no evidence for these costs when LTM representations are gated into WM, so a first aim of this study was to detect whether these costs exist.

A second question of high theoretical importance is whether there is a single shared, or two separate gating mechanisms responsible for updating WM with information from perception vs. LTM (see Fig. 2A-B). At first blush, dual gates seem necessary. For example, when the gate to WM is opened for perceptual information, distracting information from LTM would potentially be able to enter in the case of a single gate. Alternatively, a single gate suffices if the correct source of information can be selected independently of the gating process itself. Evidence for such a source selection mechanism has recently been observed (Verschooren, Liefoghe, Brass, & Pourtois, 2019; Verschooren, Pourtois, & Egner, 2020; Verschooren, Schindler, De Raedt, & Pourtois, 2019). Verschooren, Liefoghe, et al. (2019) instructed participants to commit four non-verbalizable drawings to LTM before the start of the experiment and to perform a probe-to-target matching task where the target, on a trial-by-trial basis, was either a figure presented on screen (perception trial) or a cue referring to a previously memorized figure (memory trial). A reliable cost was observed for switching between perception and memory referents, suggesting an attentional selection mechanism that switches between relevant information sources (see also Burgess, Dumontheil, & Gilbert, 2007). This type of source selection could in principle also be carried out before information is gated into WM. Moreover, there is evidence indicating that merely attending an item is not sufficient for encoding that item in WM (see discussion in Oberauer, 2019); thus, encoding of information into WM requires not only attentional selection, but also an open gate to WM. This implies that attentional source selection can take place independently of gating operations, which is a key assumption for the predictions we spell out below. That is, given this assumption, the relationship between source

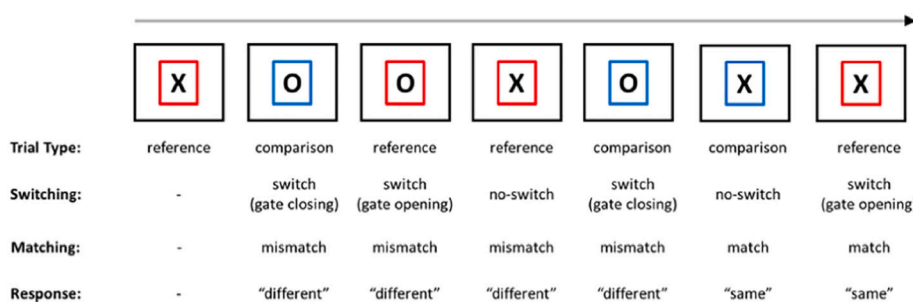


Fig. 1. The reference-back paradigm.

Participants randomly switch between reference and comparison trials. On both trial types, the referent in WM needs to be compared with the letter on screen. On reference trials, the referent is also updated with the letter. The relevant trial transitions reveal the gate opening and closing costs, independently of the updating cost (taken from Rac-Lubashevsky & Kessler, 2016a).

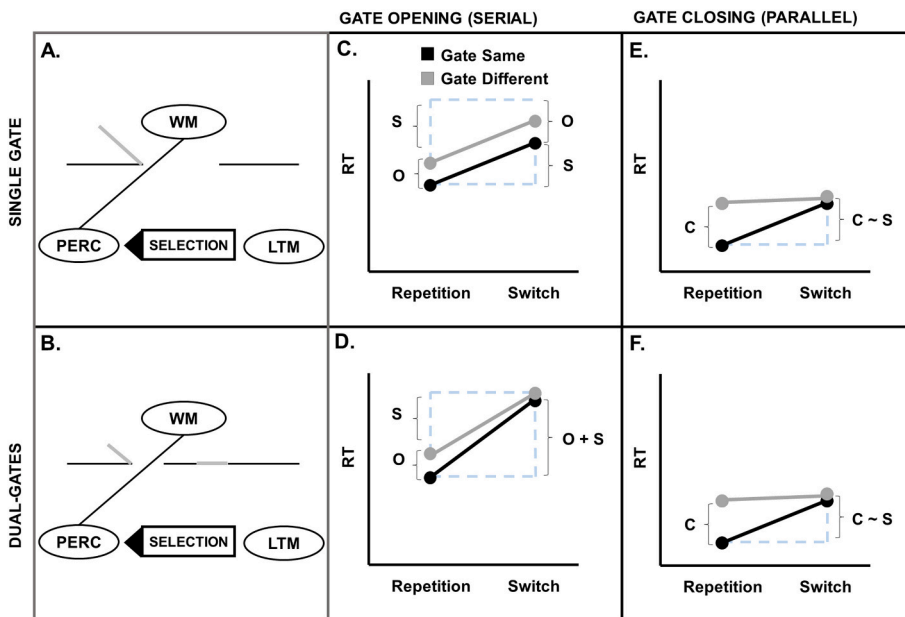


Fig. 2. Predictions concerning the interaction between gating and switching costs.

“Gate same” (comparison following comparison or reference following reference) trials are shown in black and “gate different” trials are shown in gray color. X-axis: Repetition of source (perception following perception or memory following memory) on left-hand side and switch of source on right-hand side. Y-axis: predicted response times. S = switch cost, O = gate opening cost, C = gate closing cost, PERC = perception. A. A single gate controls input into WM from both perception and LTM, but the relevant source (here: perception) is selected before gating by a dedicated selection/switching mechanism. B. In addition to this dedicated switching mechanism, a dual-gate mechanism controls perceptual and LTM selection. C. Gate opening is predicted to operate serially with switch costs, resulting in an additive effect for a single gate. D. Dual gates opening serially with switch costs predict an increase in RTs on trials where the source is switches but the gating operation is repeated (i.e., repeated comparison or reference trials), similar to the RTs on trials where both need to be switched. E, F. Gate closing is predicted to operate in parallel with switch costs. Both single and dual gates predict an underadditive interaction. Note that in these predictions, comparison trials are overall faster, but show a larger gating (closing) cost than reference

(opening) trials, in line with empirical observations in the standard reference-back task (Rac-Lubashevsky & Kessler, 2016a).

switch costs and gating costs can in principle reveal whether there is a single or there are dual gates for regulating the inflow of perceptual and mnemonic information into WM.

