# Concurrent visual working memory bias in perception and decision making

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Abstract

Previous work has shown bidirectional crosstalk between Working Memory (WM) and perception such that the contents of WM can alter what we perceive and vice versa. However, it remains unclear to what extent such interactions reflect changes in sensory and mnemonic signals and/or biases in their decisional evaluation and subjective reporting. Here, using an extended visuospatial number integration task, we report evidence for both sensory and decisional WM-perception interactions and show that they appear to be functionally independent. Spatiotemporally resolved psychometrics during concurrent WM maintenance disclosed (i) a brief visuospatial gain modulation after attending the WM information and (ii) categorical choice biases, in both perceptual and mnemonic decisions, after prolonged unattended storage. The findings highlight a role of decisional processing in behaviorally relevant WM-perception interactions and support a view that attended and unattended WM states may rely on representation at different levels of abstraction.

## Introduction

What is on our mind can affect how we perceive the physical world. In line with this intuition, laboratory experiments have shown that the contents of working memory (WM) can interact with intervening perceptual tasks. For instance, when actively maintaining a red item in WM while searching for a target shape, response times are slowed when a red distractor is present in the search array[1,2], indicating attentional capture by perceptual input that matches the concurrent WM content[1–4]. WM-perception interactions have also been found to occur in the opposite direction, such that intervening stimuli can bias memory recall of concurrently maintained material[5–8]. Findings of this type have often been interpreted as evidence that WM storage recruits early sensory processes similar to those involved in perception of actual physical input[9–13].

However, from a decision-theoretic perspective, changes in perceptual and/or mnemonic reports can be of at least two distinct origins: (i) alterations of the to-be-judged sensory or mnemonic signal or (ii) biases in its decisional evaluation in terms of e.g., subjective categorization and/or response selection[e.g., 14–16]. Critically, the two scenarios can lead to different conclusions regarding the presumed locus of interference in WM-perception interactions. Whereas alterations of to-be-evaluated signals may plausibly be attributed to early sensory processing stages, decision biases are often assumed to emerge at a post-perceptual level of processing, e.g., in fronto-parietal decision circuits[17–19,but see 20]. To date, only few studies have sought to distinguish the sensory/mnemonic and decisional aspects of WM-perception interactions[e.g., 21,22].

According to one view, WM contents interact with perception mostly while they are held active for immediate goal-directed use, in so-called attended WM[1]. The capacity of attended WM is assumed to hold only a single content at a time[23,24]. WM contents outside the current focus of attention can be stored for prospective use on later occasion, but evidence suggests that they do not bias attention in concurrent perceptual tasks[1,25]. A potential implication is that unattended WM may rely less on low-level sensory processes[26], and/or involve different storage formats that are less prone to interference with concurrent sensation[1,27,28]. If and how on the other hand, WM-perception biases in decisional evaluation and -reporting depend on the WM content's attentional state is not known yet.

Here, we examined WM maintenance of both high-precision (spatial) and categorical (color) information during a prolonged spatiotemporal number integration task to track sensory and decisional WM-perception interactions throughout attended and unattended storage. Using spatiotemporally resolved psychometrics, we found ephemeral visuospatial gain modulations associated with attended WM, and categorical decision biases, both in perceptual and mnemonic reports, after unattended storage. The results support a view that attended and unattended WM contents are represented at different levels of abstraction and may interact distinctly with the sensory and decisional aspects of subjective reports.

Results

Participants (n=68) were asked to remember the color and location of a WM sample stimulus (Fig. 1a, *left*) while deciding whether an intervening stream of random dots displays (n=6, 0.3 s/display) contained relatively more blue or red dots (Fig. 1a, *middle*). After choice, subjects were asked to reproduce the color and spatial location of the WM sample from memory (Fig. 1a, *right*). Thus, the WM task involved maintaining both categorical information about a feature that was independently task-relevant also in the decision task (red/blue) and high-precision information about stimulus location, which was not to be judged or reported in the intermittent choice task. Decision- and WM reports were entered with different hands and using distinct button operation procedures (see *Methods*) to avoid motor response confusion between the two task components.

