

Prospective task knowledge improves working memory-guided behaviour

Frida A.B. Printzlau¹, Nicholas E. Myers¹, Paul S. Muhle-Karbe¹, Sanjay G. Manohar^{1, 2} & Mark G. Stokes¹

1. Department of Experimental Psychology, University of Oxford, UK
2. Nuffield Department of Clinical Neurosciences, University of Oxford, UK

Working memory (WM) is the ability to keep information online for a forthcoming task. WM theories have tended to focus on how sensory information is maintained, and less on how WM content is used for guiding behaviour. Here we ask if WM is supported by a transformation of sensory memoranda into task-sets that are optimised for task-dependent responses. Thirty participants performed two different WM tasks; they remembered the tilt of oriented bars for either a rotation-discrimination task or a change-detection task. Task context was instructed either in advance (fixed task blocks) or at probe onset (mixed task blocks). If WM content is configured in a task-dependent format, performance should benefit from foreknowledge of the upcoming task. In line with this prediction, we found that WM accuracy was higher when participants had advance knowledge of the task context. Even if WM content can be configured as a task-set, perhaps only one item is optimised for guiding behaviour. If so, retro-cued prioritization may be supported by a transformation of the selected item from a sensory to a task-oriented code. We included a retro-cue on half of the trials to test the second hypothesis that task-foreknowledge enhances retro-cued prioritization. Interestingly, the benefits of task foreknowledge were independent of the benefits incurred by retro-cueing, indicating that attentional selection is sufficient for prioritization of WM content. Together, these results provide preliminary evidence that WM coding may be task-dependent, but neuroimaging studies are needed to elucidate the precise mechanisms by which task foreknowledge facilitates WM-guided behaviour.

Introduction

Working memory (WM) is the ability to maintain and manipulate information in the short-term for future action¹. Traditionally, WM has been conceived as a retrospective mechanism by which the brain represents sensory information that is no longer present in the environment²⁻⁶. However, a crucial function of WM is to maintain information *for* a forthcoming task. This prospective aspect of WM has received relatively less attention in the literature. Previous work has shown that WM is flexible: humans can use knowledge about a current goal to selectively encode and maintain relevant information, thereby increasing the odds of successful behaviour despite WM capacity limits⁷. This is highlighted by studies showing that information already encoded in WM can be selected and prioritized temporarily to improve performance, for example by a retrospective cue (“retro-cue”)⁸⁻¹⁰. This suggests that prospective knowledge about task requirements can influence *what* information is stored. Whether it also affects *how* the relevant information is stored remains an open question.

Early evidence for prospective coding of WM content comes from monkey behaviour and neurophysiology. In a behavioural study, monkeys performed an auditory-visual delayed-match to sample task, with auditory sample stimuli and visual target stimuli¹¹. Either auditory or visual distractors were presented during the delay, but only visual distractors interfered with performance on the task, suggesting that monkeys were storing a prospective code for comparison with the visual targets rather than a retrospective code of the auditory cue. Rainer and Miller (1999) provided neurophysiological evidence in support of prospective WM coding¹². They compared neural responses in PFC while monkeys performed a delayed paired-associate task (DPA), where each sample image was associated with a different target image, to discriminate neural activity associated with the sample and the target. PFC activity reflected the sample stimulus early in the delay, but the target stimulus later in the delay, indicative of a transition from a retrospective to a prospective code. Together, these results suggest that the nature of WM representations may depend on their future use, in a way that optimises performance for the upcoming task.

Some WM tasks allow preparation of the appropriate motor response immediately after encoding, for example some versions of the delayed-saccade task², where a subject is asked to reproduce the location of a memorised stimulus with an eye-movement. In these tasks, the response demands are fully predictable from trial onset. Consequently, neural delay activity may reflect prospective motor preparation rather than stimulus features. A recent EEG study showed that in situations where different WM contents are associated with specific actions, the selection of task-relevant sensory representations and appropriate motor plans may occur in parallel and not serially as would be expected if the WM code was primarily sensory in nature¹³. Instead, these results are consistent with a model of WM in which the brain, when possible, will link sensory representations to their motor plan to guide future behaviour, further integrating the WM literature to literature on motor planning^{14,15}. However, many WM tasks, such as continuous report tasks¹⁶ or change-detection tasks⁷, do not allow for motor preparation at encoding, but instead require a comparison between a WM stimulus and an unpredictable post-delay target. Prospective coding in these tasks would require preparation of a more abstract task-set for items in WM, i.e. linking each stimulus with the context-dependent action¹⁷.