To address these questions, we used a modified reference-back paradigm in which, orthogonal to the trial type (comparison vs. reference trials), the target stimulus was either presented on screen or retrieved from LTM (see Fig. 3C). That is, participants either repeated or switched between comparison and reference trials, using either stimuli presented on screen or representations retrieved from LTM. Not only did this allow us to test for differences in gating for perceptual and LTM information, but also more generally to investigate how gate opening and closing operations interact with attentional switches between perception and LTM input sources. Using the additive factors logic (Sternberg, 1969), different conclusions concerning a single vs. dual gating mechanisms can be drawn from distinct possible data patterns. In particular, we here derive rival RT pattern predictions based on different WM architectures (shared or dual gates for perceptual vs. LTM inputs to WM, see Fig. 2A, B) and different assumptions regarding the relationship between gating processes and source switch processes (whether they must proceed in series or can be carried out in parallel, see Fig. 2C-F). Before detailing the key predictions distinguishing between these architectures, note that, in line with findings on the “standard” reference-back task, we expected participants to generally respond faster on comparison than on reference trials, but to show a larger gating cost (gate-closing) on comparison than on reference trials (gate-opening) (see Fig. 2C-F; e.g., Rac-Lubashevsky & Kessler, 2016a).

We first provide arguments for making distinct predictions for gate opening and closing, and subsequently present the different RT patterns. Specifically, there is an important a priori difference between gate opening and closing that motivates different predictions for them. Goal-directed gate opening, by definition, is a selective process, as it needs to select whether WM will be updated with the upcoming information or not (Frank et al., 2001; O’Reilly & Frank, 2006). The selection of the input source to WM, by definition, is also a selective process. Assuming that these selection processes are both attentional in nature leads to the prediction that source switches and gate opening are likely to operate serially. Gate closing, on the other hand, can be non-selective (i.e., a

closed gate blocks all inputs), and could thus occur in parallel with attentional switches between perception and memory.

As source selection and gate opening operate serially, we would expect their costs to be *additive* (Fig. 2C, D). When we combine this serial processing assumption with a single-gate architecture (Fig. 2A), we would expect the costs of gate-opening and source-switching to add up when both processes have to be carried out on the same trial. When the input source is switched but the gating state is repeated (i.e., when reference trials are repeated), no additional cost for gating is expected: a single gate can remain open or closed, even when the relevant input source is switched, given the assumption of independence of source selection and gate state (Oberauer, 2019) (Fig. 2C). On the other hand, when we combine the serial processing assumption with a dual-gates architecture (Fig. 2B), the relevant gate to WM would need to be opened whenever the input source is switched. This would entail a gate opening cost when attention is switched between input sources, even when the gating operation is repeated (i.e., a repetition of a reference trial). As a result, we would expect increased RTs in this particular condition, similar to the one where attention is switched and a change in the gate state takes place (i.e., a switch towards a reference trials). That is, even though the gating and switching processes here are assumed to be independent and operating in series, the resulting RT pattern would not be additive (see Fig. 2D).

Gate closing is expected to proceed in parallel with source selection, in which case one would predict their costs to produce an *underadditive* interaction (e.g., Kessler, 2017; Souza, Oberauer, Gade, & Druey, 2012). Under this parallel-processing assumption, it is not possible to distinguish between a single vs. dual-gates architecture, as both would predict similar RT patterns (see Fig. 2E, F). That is, it would not be possible to determine whether an additional gating cost is present when the gating operation is repeated (i.e., a repetition of a comparison trial) but attention is switched between the input sources (forcing the closing of the irrelevant gate). Even though we predict that a cost associated with closing/opening the gate would still be present for a dual-gates architecture, it would coincide with the attention switch cost (see Fig. 2F), thus making the RT pattern indistinguishable from the one predicted under a single-gate architecture (see Fig. 2E).

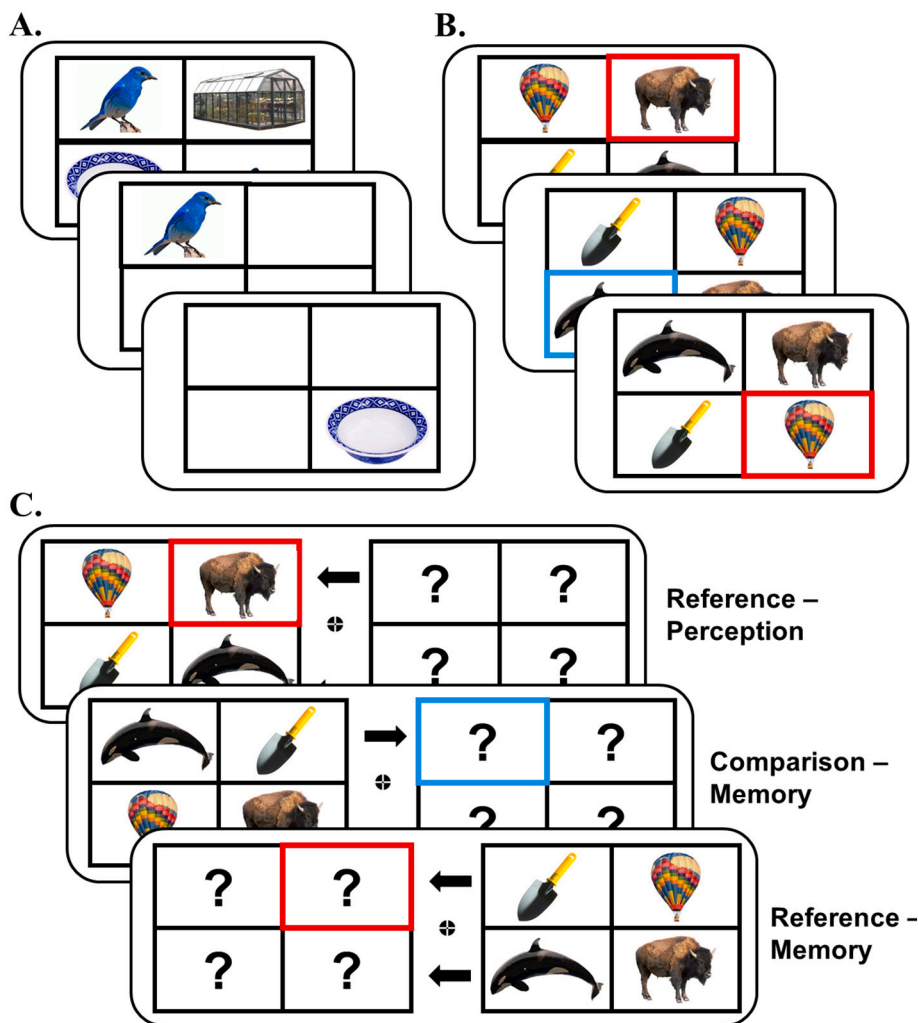


Fig. 3. Experimental paradigm.