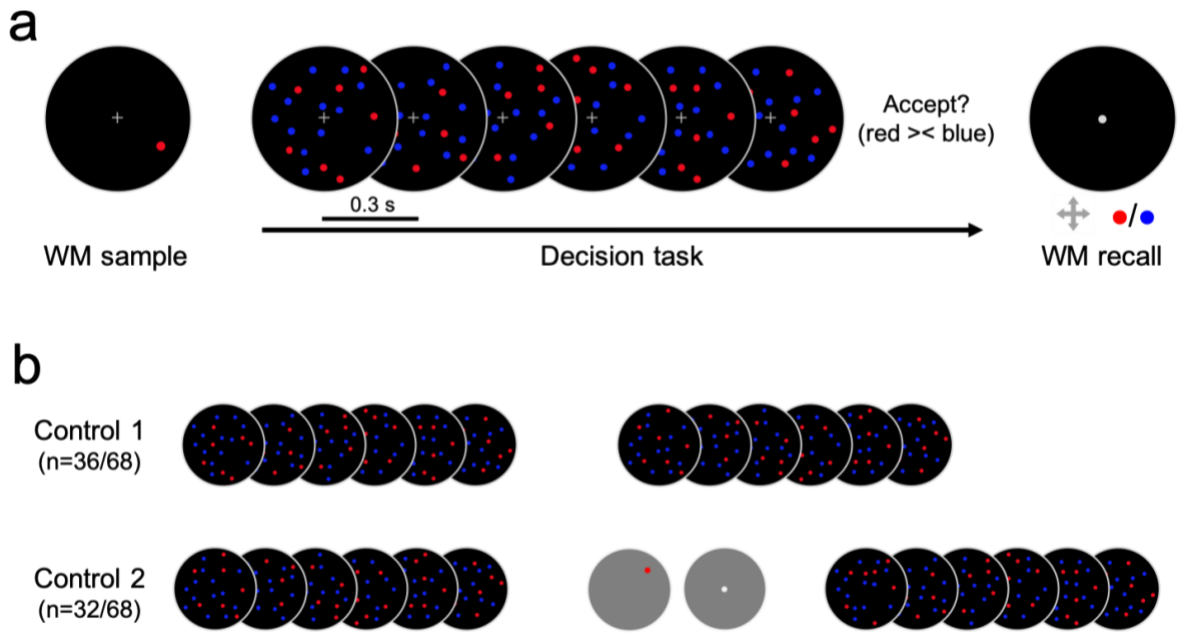


**Figure 1. Experimental paradigm**. **a,** Schematic outline of a trial in the WM interference condition. *Left*, the to-be-maintained WM sample was a single dot (red or blue) presented at a random position on an invisible circular path around fixation. *Middle*, During WM maintenance, a stream of 6 random dots displays was presented. Each display contained 20 dots, a variable number of which was blue, the others red. Participants were asked to evaluate whether the stream contained relatively more blue or red dots (see *Methods* for details). *Right*, both the color and location of the WM sample were to be reproduced from memory at the end of the trial. **b,** Within-subjects control conditions. In Control 1, the WM task elements were omitted. In Control 2, the WM- and decision task elements were rearranged such that the two tasks were not concurrent.

We asked if the concurrently memorized WM sample altered visuospatial processing of the decision stream. First, we mapped our participants' overall spatial decision weighting through logistic regression of choice against the trial-by-trial varying color value in each pixel of the decision displays. The spatial weights were compared against those predicted by an individually fitted null model as unbiased baseline (see *Methods*). Figure 2b illustrates the grand mean weighting map, collapsed across all experimental conditions (WM and controls) and display positions (1-6). Participants were most sensitive towards information in a central vertical region

of the display (p<0.05, FDR-corrected across pixels) while giving less weight to the lateral periphery, especially at the right-hand side of the display area (p<0.05, FDR-corrected). The pattern differs from classic findings of heightened sensitivity along the horizontal meridian in studies of low-level visual acuity[29–31]. We anticipate this incidental observation in our extended integration task to be of interest for vision- and numerical cognition scientists using similar stimuli. To verify if the weighting pattern was stable throughout the stream sequence, we examined the pairwise spatial correlations between the weight distributions in each of the six displays. All pairwise correlations were positive (mean R=0.65, min 0.52, max 0.78) and remained all positive when subtracting the mean correlations obtained after randomly rotating each map (1000 iterations; which excludes center-bias; mean R=0.32, min 0.17, max 0.44). Our method thus proved efficient in disclosing a robust and stable spatial weighting pattern in the stream task.

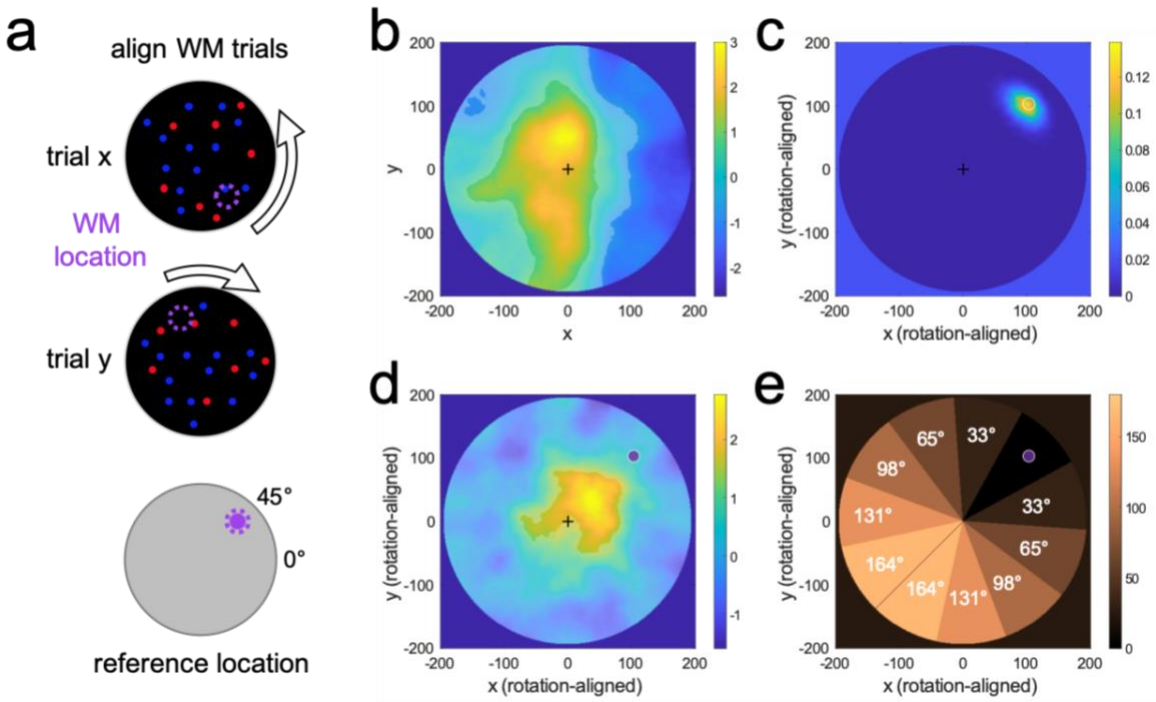


**Figure 2. Spatial weighting analysis. a,** Rotational alignment of trials. Displays were rotated offline such that the trial-specific WM sample positions matched the same (virtual) reference location (arbitrarily set to 45°, cf. purple markers). **b,** Spatial weighting of the decision displays before rotational alignment, collapsed across all trials (WM and control conditions) and displays (1-6). Positive values indicate overweighting, negative values underweighting, relative to an unbiased observer model fitted to each individual (see *Methods*). Transparent mask indicates significant regional over- or underweighting (p<0.05, two-tailed, FDR-corrected across pixels). **c,** Spatial distribution of WM positions reported on WM recall (cf. Fig. 1a, *right*) after rotational alignment, aggregated across all participants. White circle indicates true position (rotation-aligned) of the WM sample. **d,** Spatial weighting on WM trials after rotational alignment, same conventions as in b. Purple dot indicates (rotation-aligned) location of the concurrently maintained WM sample. **e,** Pie masks for angular tuning analysis. Spatial weights within each segment were averaged and examined as a function of the absolute angular distance from the WM-sample (see Fig. 3b below for results).