A task set refers to the prospective configuration of cognitive processes, such as perception, attention, memory and motor planning, for a specific task^{17,18}. Task-sets are traditionally studied in task-switching paradigms, where participants are asked to switch between tasks involving the same stimulus set and the same response outputs, for example, to classify numbers based on their magnitude or parity¹⁹. Performance costs following switches relative to repeats, “switch-costs”¹⁷, may be reduced (but not abolished) by cueing the task before target onset, perhaps by allowing the neural state to be re-configured for the new task ahead of time^{20,21} (but c.f. ²²).

Configuration of a task-set can be conceptualized as retrieval of the relevant rule-dependent stimulus-response (S-R) mappings ahead of time (e.g. for the magnitude task rule: ‘press LEFT if the number is lower than 5 and press RIGHT if the number is greater than 5’), allowing for a faster and more accurate translation to a motor output once the target appears. In WM paradigms, memory items could similarly be translated into S-R mappings in preparation for an upcoming target. For example, in a change-detection task, a red memory item may be translated into the

task-set ‘press RIGHT if the target is also red, press LEFT for any other colour’. Here we ask if WM is, in part, supported by a re-configuration of maintained items into prospective task-sets. If this is the case, we would expect WM to benefit from having prospective knowledge of the task context relative to when the task is uncertain. On the other hand, if WM function is primarily supported by a sensory representation of the stored items, we would not expect task-foreknowledge to improve performance, as the full translation from sensory code to motor output would have to occur following target onset whether the task is known in advance or not.

To test our hypotheses that advance task knowledge improves WM-guided behaviour, participants were asked to remember the angle of tilted bars for two different WM tasks: a rotation-discrimination task requiring clockwise/counter-clockwise (CW/CCW) decisions and a change-detection task requiring match/non-match (M/NM) decisions. Task-sets may differ between the two tasks. For example, in the rotation-discrimination task, a task-set may consist of a mental map of the span of target tilts that should trigger a clockwise vs a counter-clockwise response, whereas for the change-detection task, a task-set may consist of a template for acceptance vs rejection of the target. Participants either had advance knowledge of which task they would perform (fixed task blocks) or not (mixed task blocks). If WM content, when possible, is configured into a task-specific code in preparation for the target, we would expect a main effect of task-foreknowledge with more accurate performance on the fixed than on the mixed task blocks.

Even if WM content can be configured in a task-specific format, recent theoretical and experimental work suggests that only one item is optimised for guiding behaviour^{23–25}. Not all items are represented equally in WM²⁵. For example, content prioritized by a retro-cue is reported faster and more precisely^{8,9} and is associated with improved neural decoding²⁶. Myers et al suggest WM prioritization involves two steps: selection and preparation. First, the relevant item in WM is selected by focusing attention to the cued feature. Second, the representation of the relevant item is transformed into an action-oriented code that is optimized to guide behaviour i.e. a stimulus-specific task-set. Preliminary support for this theory of WM prioritization comes from neuroimaging studies of the retro-cue effect that highlight a role of neural areas often associated with motor planning and task-set preparation, such as striatum and cingulo-opercular