A. Memory training for the four figures. Participants were first presented with four figures, followed by a test. On each trial of this test, they decided whether the picture was in the correct location. B. Training for the reference back task. A reference back task with only perceptual stimuli. On comparison trials (blue), the category (“living” vs. “non-living”) of the selected item needs to be compared to the category of item currently held in WM. On reference trials (red), in addition to the comparison, WM needs to be updated with the selected item. C. Experimental task. The same reference-back logic applies, but when the selected item is a question mark, it needs to be retrieved from a list of four items memorized before the onset of the task. Perception and Memory trials are interleaved as well, creating Repetition and Switch conditions. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

To summarize, the modified reference-back paradigm developed here can be used to (i) determine whether gate opening and closing costs can be detected for both perceptual and LTM sources and to (ii) differentiate between a single vs. dual WM gates for perception and LTM. We derived these predictions by assuming (a) that previously demonstrated costs of gate opening and closing (e.g., [Rac-Lubashevsky & Kessler, 2016a, 2016b](#)) and of source switching ([Verschooren et al., 2020](#); [Verschooren, Liefoghe, et al., 2019](#); [Verschooren, Schindler, et al., 2019](#)) will be evident in the present task, and (b) that attentional selection can be independent from gating ([Oberauer, 2019](#)). As both gating and source switching produce a cost, we can infer that this cost is hidden by some other factors (e.g. parallel processing) in situations when it is not observed directly. We here report a single experiment, but it represents a higher-powered replication of a pilot experiment that we report in the Supplementary Materials. The combined analysis, included in the Supplementary Materials as well, confirms the robustness of the results reported below.

2. Methods

2.1. Participants

A power analysis (MorePower; [Campbell & Thompson, 2012](#)) on the results from the pilot study revealed that we needed a sample of 50 participants to detect a partial η^2 of 0.16 with 85% power (based on the observed the three-way interaction between Trialtype, Gating, and Source-Switching; see Supplementary Materials). We recruited 72

participants on Amazon Mechanical Turk, an online testing platform. Participants that responded correctly in less than 60% of the trials were rejected. The sample included in the analysis consisted of 52 participants. This study was approved by Duke University’s Institutional Review Board. Participants signed an informed consent before starting the experiment and received \$4.1 for participation (+\$1 bonus if accuracy was higher than 80%).

2.2. Materials

The experiment was programmed in JavaScript, using the jQuery library (see <https://osf.io/nyv6m/>). We used 16 picture stimuli from an existing picture database ([Bejjani & Egner, 2019](#)). The pictures belonged to two categories living (animals) or non-living (objects; see [Fig. 1](#)). The experiment was presented within a 900×900 -pixel window and the pictures were 100×166 -pixel in size. On each run, eight unique pictures were used (four for the memory and four for the perceptual trials) and the pictures used for the memory and perceptual trials were randomized for each participant. For half the participants, one set of eight pictures was used and for the other half a different one.

2.3. Procedure

Participants started with a training phase for the memory set and for the reference back task. At the start of the memory training, four pictures were presented in a 2×2 grid on screen and participants were instructed to press the space bar once they had memorized the picture’s identity

and grid location (see Fig. 3A). On each trial of the memory training phase, after a 300 ms fixation cross, one of the memorized pictures was presented in a correct or incorrect location until response (or for maximum 15 s). Participants decided whether the picture was in the correct location by pressing the 'd'- or 'k'-key (counterbalanced over participants). New trials were presented until participants responded correctly to at least 18 trials total and reached an accuracy level of at least 0.85 (averaged over all the completed trials). Subsequently, participants completed a training phase for a (perceptual) reference back task (see Fig. 3B). On each trial, one of four unique picture stimuli presented on screen was selected in a colored frame. Dependent on the color of the frame, the trial was either a comparison or reference trial (e.g. red for reference trials and blue for comparison trials). On reference trials, participants compared the category (living or non-living) of the picture currently in WM to the category of the picture in the colored frame on screen and updated WM with that picture. On comparison trials, a similar comparison was carried out, but WM was not updated. These trials succeeded each other in random order, but the first trial of the block was always a reference trial on which no comparison was made but WM was updated with the picture in the colored frame. The location of the picture stimulus on each trial was random. A new trial was presented until participants had responded correctly to at least 18 trials total and achieved an overall accuracy of at least 0.70 (averaged over all the completed trials).

Following the practice tasks, in the actual experimental task, perception and memory trials for the reference back task were combined (see Fig. 3C). Before the first trial of each block, the four memorized pictures were presented once more (until a space bar press) to allow participants to re-commit them to memory if necessary. On each trial, after a 350 ms fixation cross, one 2×2 grid was presented on the left and one on the right side of the screen. Two arrows pointed either towards the grid filled with four picture stimuli (perceptual trial) or the grid that was filled with question marks (memory trial). The within-grid locations of the four picture stimuli were randomized on each trial. In the selected grid, one of the four locations was highlighted in a red- or blue-colored frame. The stimuli remained on screen for 4500 ms or until response. The color of the frame indicated whether the trial was a reference or comparison trial. On comparison trials, participants compared the category of the selected picture with the category of the picture currently in WM. On reference trials, they additionally updated WM with the selected picture. On perceptual trials, this comparison and/or updating was carried out for the stimulus picture in the selected location, whereas on memory trials this was carried out on the stimulus that was previously memorized in the cued location.

The first trial of each experimental task block was always a perceptual reference trial on which the selected picture was placed in WM. Each subsequent trial had a 50% probability to be a comparison or reference trial. Similarly, each trial had a 50% probability to be perception or memory, match or mismatch (for target and probe category), perceptual stimuli to be on the left side vs. right side, and whether the trial type (comparison or reference) and source (perception or memory) were switched. Finally, each location within each square and each target picture had a 25% probability to be selected, but neither target nor location repetitions were allowed. We restricted the randomization to have an approximately balanced number of observations for each participant in each experimental cell.

Participants completed one practice block and 18 experimental blocks. Each block consisted of 65 trials. In the practice block, participants received feedback ("correct", "incorrect", "too slow" on screen for 1 s). The memory and reference-back training phases were presented before the practice block, and feedback was provided after each trial in the training phases. Participants pressed the 'd'- and 'k'-key for match and mismatch responses (counterbalanced over participants).

2.4. Design

The experiment had a 2 (Trialttype: comparison, reference) \times 2 (Gating: same, different) \times 2 (Source: perception, memory) \times 2 (Source-Switching: repetition, switch) within-subjects design. The dependent variables were the response times (RTs) and error rates (ERs).