Comparing the overall weighting pattern in Fig. 2b between trials with and without a concurrent WM load, we found no significant differences (no pixels p<0.05, FDR-corrected for multiple

comparisons). However, our main question was whether on WM trials, the allocation of processing gain in visual space was shifted towards (or away from) the location of the concurrently memorized WM sample. To this end, we offline rotated the circular displays from all trials such that they were all aligned to the same WM sample position (Fig. 2a). We arbitrarily set this common reference position to 45° for illustration purposes. The weighting map computed from the thus aligned displays, averaged across displays (1-6), indeed showed a concentration of sensitivity towards the WM sample location (Fig. 2d, $p<0.05$, FDR-corrected across pixels). In other words, concurrent WM directly modulated the gain of perceptual processing in concrete visual space. This effect manifested as a moderate shift of sensitivity away from fixation in the direction of the WM sample, rather than a concentration at its actual physical position (which was more peripheral and reproduced with high accuracy on later recall, cf. Fig. 2c). Unlike the overall spatial weighting pattern (cf. Fig. 2b), the WM-related spatial bias (Fig. 2d) appeared not to be stable over time (mean inter-display correlation R=-0.03, min -0.30, max 0.17), indicating that the effect was transient rather than persistent.

For further inspection, we split the display area into equal-sized "pie" segments, with a target segment centered around the WM sample location at 45° (Fig. 2e). Averaging weight within segments allowed us to examine the "tuning" of spatial weighting, in terms of its mean angular distance from the WM sample location. Figure 3b illustrates the angular tuning separately for each of the six displays in the decision stream. Statistical analysis of the mean weight in the WM sample segment compared to the remaining segments showed a significant effect in the first stream display (display 1; $p<0.001$, paired t-test). This angular tuning was even discernable directly in the weighting map of display 1, with significantly increased sensitivity ($p<0.05$, FDR-corrected across pixels) along the trajectory between fixation and WM-sample location (leftmost in Fig. 3a). However, no indication of such effect was evident in any of the subsequent displays (2-6), neither in pixel-level weighting maps (no pixels $p<0.05$, FDR-corrected) nor in terms of angular tuning (all p's >0.10). Bayes factor analysis indicated anecdotal to moderate evidence for the absence of an angular tuning effect in displays 2-6 ($BF_{01}$ ranging from 2.06 to 4.85), but strong evidence for its presence in display 1 ($BF_{01}=0.004$). For further validation, we pseudo-aligned the trials from control conditions to the same WM sample locations as the WM trials (i.e., *as if* each WM sample had been presented on a control trial, too). We observed no (pseudo-) angular tuning for any of the six displays in this control analysis (yellow in Fig. 3b, all p's >0.05).

To verify if the spatial weighting shift towards the WM location was related to active WM processing, we median-split each participant's trial data according to the precision of location reports on subsequent WM recall. We observed significant angular tuning in display 1 on high-precision WM trials ($p<0.001$, $BF_{01}=0.001$) but not on low-precision WM trials ($p=0.23$, $BF_{01}=3.74$). In other words, the physical presentation of a WM sample alone was not sufficient to explain the weighting shift on WM trials. This finding, together with the relatively small radius of the shift, also renders the effect in display 1 unlikely to have resulted from inadvertent saccades to the preceding WM sample.

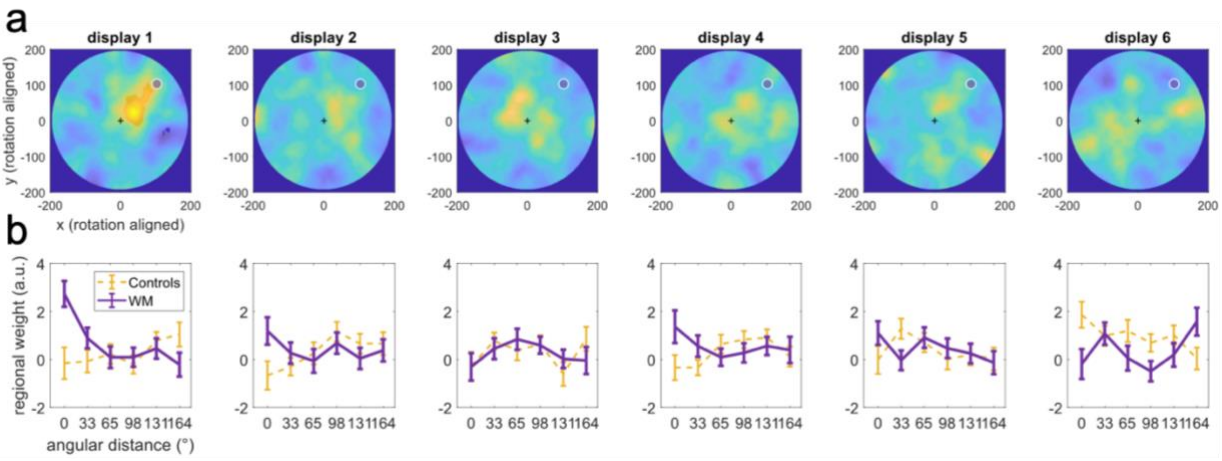


**Figure 3. Regional weight concentration – time course. a,** spatial weighting on WM trials after rotational alignment as in Fig. 2d but shown separately for each of the six displays in the decision stream. A significant regional gain concentration ($p<0.05$, two-tailed, FDR-corrected, indicated by transparent mask) was observed in display 1 only. **b,** *Purple:* angular tuning of spatial weighting in terms of mean angular distance from the WM sample (cf. Fig. 2e). Significant tuning was evident exclusively in display 1. Yellow curves show analogue analysis of control trials (pooled over control conditions 1 & 2) pseudo-aligned to the same WM-locations as the WM-trials.