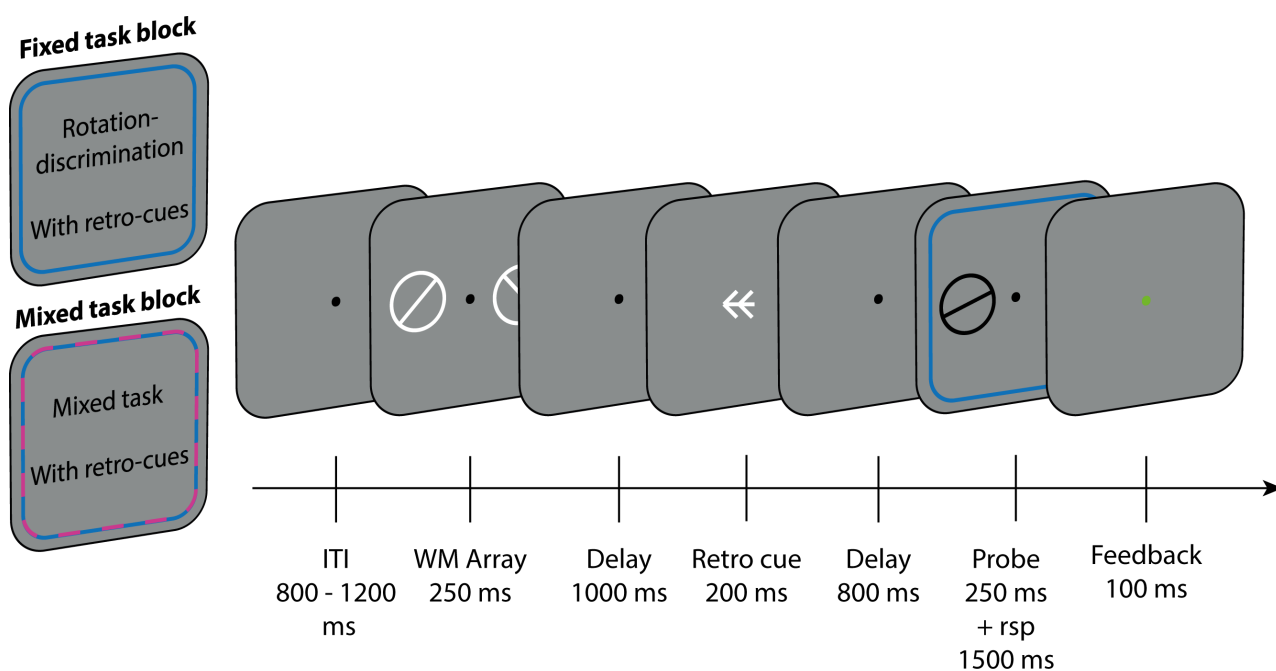
network^{24,27–30}. Wallis et al. (2015) compared the spatiotemporal neural signatures in MEG associated with pre-cues and retro-cues in WM. Retro-cues were uniquely associated with activity in pre-supplementary motor area, anterior insula and frontal operculum, perhaps indicative of “output gating” (i.e. selecting a WM item for guiding behaviour)²⁸. If only one item can be stored in a task-specific format, and retro-cued prioritization stems, in part, from the ability to transform a selected item in memory from a stimulus- to an action-oriented representation, the retro-cue benefit should be larger when the task-context is known in advance. To test this second hypothesis, we also included a retro-cue to signal which item would be probed. If only one item can be configured for an upcoming task and if such a task-specific re-configuration supports prioritization of content in WM, we would expect task-foreknowledge to enhance retro-cued prioritization, with a stronger retro-cue benefit in fixed task blocks than in mixed task blocks.

In summary, we found that task-foreknowledge improves WM accuracy, suggesting it may be advantageous to configure WM content in a task-oriented code. Retro-cued prioritization was found irrespective of task foreknowledge, suggesting attentional selection may be sufficient for effective prioritization of content in WM.

Methods

Participants

Thirty-five participants took part in the experiment. Five participants performed below chance in one of the experimental conditions and were therefore excluded from subsequent analyses. The remaining thirty participants (18 female) were included in the analyses. They were aged 18-35 ($M = 26.03$, $SD = 5.014$), had normal or corrected-to-normal vision (including normal colour vision), and no history of neurological or neuropsychiatric disorders. 28 were right-handed and two were left-handed. The study has been approved by Oxford Central University Research Ethics Committee (CUREC) and all participants provided informed consent prior to participating in the study. Participants were reimbursed for their time.



Conditions			Rotation-discrimination	Change-detection
Task context	Task foreknowledge	Retro-cue	<div> <div>CCW</div> <div>CW</div> <div>+/- 5°, 10°, 16°, 24°, 32°, 40°</div> </div>	<div> <div>M</div> <div>NM</div> <div>+/- 10°, 20°, 32°, 48°, 64°, 80°</div> </div>
<div> <div>Rotation-discrimination</div> <div>Change-detection</div> </div>	<div> <div>Yes (fixed blocks)</div> <div>No (mixed blocks)</div> </div>	<div> <div>← → Informative</div> <div>⊗ Neutral</div> </div>		

Figure 1. Task design and experimental conditions. CW = clockwise, CCW = counter-clockwise, M = match, NM = non-match.

Apparatus and stimuli

The task was programmed and stimuli presented in Matlab R2017b (Mathworks) and Psychtoolbox 3.0.14³¹. It was presented on a 24 inch, 1920x1080 pixel monitor running at 100 Hz and participants were seated 60 cm from the screen.