2.5. Data analysis

Only trials from the main task (i.e., no training or practice data) were analyzed. In addition, we did not include the first trial in each block, trials on which an error was committed, and those preceded by an error, and we filtered out response times below 200 ms. Given the similar pattern for RTs and ERs and the low overall ERs (<0.10 ; see Table 1), we focus our analysis on the RTs; this also corresponds to the main focus of prior reference-back studies (Rac-Lubashevsky & Kessler, 2016a, 2016b).

We analyzed the data with a generalized linear multilevel model (GLMM) approach, using the lme4 (Bates, Mächler, Bolker, & Walker, 2015) and emmeans (Lenth, 2019) libraries in R (RStudio Team, 2016; for data analysis scripts, see <https://osf.io/nyv6m/>). For repeated observations for each participant, such a linear multilevel model is preferable over ordinary linear regression, as it considers variability at different levels of the dataset and allows the levels to inform each other (Nalborczyk, Batailler, Vilain, & Bürkner, 2018). In addition, GLMMs provide a powerful method for analyzing RT data, which are rarely normally distributed and often show a skewed distribution (Lo & Andrews, 2015). We opted for a GLMM with an inverse Gaussian distribution, which we previously found to describe RT data on this type of protocol best (see Verschooren, Liefoghe, et al., 2019).

We specified a model containing all fixed effects, i.e. Trialttype (comparison, reference), Gating (same, different), Source (perception, memory), and Source-Switching (repetition, switch), and their

Table 1
Reaction times (ms) and error rates.

Source	Switch	Trialttype	Gating	RT (95% CI)	ER (95% CI)
Perception	Repetition	Comparison	Same	994 (± 15)	0.09 (± 0.009)
Perception	Repetition	Comparison	Different	1103 (± 16)	0.06 (± 0.007)
Perception	Switch	Comparison	Same	1062 (± 15)	0.09 (± 0.009)
Perception	Switch	Comparison	Different	1153 (± 19)	0.06 (± 0.008)
Perception	Repetition	Reference	Same	1092 (± 17)	0.08 (± 0.008)
Perception	Repetition	Reference	Different	1143 (± 18)	0.08 (± 0.009)
Perception	Switch	Reference	Same	1127 (± 18)	0.06 (± 0.008)
Perception	Switch	Reference	Different	1209 (± 19)	0.10 (± 0.010)
Memory	Repetition	Comparison	Same	1162 (± 17)	0.08 (± 0.009)
Memory	Repetition	Comparison	Different	1391 (± 21)	0.07 (± 0.008)
Memory	Switch	Comparison	Same	1330 (± 19)	0.10 (± 0.010)
Memory	Switch	Comparison	Different	1400 (± 20)	0.08 (± 0.009)
Memory	Repetition	Reference	Same	1306 (± 21)	0.06 (± 0.008)
Memory	Repetition	Reference	Different	1398 (± 22)	0.10 (± 0.009)
Memory	Switch	Reference	Same	1398 (± 21)	0.09 (± 0.009)
Memory	Switch	Reference	Different	1446 (± 22)	0.10 (± 0.010)

interactions (e.g., the interaction between Trialtype and Gating reveals the gate opening and costs). Given the complexity of the model, we did not include random slopes for these effects. We provide the model summary using effect coding (see Fig. 4) and planned contrasts for the different gating costs (see following paragraph).

3. Results

The RTs and ERs (with their 95% CI) for all the conditions are displayed in Table 1. Fig. 4 shows the coefficients for the model. For ease of interpretation, we first present the theoretically relevant effects, i.e., (i) those assessing the presence of gating costs for perception as well as LTM, and (ii) those evaluating the interaction between the gating and switch costs.

3.1. WM gating costs for perceptual and LTM information

To begin with, we found evidence for the presence of gating costs (-48 ms, $T = -19.6$, $p < 0.001$; see Fig. 4 and Fig. 5A). That is, participants were slower on Different than Same trials (96 ms, 95% CI = [87;106]). In addition, there was a main effect of Source (-122 ms, $T = -49.5$, $p < 0.001$; see Fig. 4), with participants being slower on memory than perception trials (243 ms, 95% CI = [234;253]). Crucially, these effects of Gating and Source interacted (6 ms, $T = 2.7$, $p = 0.007$; see Fig. 4), in that the cost for gating was smaller on perception (83 ms, 95% CI = [68;98]) than memory (109 ms, 95% CI = [89;130]) trials (see Fig. 5B). In addition, Gating interacted with Trialtype (-14 ms, $T = -5.7$, $p < 0.001$; see Fig. 4A), replicating the often observed finding that gate closing costs (125 ms, 95% CI = [107;142]) are larger than gate opening costs (68 ms, 95% CI = [50;87]; see Rac-Lubashevsky & Kessler, 2016a, 2016b). This two-way interaction also further interacted with Source (6 ms, $T = 2.3$, $p = 0.02$; see Fig. 4A and Fig. 5C). For gate opening, the costs for perception and memory were similar (67 ms, 95% CI = [44;89]; 70 ms, 95% CI = [40;100], respectively), whereas for gate closing the cost was smaller for perception than for memory (99 ms, 95% CI = [79;120], 149 ms, 95% CI = [122;177], respectively, see Fig. 5C). This three-way interaction did not further interact with the effect of Switch (4 ms, $SE = 0.028$, $T = 1.7$, $p = 0.10$; see Fig. 4A). In sum, these

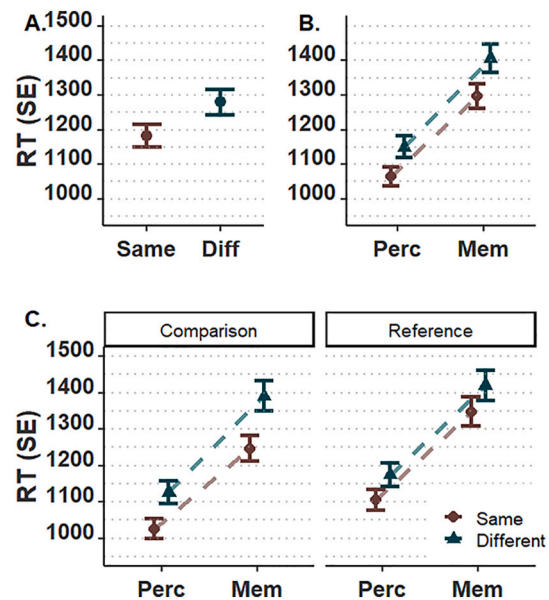


Fig. 5. Reaction times (standard error).