Together, perceptual processing was temporarily biased towards the location of the concurrently stored WM sample, but this bias was ephemeral and dissipated quickly with new perceptual decision information. Visuospatial processing of the remainder of the stream appeared unaffected by the concurrently maintained spatial WM information. The pattern suggests that the spatial WM information was swiftly transferred from attended to unattended storage when the decision task stream commenced.

Our analysis has thus far focused on interactions with the spatial information in the WM sample. We next asked to what extent the concurrently memorized categorical color information, which was also remembered with high accuracy (mean percentage correct 93.1 %, SE=0.006), may have biased perceptual judgment. To this end, we examined psychometric weighting of the red-blue composition of the stream displays using conventional reverse correlation analysis[32–34]. The weighting functions in Figure 4a indicate the proportion of blue>red choices as a function of the relative blue-red dot count in a display. Descriptively, the mean weighting functions were near-linear and appeared parallelly shifted towards the color of the WM sample (blue or red), indicating an additive decision bias, compared to control conditions without concurrent WM maintenance (Fig. 4a). We next fitted a logistic choice model (see *Methods*) to independently quantify the psychophysical sensitivity (slope) towards the stream displays' color composition, and the strength of an additive choice bias (intercept) associated with maintaining a blue or red WM sample, respectively.

Statistical analysis of the model coefficients corroborated a significant choice bias towards the WM sample color (Fig. 4b, intercepts; WM blue: $p=0.01$, WM red: $p<0.001$, paired t-tests against pooled control conditions). We confirmed that this additive effect was associated with active WM maintenance and not merely with the presentation of a WM sample: the choice bias

(WM blue – WM red) was significantly enhanced when restricting the analysis to those trials in which the WM color was subsequently recalled correctly (0.598 vs. 0.521, $p<0.001$, paired t-test). As by task design, the excess of blue (or red) dots in a display was always mirrored in the number of blue and red dots alike ($n_{blue}$ was 20-$n_{red}$ and vice versa, see *Methods*), the additive choice bias is not easily explained by selective encoding of the WM-matching color inputs in the stream (see *Discussion*).

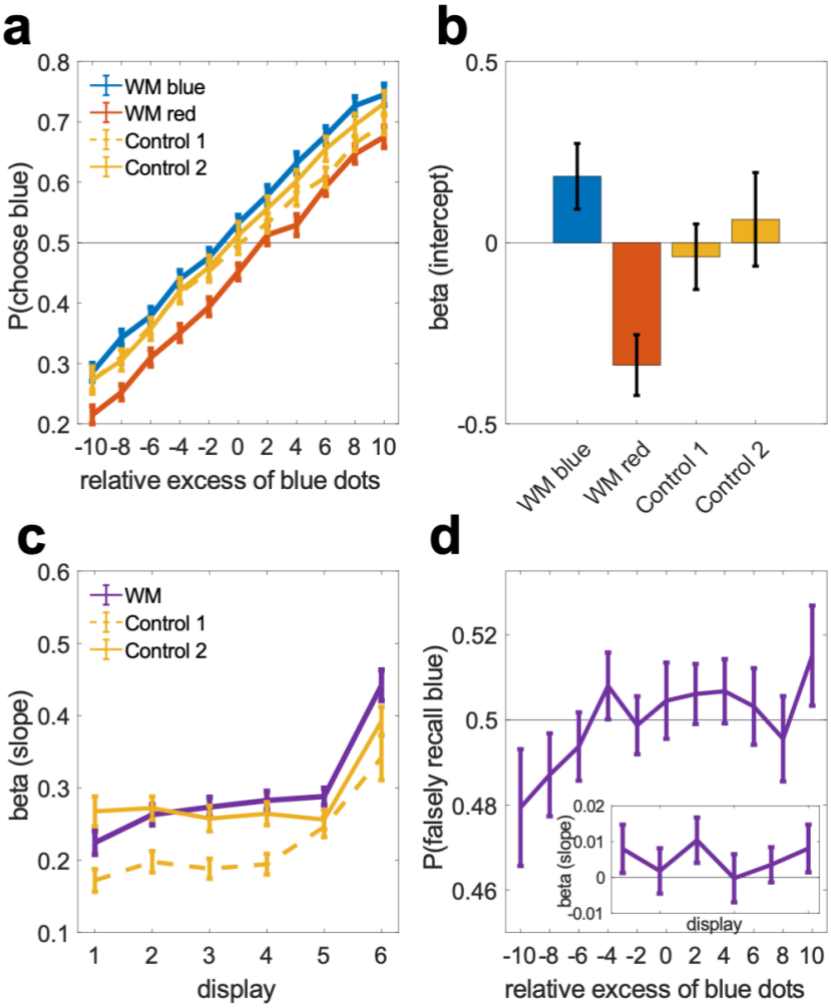


**Figure 4. Bidirectional biases of WM and decision making – color information. a,** psychometric weighting functions averaged over the six displays in the decision task, plotted separately for trials where the concurrently maintained WM sample was red or blue, and for control conditions without a concurrent WM task (cf. Fig. 1). **b,** bias terms (intercepts) derived from logistic regression of choice. **c,** choice sensitivity (slopes) to the red-blue information in each of the six displays in the decision stream. **d,** Memory recall bias. Probability of (erroneous) blue/red report in WM recall as a function of the blue-red composition of the intervening decision displays. Small inset plot shows the time-course of this relation over the six stream displays in terms of logistic regression coefficients. Error bars in all panels show standard error of the mean.

Turning to sensitivity (Fig. 4c, slopes), we observed an overall recency effect[35,36] with heightened sensitivity towards the end of the decision stream (main effect of display position:

both $p<0.001$, repeated measures ANOVAs), which may reflect memory loss or "leakage" of early presented decision information[36,37]. The recency effect was stronger on WM trials, with a steeper time course compared to controls (difference in linear slope, $p=0.02$), indicating that the concurrent WM load interfered with the general mnemonic demands of the stream task (see Fig. 5b below for further analysis). Interestingly, however, we found no reduction in overall sensitivity during WM maintenance compared to control conditions without a concurrent WM load. In fact, in one of the control conditions (Control 1), sensitivity was even significantly lower than on WM trials (main effect of condition, $p<0.001$). This unexpected observation might be attributed post-hoc to procedural aspects (decision trials occurred in faster succession in this condition). In our second control condition (Control 2), which controlled for this aspect (cf. Fig. 1b), overall sensitivity was statistically indistinguishable from that on WM trials (main effect of condition, $p=0.40$). To summarize, concurrent WM maintenance robustly biased choices and slightly increased recency effects, but it did not impair overall perceptual-discriminative acuity.

We analogously examined whether information in the decision stream would bias subsequent recall of the WM sample color (Fig. 4d). A logistic regression of WM color reports (blue/red) against the relative blue-red dot count in the intermittent stream displays showed a significant positive effect ($p=0.036$, t-test of pooled slope coefficients against zero). Thus, the more blue (or red) dots were contained in a stream display, the more likely the WM sample was erroneously recalled as blue (or red). The time course of this effect showed no significant variation across the six stream displays (inset in Fig. 4d; $F<1$, repeated measures ANOVA), suggesting that the bias was not only driven by (e.g.) early displays that occurred in temporal proximity to the WM sample. Together, our data indicate bidirectional reporting biases after accessory WM storage: decision task responses were biased towards concurrent WM content and vice versa, WM recall was categorically biased towards the intervening decision information.

We explored yet another decision-theoretic aspect in our task: one group of participants was asked to judge if the stream contained more blue (or red) dots on average ("averaging" condition) which mirrors the typical task requirement in perceptual choice experiments. Another group was asked to decide if they were willing to receive the value of one randomly drawn sample from the just presented stream ("gambling" condition), which mimics the scenario of an economic "risky" choice task. Normatively, observers in both these conditions should behave identically in order to maximize long-term returns. However, we hypothesized that the gambling scenario would promote a more discretized representation of the individual stream displays and thus load more strongly on WM storage processes[38]. The averaging condition, in contrast, may promote a more continuous updating of a running decision variable[36,39,40], potentially posing a lower WM load. We therefore anticipated the gambling task to be more susceptible to interference with the concurrent WM task.

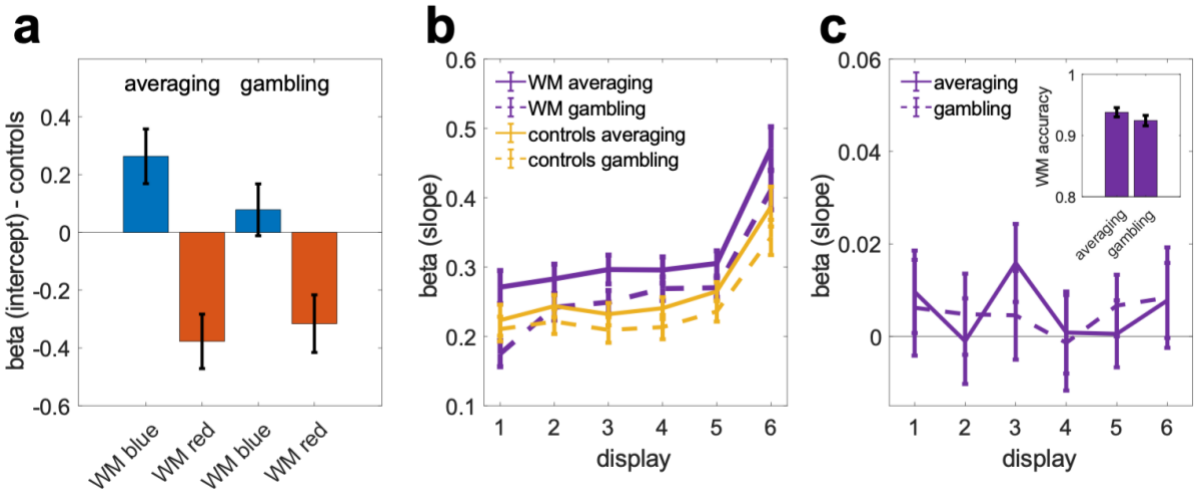


**Figure 5. Averaging or gambling – color information. a,** WM-induced choice bias relative to pooled control conditions (cf. Fig. 4b), plotted separately for "averaging" (left bars, n=35) and "gambling" variants (right bars, n=33) of the decision task. **b,** choice sensitivity (slopes) for each of the six displays in the decision stream (cf. Fig. 4c), plotted separately for the averaging and gambling tasks. Yellow curves show pooled control conditions (1 & 2) **c,** WM recall bias (cf. inset in Fig. 4d) plotted separately for the averaging and gambling conditions. Small inset plot shows proportion correct color recall. Error bars in all panels show standard error of the mean.

We observed no differences in spatial weighting (cf. Fig. 2b) or angular tuning (cf. Fig. 2d) between the two task variants (no pixels $p<0.05$, FDR-corrected). We also found no reliable differences in color bias (Fig. 5a), neither in terms of its magnitude ($p=0.08$, two-sample t-test) nor direction ($p=0.59$, two-sample t-test). However, overall choice sensitivity (Fig. 5b) was significantly lower in gambling than in averaging ($p=0.01$, two-sample t-test) which replicates and extends previous findings[41]. Furthermore, the analysis showed a robust WM-induced enhancement of recency in the gambling group only ($p=0.003$, paired t-test of slope difference between WM- and control conditions). No indication of such effect was evident in the averaging group ($p=0.47$). The between-group difference was not significant ($p=0.19$, two-sample t-test), but the pattern suggests that the overall WM-induced recency enhancement (cf. Fig. 4c) was primarily driven by the gambling condition, which is tentatively consistent with stronger mnemonic demands in the gambling scenario.

Examining the bias in subsequent WM-color recall (cf. Fig. 4d) separately for the averaging- and gambling groups, we found no difference between the two (Fig. 5d, $p=0.88$; two-sample t-test of regression coefficients pooled over displays). Overall WM color recall appeared numerically slightly less accurate after gambling (0.92) than after averaging (0.94, cf. inset in Fig. 5d) but the difference was non-significant ($p=0.23$, two-sample t-test). Lastly, we asked if WM location recall (cf. Fig. 2c) differed between the two variants of the intermittent decision task. We found that participants in the gambling condition tended to report the WM-sample locations less precisely (Fig. 6), adding to the overall tendencies for the risky choice task to interfere more strongly with concurrent WM than the averaging task.