A. Gating: Same and Different (Diff) trials on x-axis. B. Gating x Source. Perception (Perc) and Memory (Mem) trials on x-axis. C. Trialtype x Gating x Source. Left inset: Comparison (gate closing) trials, right inset: Reference (gate opening) trials.

findings indicate that participants showed gating costs on both memory and perception trials, but that the cost for closing the gate is larger for memory inputs (see Fig. 5C).

3.2. Evidence for a shared WM gate between perceptual and LTM sources

To determine whether a shared gate or dual gates are in place for controlling input from perception versus LTM to WM, we investigated the relationship between the costs for gating and source switching (see Introduction and Fig. 2). We found a significant effect of switching

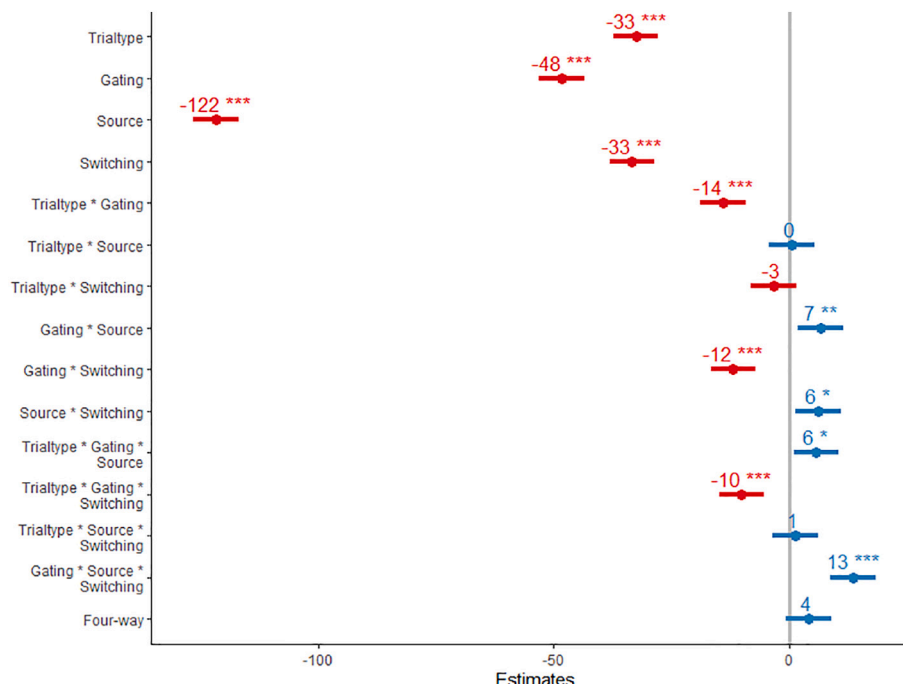


Fig. 4. Forest plot with model estimates. Significance codes: 0 (****) 0.001 (***), 0.01 (**), 0.05 (*), 1.

between sources of updating (-33 ms, $T = -13.6$; $p < 0.001$; see Fig. 4 and Fig. 6A), with participants being slower on switch than repetition trials (67 ms, 95% CI = [57;76]). This switch cost further interacted with the gating cost presented above (-12 ms, $T = -4.9$, $p < 0.001$; see Fig. 4), as the gating cost was larger on repetition (120 ms, 95% CI = [103;138]) than switch (73 ms, 95% CI = [54;91]) trials (see Fig. 6B). Moreover, this two-way interaction further interacted with Trialtype (-10 ms, $T = -4.1$, $p < 0.001$; see Fig. 4), indicating differences between gate opening and closing. More specifically, for gate opening, we found additive effects, with a similar cost on source repetition (72 ms, 95% CI = [47;97]) and switch (65 ms, 95% CI = [38;92]) trials (see Fig. 6C, right panel). For gate closing, on the other hand, the gating cost decreased on switch (80 ms; 95% CI = [55;106]) compared to repetition (169 ms, 95% CI = [146;192]) trials (see Fig. 6C, left panel). In sum, we found evidence for a single gate that operates serially with attentional switches between input sources during gate opening, but in parallel during gate closing (see General Discussion).

3.3. Additional effects

In addition to these a priori, theoretically relevant effects, there was evidence for an effect of Trialtype (-33 ms, $T = 13.3$; $p < 0.001$; see Fig. 4), with participants being slower on reference than comparison trials (65 ms, 95% CI = [56;74]), reflecting the typical cost for WM updating (Rac-Lubashevsky & Kessler, 2016a, 2016b). Trialtype did not interact with Source (0 ms, $T = 0.2$; $p = 0.86$; see Fig. 4) or with Source-Switching (-3 ms, $T = -1.4$; $p = 0.17$; see Fig. 4). The two-way interaction between Source and Source-Switching was significant (6 ms, $T = 2.5$; $p = 0.01$; see Fig. 4), with participants showing a larger cost when switching towards memory (79 ms, 95% CI = [59;99]) compared to switching towards perception (54 ms, 95% CI = [39;70]) trials (see also Verschooren et al., 2020; Verschooren, Liefoghe, et al., 2019). This two-way interaction did not interact with Trialtype (1 ms, $T = 0.5$; $p = 0.61$; see Fig. 4), but did interact with Gating (13 ms, $T = 5.5$; $p < 0.001$; see Fig. 4). That is, on perceptual trials, the cost for switching and gating was additive (80 ms, 95% CI = [60;101]) on repetition and 86 ms, 95% CI = [64;109] on switch trials). On memory trials, on the other hand, these costs interacted underadditively: 160 ms (95% CI = [133;188]) on

repetition and 59 ms (95% CI = [29;89]) on switch trials.

3.4. Exploratory correlational analysis

The evidence for a shared gate presented in Section 3.2 would in principle suggest that gate opening and closing costs for one source should be correlated across individuals with these costs for the other source. To test this, we ran an exploratory Pearson partial correlation analysis, controlling for baseline RTs, using the ppcor R library (Kim, 2015). Gate opening on perceptual trials was indeed positively correlated with gate opening on LTM trials ($r = 0.39$, $p < 0.001$). Similarly, gate closing on perceptual trials was positively correlated with gate closing on LTM trials ($r = 0.69$, $p < 0.001$). These results support our interpretation of a shared gate. As a caveat, the sample size ($N = 52$) was not originally calculated for supporting individual difference analyses. To increase power, we increased the sample size by collapsing the data with the pilot experiment ($N = 86$, see Supplementary Materials). The above reported correlations become more pronounced, as a consequence, with gating operations on perceptual and LTM trials remaining positively correlated ($r = 0.39$, $p < 0.001$; $r = 0.52$, $p < 0.001$, for opening and closing, respectively).