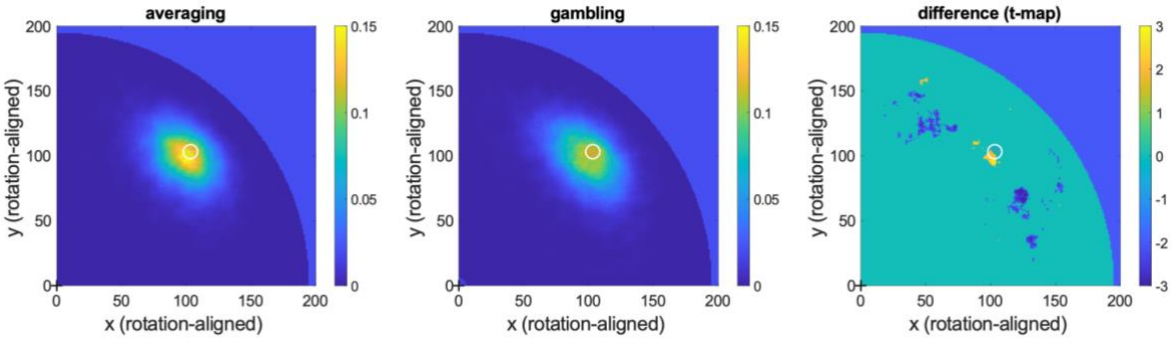


**Figure 6. Averaging or gambling – spatial WM precision. a,** Spatial distribution of WM positions reported on WM recall (rotation-aligned, as in Fig. 2d), shown separately for the averaging- (*left*) and gambling (*middle*) variants of the intermittent decision task. *Right* panel shows statistical map of the difference between the two, thresholded at $p<0.05$ (two-tailed, uncorrected). White circles indicate true original position (rotation-aligned) of the WM sample. Participants in the averaging condition tended to report more locations near to the target and fewer locations afar from it, compared to the gambling condition.

## Discussion

To summarize our findings, we report an array of WM-perception interactions, including (i) a short-lived shift of visual sensitivity towards the just-encoded WM information in concrete visual space, (ii) a bidirectional bias to categorically (mis-)judge decision information according to the concurrent WM information and vice versa, and (iii) mild WM interference with the mnemonic demands of the decision task, in terms of enhanced recency and reduced spatial recall precision. Alongside this multifaceted crosstalk between WM and perception, we did not observe any reduction in overall perceptual sensitivity.

Using a sequential visuospatial integration task enabled us to track the transition of concurrent WM information from attended to unattended storage. Spatiotemporally resolved sensitivity indicated that the spatial WM information effectively ceased to guide attention already after the first decisional input that followed it. A modulation of regional sensitivity was evident during this very first input only. These new observations in spatial weighting conceptually replicate and extend previous findings in spatial WM[42] and in visual search speed[1–4]. At the same time, they indicate that attentional WM state adapts rapidly according to momentary task (ir-)relevance. The time course of spatial gain modulations reported here seemingly contrasts with occasional reports of longer lasting attention- or sensation effects that persisted throughout several successive search- or choice displays after WM sample presentation[43,44]. However, in these previous studies, each display was to be judged separately before succeeding to the next, which may have enabled participants to periodically refocus on the WM information. Our challenging sequential integration task likely precluded such endogenous reorienting and forced the spatial WM information more persistently into unattendance[see also 45]. Consistently, concurrent WM maintenance did not impair overall psychometric sensitivity[see also 46]. Participants nevertheless accurately reproduced the WM location on later recall, in line with previous evidence that temporary withdrawal of attention does not necessarily disrupt memory performance[47–49].

After prolonged, presumedly unattended storage, the concurrent WM information still showed a marked influence on choice behavior in terms of a robust bias in categorical color judgments. Unlike the modulation of spatial sensitivity, the effect of WM color was additive in nature, that is, it altered choices independent of the very decision information on display[15]. This effect is unlikely to result from alterations in fine visual color tuning [cf. 7], which would be expected to show in more local psychometric distortions, if at all in our discrete dots task. In other words, while prolonged WM storage hardly interfered with sensory stimulus processing, it did seem to influence post-perceptual decision making. Furthermore, decision information arriving during prolonged storage also biased subsequent color memory reports. Given the categorical nature of these (mis-)reports, we assume that they likewise reflected high-level conceptual interference (and/or -confusion), rather than the subtle alterations of a sensory memory trace[cf. 7]. Together, these findings suggest decisional processing as a locus of WM-perception interactions that appear distinct from low-level sensory-mnemonic crosstalk.

Our results integrate well with the view that WM contents can be flexibly maintained at different levels of abstraction according to momentary task requirements[10,12,26,50]. Here, during a challenging visuospatial integration task, the concurrent color information may have been stored in a rather asensory (e.g., abstract-categorical, or verbal) format, which avoids low-level perceptual interference[50] but may interact with task aspects that rely on similar levels of abstraction, such as decisional categorization along a shared feature dimension. The precise location of a stimulus in visual space may seem less amenable to endogenous transformation, but some descriptive aspects of our data suggest that the spatial WM information might have been partially abstracted, too. When still visible in spatial sensitivity patterns, the fading signature of the WM item was more that of an angular pointer than of the item's precise location in Euclidean space. At later WM recall, location reports were remarkably accurate in terms of both angular and radial position (cf. Fig 2c and 6), the latter of which our task allowed to be inferred from long-term memory. In other words, at WM recall, the sample's concrete physical appearance (color and location) may partially have been reconstructed from abstract memoranda.