4. Discussion

4.1. A single WM gate

In the present study we demonstrated, to the best of our knowledge for the first time, costs for opening and closing the gate between WM and LTM, in addition to the previously reported costs for gating perceptual information into WM. Moreover, we observed an interaction between these opening and closing costs, on the one hand, and the cost for switching attention between a perceptual and an LTM source, on the other hand. Together, this pattern of interaction effects is indicative of a single WM gate that is shared between perception and LTM, rather than a separate gate for each source (Fig. 2A, C, E).

Our results have several important implications. To begin with, a gating mechanism for LTM can provide a mechanistic account for how relevant information is represented and protected in different functional states within LTM and WM, which is a central question in “embedded component” models of WM (Cowan, 1999; Oberauer, 2002, 2009). These models distinguish between different levels of “activation” of LTM representation, consisting of a potentially very large set of items in “activated LTM”, and a much smaller subset of those items that are more highly activated (or attended to) and are therefore immediately accessible, and the latter correspond to items being held in WM (Cowan, 1999; Oberauer, 2002, 2009). Finally, in one influential model, a single item among those held in WM is prioritized for guiding behavior, embedded in what has been called the “focus of attention” (Oberauer, 2002, 2009). The LTM gating costs reported here indicate that memory representations in more activated states are protected against potential interference from representations in less activated states through a gating mechanism. More specifically, in the paradigm used here, WM is updated with one among several items maintained in (activated) LTM, corresponding to that item being in the focus of attention. The fact that a gate opening cost can be detected on top of the updating costs themselves provides clear support for the notion that the transition of items being in activated LTM to being in the focus of attention is regulated by a gate. Similarly, when WM switches into a maintenance mode following updating from LTM, a gate closing cost was detected, indicating that these most activated items are protected by a closed gate.

Another key implication deriving from gating costs for LTM is that the selection of WM contents from both perceptual and LTM sources is likely controlled by a similar mechanism. The PBWM model and its’ gating mechanism have motivated a broad range of theoretical and empirical research, primarily applied to gating operations between perception and WM (e.g., (Chatham & Badre, 2015; Chatham, Frank, &

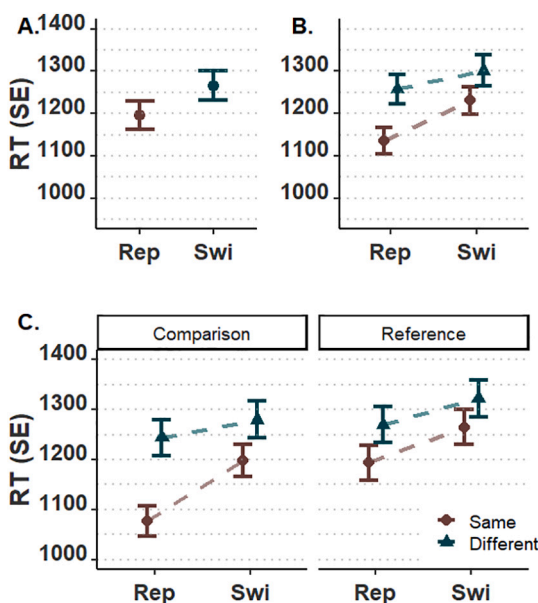


Fig. 6. Reaction times (standard error). A. Source-Switching: Repetition (Rep) and Switch trials on x-axis. B. Gating x Source-Switching. C. Trialtype x Gating x Source-Switching. Left inset: Comparison (gate closing) trials, right inset: Reference (gate opening) trials.

Badre, 2014; Frank & Badre, 2012; Jongkees, 2020; Rac-Lubashevsky & Kessler, 2016a, 2016b). For example, this research has demonstrated that the gating mechanism controlling the input into WM can be extended to selection within WM, when one item is prioritized to bias behavior, i.e., “output gating” (Chatham & Badre, 2015; Myers, Stokes, & Nobre, 2017). Our findings entail that, to some degree, the progress booked in those research lines might also be applied to understanding selection from LTM as well. That being said, some differences between the costs for perceptual and LTM gating remain, which need to be more closely scrutinized in future research (as discussed below).

Our second aim was to determine whether a single gate or dual-gating mechanism is in place for perceptual vs. LTM information. Even though the presence of gating costs for both sources suggests similar mechanisms, it does not necessarily imply a single gate. To establish whether this was actually the case, we explored how gating costs interacted with the cost associated with switches between perception and LTM sources of WM inputs. In the case of gate opening, our assumption that source switching and gate opening operate serially was confirmed by their additive costs. As stated in the Introduction, we interpret this serial effect as reflecting a bottleneck in the recruitment of attention, which is likely required both for switching between input sources as well as for allowing a task-relevant item to enter WM (i.e., gate-opening). Crucially, this additive effect entails that the hypotheses of single vs. dual gates can be differentiated (see Introduction and Fig. 2). For a single gate, the costs for source switches and switching towards a reference trial (i.e., gate opening), would add up when both have to be performed on the same trial. Importantly, when a source switch occurs and a reference trial is repeated, there would only be a source switch cost, as the single gate can remain open (see Fig. 2C). Dual gates, on the other hand, predict that in this latter case, there would be both a switch cost and a gate opening cost, as the switched-to gate would need to be opened on source switch trials (see Fig. 2D). The additive effects for gate opening and switching observed here therefore suggest that a single WM gate is shared between perception and LTM, which remains open when the information source is switched (see Fig. 6C, right panel). This type of architecture would facilitate speedy WM updating from distinct sources at the risk of some mutual interference between mnemonic and perceptual inputs to WM.

Gate closing, on the other hand, interacted underadditively with switch costs between perception and LTM (see Fig. 6C, left panel). Even though this underadditive interaction by itself does not allow us to differentiate between a single vs. dual-gates interpretation (see Fig. 2E, F), the evidence acquired for a single gate in the case of gate-opening rendered this question redundant for gate closing. Under assumption of a shared gate then, the underadditive effect for gate closing implies that the gate closing process and source switches can occur in parallel. This finding confirms that gate-closing in a single-gate architecture is a non-selective process by nature; a closed gate blocks information from either source (see Introduction). Moreover, this is in line with the assumption of the PBWM model that the default state of the WM gate is closed (O’Reilly & Frank, 2006). A gate closing process that is not disrupted by other ongoing cognitive operations indeed suggests a default state. Furthermore, in addition to the findings presented here, a recent neuroimaging study reported evidence in favor of a default closed-gate state (Nir-Cohen, Kessler, & Egner, 2020).

Taken together, these findings can be tied back to the PBWM model. A single WM gate fits well with this model, which states that many “stripes” or parallel loops exist between the PFC and BG (O’Reilly & Frank, 2006). These parallel loops allow for selective updating. For example, sometimes contextual information (e.g., task demand) needs to be maintained while other information (e.g., the relevant stimulus) is updated. Our results extend this notion by suggesting that different BG-PFC loops can selectively update WM with different items regardless of their perceptual versus memory source, aided by an independent source-selection mechanism. That being said, future neuro-computational and -imaging research with this modification of the reference-back paradigm

should be used to complement our additive factors logic (see also Trutti, Verschooren, Forstmann, & Boag, 2021). For example, on reference repetition trials that involve a source switch, a lack of activation of the neural correlates of gate closing would confirm that a single gate remains open.

Finally, it should be noted that we also observed some intriguing differences between LTM and perceptual gating. Most importantly, even though the gate opening costs were equivalent between perception and LTM, the gate closing cost for LTM was larger than the one for perception. This is a surprising finding from the perspective of a single gate that is by default closed to both perception and LTM. However, it is not yet clear whether this finding is robust, as this larger gate closing cost for LTM was neither present in the pilot study nor in the combined analysis (see Supplementary Materials), so further research into the robustness of this specific finding is necessary. That being said, a possibly larger gate closing cost for the LTM source would represent an interesting commonality with the cost for attention switches between perception and LTM outside of the WM domain. In this literature, a small cost for switches from LTM towards perception, but a large cost for switches from perception towards LTM has been reported (Verschooren et al., 2020; Verschooren, Liefvooghe, et al., 2019). This can potentially be attributed to the fact that internal memory representations are usually of lower fidelity than perception of external, currently present stimuli (but see Verschooren et al., 2020). This may mean that more attentional effort – and thus, time – is required to boost LTM representations’ activation level to enter WM (compared to the sensory-driven entry of external stimuli), which in turn would result in a slight delay in gate-closing for LTM compared to perceptual items. More research into the potentially common factor underlying these differences between the processing of internal vs. external information is required.

4.2. Alternative interpretations

The (modified) reference-back paradigm used here superficially resembles a task-switching paradigm. In this interpretation, the observed processing costs would actually reflect task- or cue-switching and not gate opening/closing or source-switching. However, we argue that our findings cannot be accounted for as simple task-switching effects. To begin with, gate opening and closing costs can be dissociated in their interaction with attention switches. This suggests that these costs do not reflect mere task-switching effects, for which no differential interaction would be expected. In addition, a task-switching account predicts similar neural signatures for gate opening and closing, whereas previous work provided evidence for differential EEG (Rac-Lubashevsky & Kessler, 2018) and fMRI (Nir-Cohen, Kessler, & Egner, 2020) correlates of these operations.

Likewise, cue-switching (or other superficial changes in low-level visual features between trial types) cannot easily account for our findings. If gating costs were driven by cue switches, this would predict symmetrical findings for gate opening/closing, which is not the case. That is, switching to a reference trial (gate opening) and a switching to a comparison trial (gate closing) are both indicated by a change in the cue color. The mere effect of this low-level perceptual change cannot lead to different RT costs in the two cases. Similarly, the source-switch costs observed here cannot be merely due to task switching or differences in low-level visual features. That is, even though the stimulus source changes (perception vs. memory), the actual task set remains the same (i.e., probe-to-target matching on comparison or reference trials). The source switch cost then is more parsimoniously interpreted as reflecting the additional process of selecting the correct input source (perception vs. LTM) when a change in input source is required (Burgess et al., 2007; Verschooren, Schindler, et al., 2019).

Another alternative interpretation for the gating costs observed here is in terms of a decision conflict between gating policies, resolving the question whether the gate should be opened or closed. However, in the reference-back paradigm, participants have to decide on each trial

whether or not the gate needs to be opened, not just on trials where the gate-state has to be changed. Given that this putative decision process thus has to take place on both gate-repetition and -switch trials, it cannot contribute to the cost of gate switching (as it would be subtracted out in the calculation of this cost). Furthermore, previous studies using the reference-back paradigm have revealed a differential neural signature of gate opening and closing, which makes the interpretation in terms of an elevated decision conflict in switch trials unlikely (Nir-Cohen, Kessler, & Egner, 2020; Rac-Lubashevsky & Kessler, 2018).

5. Conclusions

In the current study, we provided evidence for the existence of a gating mechanism that controls how content of LTM is selected for entry to WM. In addition, our data suggest that a single gate and a shared attentional selection mechanism likely control the access to WM for both perceptual and LTM sources. These findings provide an important building block for future, more complete models of WM encompassing different input sources of information.

Open practices statement

Raw data and analysis scripts for the experiments can be found at <https://osf.io/nyv6m/>. The experiments were not preregistered.

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Declaration of Competing Interest

None.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.cognition.2021.104668>.