Why should abstractions in unattended WM have evolved to interact with concurrent decision processes? While the present choice biases appear suboptimal in the context of a dual-task paradigm, our findings connect to literatures on the role of trial history[51–55], and of past experience more generally, in adaptive decision making. Prominent models, often in a Bayesian tradition, have characterized how prior experience shapes current percepts, and vice versa, how prior distributions are continuously updated through new experience[56–58]. Observing similar dynamics here in a concurrent WM task, we may speculate that the mechanisms behind unattended WM overlap with those that inject latent context information in adaptive decisions (for related discussion, see[59]), likely in close exchange with longer-term memory and -knowledge[23,24,60]. Tentatively consistent with such idea, decision-biasing information from previous trials was recently found to be represented in parietal areas that had traditionally been considered a central part of the WM circuitry in mammalian cortex[61].

The additive biases reported here are open to alternative interpretations, e.g., that the WM sample might have pre-activated matching visual information[62] such that ensuing decision bias may result from a baseline shift[63] from the outset of evidence accumulation in our stream task.

Such account can explain why WM-matching stimuli seem to enter visual awareness more easily e.g., after interocular suppression[13,64,but see 65,66,22]. Under this account, WM sample information would effectively have been carried along in decisional accumulation processes engaged in our sequential integration task. While an intriguing possibility, it remains unclear how pre-activation of visual color information would offset evidence accumulation with regard to whether stimuli were more (or less) *numerous*[67] (see *Stimuli and Task*). A related possibility is that participants might have selectively focused on the WM-color matching dots (inadvertently, or as a deliberate memory aid) in our decision streams. Here too, it is not clear if such selective processing could lead to the invariant overestimation (and not underestimation, or more accurate assessment) of numerosity we observed across the entire number range. Further work will be needed to scrutinize the viability of these alternative accounts for the classic categorical decision biases in our psychometric data.

We did not record neural activity in the present study and can only speculate where and how in the brain the WM information was stored throughout inattention. Ample neuroscientific evidence indicates that abstract-categorical information recruits high-level frontoparietal networks[10,68–70]. Our findings appear consistent with the proposal that these networks might be relied on especially in unattended WM storage, while attended storage may more strongly engage sensory cortices[26]. However, new evidence exists that also sensory areas could be equipped with machinery to maintain representations in interference-proof formats[71], potentially even during periods of inattention[27,72,73]. A latent persistence of concrete visual information in such formats may add to the high precision of WM recall we observed after attention was temporarily withdrawn. For instance, recent fMRI evidence suggests that attended and unattended WM information could be represented in opposite patterns within shared content-coding areas[27,73]. Here, in terms of interactions with perception, we observed no behavioral indices of repulsion or suppression, but a pattern of attraction biases consistent with crosstalk at different levels of the cortical processing hierarchy (but see[74] for evidence that behavioral attraction and neural repulsion are not mutually exclusive). How the interactions reported here relate to the representational nature of mnemonic- and decisional information on the neural level ultimately remains a question for future work using e.g., fMRI- and/or EEG recordings.

To conclude, our report highlights decisional processing stages as a locus of behaviorally relevant interactions between perception and concurrent WM. The findings complement and extend previous work on lower-level biases associated with attended WM, and support a multiplexed view of adaptive WM storage across the cortical hierarchy. We hope that the new approaches and methodologies introduced here will also prove instrumental in the continuing search for the neural substrates of WM.

## Methods

### Participants

A total of n=80 healthy volunteers (43 female, 37 male; age 26.61 +/- 4.35) participated with written informed consent. Participants who failed to perform above chance level in WM color- (n=7) and/or location recall (n=2) were excluded from analysis. We further excluded n=3

participants whose choices in the decision task were not robustly driven by the red-blue composition of the stream displays ($p<0.001$, logistic regression of choice). Results are reported for the remaining n=68 participants (36 female, 32 male).

Stimuli and Task

Decision task. On each trial, participants viewed a stream of six circular displays (cf. Fig. 1, *middle*; outer circle diameter 10.6° visual angle). Each display contained 20 circular dots (diameter 0.3°), a varying number of which was colored blue, the others red. The difference in the number of blue – red dots in each display was randomly drawn from a normal distribution that was truncated to one standard deviation (SD=10). The mean of the distribution was randomly varied across trials to be either -4 or +4, however, due to an error in the presentation code it was consistently shifted by 1 dot towards red (in half of the subjects) or blue (in the remaining subjects). As this shift was small and constant in all trials and conditions of interest, we consider it inconsequential for the reported results. Control analyses confirmed that the overall color weighting functions in the two subgroups were virtually identical. The spatial positions of dots in each display were randomly assigned (independent of color) and uniformly distributed across the display area, with the restrictions that no dots overlapped and that the minimum distance to the outer border of the display area was 0.3°. Each display was presented for 0.2s, followed by a blank period (empty display area) of 0.1s. The outer circle and a central fixation cross remained on screen for the entire trial.

To foster participants' motivation in the decision task, the red-blue comparison was instructed in an incentivized choice frame. One of the colors (red/blue, counterbalanced across participants) was designated as gain-, the other as loss color. Participants were instructed to accept the stream if it contained more gains, and to reject it otherwise, via left-hand button press (key "C" or "X", respectively). After choice, full informative feedback was displayed, and accepted gains were credited to the participant's running bonus balance. Feedback was based on the mean of the stimulus set (see above). In half of the participants, the task was framed as a gamble where the outcome (in terms of both feedback and bonus) was based on that of a randomly drawn display from the just-presented stream.

WM task. WM trials started with presentation of a single dot (diameter 0.3°; cf. Fig. 1 *left*) for 0.5 s, the color (red/blue, randomly varied across trials) and spatial location of which were to-be-remembered for later recall. The location of the WM sample varied randomly across trials but was restricted to a circular path of 3.8° radius around fixation. In WM interference blocks (Fig. 1a), the WM sample was followed after a 0.2s delay[63] by the decision task. In Control 2 blocks (Fig 1b, lower), the WM sample was immediately followed by WM recall. On WM recall, a white dot appeared at the center of the display area and participants were asked to move it to the remembered location using arrow keys, and to toggle its color (red/blue) with key "0" on the numpad, all using the right hand. Participants were free to make adjustments and corrections (of both color and location) for as long as they wished before submitting their result by pressing the enter key. Thereupon, feedback of both color- and location accuracy (transformed into a percentage correct score) was displayed. Color- and location accuracy were combined into a bonus score that was surcharged on participants' running bonus balance.