References

- Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67(1). <https://doi.org/10.18637/jss.v067.i01>.
- Bejjani, C., & Egner, T. (2019). Spontaneous task structure formation results in a cost to incidental memory of task stimuli. *Frontiers in Psychology*, 10. <https://doi.org/10.3389/fpsyg.2019.02833>.
- Burgess, P. W., Dumontheil, I., & Gilbert, S. J. (2007). The gateway hypothesis of rostral prefrontal cortex (area 10) function. *Trends in Cognitive Sciences*, 11(7), 290–298. <https://doi.org/10.1016/j.tics.2007.05.004>.
- Campbell, J. I. D., & Thompson, V. A. (2012). MorePower 6.0 for ANOVA with relational confidence intervals and Bayesian analysis. *Behavior Research Methods*, 44(4), 1255–1265. <https://doi.org/10.3758/s13428-012-0186-0>.
- Chatham, C. H., & Badre, D. (2015). Multiple gates on working memory. *Current Opinion in Behavioral Sciences*, 1, 23–31. <https://doi.org/10.1016/j.cobeha.2014.08.001>.
- Chatham, C. H., Frank, M. J., & Badre, D. (2014). Corticostriatal output gating during selection from working memory. *Neuron*, 81(4), 930–942. <https://doi.org/10.1016/j.neuron.2014.01.002>.
- Chun, M. M., Golomb, J. D., & Turk-Browne, N. B. (2011). A taxonomy of external and internal attention. *Annual Review of Psychology*, 62(1), 73–101. <https://doi.org/10.1146/annurev.psych.093008.100427>.
- Cowan, N. (1999). An embedded-processes model of working memory. In *Models of working memory: Mechanisms of active maintenance and executive control* (pp. 62–101). Cambridge University Press. <https://doi.org/10.1017/CBO9781139174909.006>.
- Cowan, N. (2017). The many faces of working memory and short-term storage. *Psychonomic Bulletin & Review*, 24(4), 1158–1170. <https://doi.org/10.3758/s13423-016-1191-6>.
- Frank, M. J., Loughry, B., & O'Reilly, R. C. (2001). Interactions between frontal cortex and basal ganglia in working memory: A computational model. *Cognitive, Affective, & Behavioral Neuroscience*, 1(2), 137–160. <https://doi.org/10.3758/CABN.1.2.137>.
- Frank, M. J., & Badre, D. (2012). Mechanisms of hierarchical reinforcement learning in Corticostriatal circuits 1: Computational analysis. *Cerebral Cortex*, 22(3), 509–526. <https://doi.org/10.1093/cercor/bhr114>.
- Jongkees, B. J. (2020). Baseline-dependent effect of dopamine's precursor L-tyrosine on working memory gating but not updating. *Cognitive, Affective, & Behavioral Neuroscience*. <https://doi.org/10.3758/s13415-020-00783-8>.
- Kessler, Y. (2017). The role of working memory gating in task switching: A procedural version of the reference-back paradigm. *Frontiers in Psychology*, 8, 2260. <https://doi.org/10.3389/fpsyg.2017.02260>.
- Kim, S. (2015). Ppcor: An R package for a fast calculation to semi-partial correlation coefficients. *Communications for Statistical Applications and Methods*, 22(6), 665–674. <https://doi.org/10.5351/CSAM.2015.22.6.665>.
- Lo, S., & Andrews, S. (2015). To transform or not to transform: Using generalized linear mixed models to analyse reaction time data. *Frontiers in Psychology*, 6. <https://doi.org/10.3389/fpsyg.2015.01171>.
- Myers, N. E., Stokes, M. G., & Nobre, A. C. (2017). Prioritizing information during working memory: Beyond sustained internal attention. *Trends in Cognitive Sciences*, 21(6), 449–461. <https://doi.org/10.1016/j.tics.2017.03.010>.
- Nalborczyk, L., Batailler, C., Vilain, A., & Bürkner, P.-C. (2018). *An introduction to Bayesian multilevel models using brms: A case study of gender effects on vowel variability in standard Indonesian* (p. 18).
- Nir-Cohen, G., Kessler, Y., & Egner, T. (2020). Neural substrates of working memory updating. *Journal of Cognitive Neuroscience*, 32(12), 2285–2302. https://doi.org/10.1162/jocn_a.01625.
- 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. (2009). Chapter 2 design for a working memory. In , Vol. 51. *Psychology of learning and motivation* (pp. 45–100). Elsevier. [https://doi.org/10.1016/S0079-7421\(09\)51002-X](https://doi.org/10.1016/S0079-7421(09)51002-X).
- Oberauer, K. (2019). Working memory and attention – A conceptual analysis and review. *Journal of Cognition*, 2(1), 36. <https://doi.org/10.5334/joc.58>.
- O'Reilly, R. C., & Frank, M. J. (2006). Making working memory work: A computational model of learning in the prefrontal cortex and basal ganglia. *Neural Computation*, 18(2), 283–328. <https://doi.org/10.1162/089976606775093909>.
- Rac-Lubashevsky, R., & Kessler, Y. (2016a). Dissociating working memory updating and automatic updating: The reference-back paradigm. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 42(6), 951–969. <https://doi.org/10.1037/xlm0000219>.
- Rac-Lubashevsky, R., & Kessler, Y. (2016b). Decomposing the n-back task: An individual differences study using the reference-back paradigm. *Neuropsychologia*, 90, 190–199. <https://doi.org/10.1016/j.neuropsychologia.2016.07.013>.
- Rac-Lubashevsky, R., & Kessler, Y. (2018). Oscillatory correlates of control over working memory gating and updating: An EEG study using the reference-back paradigm. *Journal of Cognitive Neuroscience*, 30(12), 1870–1882. https://doi.org/10.1162/jocn_a.01326.
- Roth, J. K., & Courtney, S. M. (2007). Neural system for updating object working memory from different sources: Sensory stimuli or long-term memory. *NeuroImage*, 38(3), 617–630. <https://doi.org/10.1016/j.neuroimage.2007.06.037>.
- RStudio Team. (2016). *RStudio: Integrated development for R (1.1.456)*. RStudio, Inc. <http://www.rstudio.com/>.
- Sell, P., Risko, E. F., Smilek, D., & Schacter, D. L. (2016). Mind-wandering with and without intention. *Trends in Cognitive Sciences*, 20(8), 605–617. <https://doi.org/10.1016/j.tics.2016.05.010>.
- Souza, A. S., Oberauer, K., Gade, M., & Druwey, M. D. (2012). Processing of representations in declarative and procedural working memory. *Quarterly Journal of Experimental Psychology*, 65(5), 1006–1033. <https://doi.org/10.1080/17470218.2011.640403>.
- Sternberg, S. (1969). The discovery of processing stages: Extensions of Donders' method. *Acta Psychologica*, 30, 276–315. [https://doi.org/10.1016/0001-6918\(69\)90055-9](https://doi.org/10.1016/0001-6918(69)90055-9).
- Trutti, A. C., Verschooren, S., Forstmann, B. U., & Boag, R. J. (2021). Understanding subprocesses of working memory through the lens of model-based cognitive neuroscience. *Current Opinion in Behavioral Sciences*, 38, 57–65. <https://doi.org/10.1016/j.cobeha.2020.10.002>.
- Verschooren, S., Liefvooghe, B., Brass, M., & Pourtois, G. (2019). Attentional flexibility is imbalanced: Asymmetric cost for switches between external and internal attention. *Journal of Experimental Psychology: Human Perception and Performance*, 45(10), 1399–1414.
- Verschooren, S., Pourtois, G., & Egner, T. (2020). More efficient shielding for internal than external attention? Evidence from asymmetrical switch costs. *Journal of Experimental Psychology: Human Perception and Performance*, 46(9), 912–925. <https://doi.org/10.1037/xhp0000758>.
- Verschooren, S., Schindler, S., De Raedt, R., & Pourtois, G. (2019). Switching attention from internal to external information processing: A review of the literature and empirical support of the resource sharing account. *Psychonomic Bulletin & Review*, 26(2), 468–490. <https://doi.org/10.3758/s13423-019-01568-y>.