Design and Procedure

Each participant performed 3 consecutive blocks of 80 trials in the critical WM interference condition, where the decision task was presented after WM encoding and before WM recall (Fig. 1a). Half of the participants additionally performed 3 blocks in control condition 1, in which the WM task elements were omitted (Fig. 1b, upper). The remaining participants performed 3 blocks in control condition 2, in which the WM- and decision task elements were reordered so that the two tasks were not concurrent (Fig. 1b, lower). The ordering of WM interference- and control blocks was counterbalanced across participants. All between-subject assignments (control 1/2, gain/loss color, choice framing, task order) were crossed to be orthogonal.

Participants where pre-experimentally instructed to give equal priority to the WM- and decision tasks, and that performance in both task components would be combined in the final bonus score. Participants were seated at approximately 57 cm viewing distance from a 24'' TN display (BENQ XL2430, 531.36mm x 298.89mm viewing area, 144Hz refresh rate, 1920x1080 pixels resolution). A chinrest (SR Research) was used to minimize changes in viewing distance and head posture. Participants were instructed to fixate a centrally presented crosshair (10 x 10 pixels, 2 pixels linewidth) and to avoid eye movements during all task stages. After each block, summary performance feedback was provided, and participants were free to take a short break before continuing with the next block. Upon completion of the experiment, the bonus score balance was converted into a small monetary amount (2-5 Euro, depending on performance) and surcharged on the standard reimbursement for participation.

Spatiotemporal weighting analyses

For spatial weighting analysis, the stream displays were reconstructed offline as 401x401 pixel circular pseudo-color maps (blue: 1, black: 0, red: -1) and smoothed with a 20x20 pixel Gaussian kernel. Spatial decision weight was estimated at each pixel (x,y) using a logistic regression of choice (Eq. 1):

$$P(blue) = L\left(\beta_0 + \sum_{k=1}^{6} \beta_{x,y,k}\, c_{x,y,k}\right)$$

where $P(blue)$ is the probability of choosing blue>red, $L$ is the logistic function $y = 1/(1 + e^{-x})$, and $c_{x,y,k}$ is the pseudo-color value at pixel coordinate x,y in stream display k. The coefficients $\beta_{x,y,k}$ form a spatiotemporal map ($M$) of decision weight in terms of psychometric slopes at each pixel x,y and each display position k (1-6), and $\beta_0$ is the model's constant term. We estimated $M$ for each participant's choice data and contrasted it with a spatially unbiased observer map $M^*$. The unbiased map $M^*$ was estimated from the choice probabilities predicted by an individually fitted psychometric model (see *Psychometric model* below) which was uninformed by the displays' spatial dot layout. Subtracting $M - M^*$ yields a map of regional over- (positive values) or underweighting (negative values). The maps were examined statistically using t-tests against zero with false-discovery-rate (FDR) correction[75] for multiple comparisons in pixel space.

To test for concentration of decision weight at the concurrently maintained WM sample location, we recomputed $M - M^*$ from rotationally aligned stream displays. Specifically, we rotated the decision displays from each WM trial offline so that the WM sample location on any given trial was aligned at the same angular position (arbitrarily set to 45°). For instance, when the WM sample was presented at 120°, the subsequent stream displays would be re-rotated by -75°. Trials with unusually inaccurate WM location recall (>40 pixels Euclidean displacement) were excluded from the main analysis. To statistically test for angular tuning, we partitioned the display area into 11 equal-sized pie segments and compared the average weight in the segment centered around the WM sample position to that in the remaining segments. The reported results pattern was robust to varying the number (width) of segments in partitioning.

Reverse correlation analysis of psychometric weight

Psychometric weighting functions (cf. Fig. 2) were derived by computing for each relative excess count of blue (vs red) dots, in each display position (1-6), the relative frequency with which the stream was subsequently judged blue (i.e., accepted when the gain color was blue or rejected when the gain color red). The slope of the resulting psychometric curve indicates the weight with which the blue-red dot count in a display impacts on final choice. In other words, the slope of the curve indicates the observer's psychophysical *sensitivity* to this information. In contrast, an overall displacement of the function, e.g., in terms of a parallel shift away from an ideal observer function (which is point-symmetric at p=0.5) reflects an additive response bias towards one of the two choice categories, regardless of the stream's physical appearance.

Psychometric model

For quantitative analysis of choice bias and -sensitivity, we used a simple logistic choice model of the form (Eq. 2):

$$P(blue) = L\left(\beta_b c_{wm} + \beta_r(1 - c_{wm}) + \sum_{k=1}^{6} \beta_k\, c_k\right)$$

where $P(blue)$ is the probability of choosing blue>red, $L$ is the logistic function, $c_{wm}$ is a dummy variable coding the color of the WM sample (1: blue, 0: red), and $c_k$ is the color composition of stream display $k$ in terms of the excess count of blue minus red dots (ranging from -10 to +10 relative to the mean of the stimulus set, see *Stimuli and Task*). The coefficients $\beta_k$ reflect the psychophysical sensitivity (slope) with which the color composition of a stream display is weighed in choice, whereas coefficients $\beta_b$ and $\beta_r$ reflect the strength of a choice bias associated with maintaining a red or blue WM sample, respectively. In control trials without a concurrent WM item, a single intercept ($\beta_0$) was used instead.

Statistical procedures

We used conventional parametric procedures (t-tests and ANOVAs) as detailed in *Results*. Greenhouse-Geisser corrected degrees of freedom were used where appropriate. Supplementary Bayesian statistics were computed using the Bayes factor toolbox https://github.com/klabhub/bayesFactor .

Ethics Statement

The study was approved by the ethics commission of the Max Planck Institute for Human Development and was conducted in accordance with the Human Subjects Guidelines of the Declaration of Helsinki.

Data availability

The research data supporting the findings will be made available upon publication through the institutional git repository:

Code availability

The experimental and analysis code will be made available upon publication through the institutional git repository:

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