Stimuli were presented on a grey background (RGB = 0.5, 0.5, 0.5). A black fixation dot was presented at the centre of the screen (0.3° diameter) throughout each trial. Memory items were two tilted white bars within circles (6° diameter) and appeared on each side of the screen, at a distance of 6° from the fixation dot. On every trial, the orientation of each stimulus was selected at random between 1 and 180° with replacement. The probe was a black tilted bar within a circle (6°; same size as memory items) and was presented in the position of the to-be-remembered

item. The angular offset between the memory item and the probe was uniformly distributed across \pm six angle differences (except for 'match' probes in the change-detection task where the angle difference was always 0°). For the change-detection task, the set of angular offsets were $\pm 10^\circ$, $\pm 20^\circ$, $\pm 32^\circ$, $\pm 48^\circ$, $\pm 64^\circ$, and $\pm 80^\circ$. For the rotation-discrimination task, the angular offsets were $\pm 5^\circ$, $\pm 10^\circ$, $\pm 16^\circ$, $\pm 24^\circ$, $\pm 32^\circ$, and $\pm 40^\circ$. Feedback was provided at the end of each trial. The fixation dot turned green for a correct and red for an incorrect response.

Participants responded using the 'F' and 'J' keys on a standard keyboard (QWERTY configuration). For the rotation-discrimination task, participants responded 'F' for 'counter-clockwise' and 'J' for clockwise. For the change-detection task, the response mappings were counterbalanced across participants.

Procedure

Participants performed a computerised experimental task consisting of two different task contexts (*Figure 1*): a change-detection task requiring match/non-match (M/NM) judgements and a rotation-discrimination task requiring clockwise/counter-clockwise (CW/CCW) judgements. Participants compared the probe to the remembered stimulus according to the current task rule. In the change-detection task, participants responded 'match' if the probe had the same tilt as the memory item and 'non-match' if the probe had a different tilt. In the rotation-discrimination task, participants responded 'clockwise' or 'counter-clockwise' depending on the direction of tilt relative to the memory stimulus. In half of the blocks, the task context remained fixed for a block of trials (fixed task blocks) and in the other half the task context varied within the block and participants were not informed of the task rule until probe onset (mixed task blocks). Moreover, in half of the blocks, a retro-cue was presented during the delay period to inform participants which of the two items would be probed at the end of the trial.

Each trial started with a fixation dot (800-1200 ms) followed by presentation of the WM items (250 ms). After an initial delay period (1000 ms), either an informative or a neutral retro-cue appeared (200 ms) depending on the block type, followed by another delay (800 ms). The probe was presented for 250 ms and participants had 2000 ms to respond. If no response was detected

within the response window, the trial would time-out and was recorded as incorrect. Participants received feedback following the response.

There was a total of 864 trials, divided into 8 block types (36 trials per block): fixed rotation-discrimination with retro-cue, fixed rotation-discrimination without retro-cue, fixed change-detection with retro-cue, fixed change-detection without retro-cue, 2 x mixed task with retro-cue, and 2 x mixed task without retro-cue. The order of the eight block types was pseudorandomised so each block type appeared once every eight blocks, but in random order. Participants practiced the task before starting the experiment.

Analyses

Accuracy

We recorded the proportion of correct responses for each condition, averaged over the angular offsets between the memorised stimulus and the probe.

Our main analysis focused on whether task-foreknowledge benefits WM performance. Secondly, we were interested in whether the retro-cue benefit interacts with task-foreknowledge. To test this, we performed a 2x2x2 ANOVA with task-context (change-detection vs rotation-discrimination), task-foreknowledge (present vs absent) and retro-cue (informative vs neutral) as within-subject factors.

Evidence from task-switching paradigms suggest that performance is better on task-repeat trials relative to task-switch trials (switch-cost)¹⁷. Next, we also tested whether a potential main effect of task-foreknowledge in the above analysis could be accounted for by task repetition. We limited the next analysis to task-repetition trials only and ran a 2x2 repeated measures ANOVA with task-context (change-detection vs rotation-discrimination) and task-foreknowledge (present vs absent) as within-subject factors.

For completeness, we also tested the role of task-switching on WM performance in general with a 2x2x2 ANOVA on the mixed block trials only with task-context (change-detection vs rotation-

discrimination), task-switching (switch vs repeat) and retro-cue (informative vs neutral) as within-subject factors.

We complement the frequentist statistics with Bayes Factor Analysis, performed using JASP (v 0.9.0.1) with default priors³². These analyses indicate the likelihood of the data given H_1 relative to the null hypothesis H_0 (reported here as BF_{10} ; values larger than 1 suggest evidence in favour of the H_1). For the Bayesian repeated measures analyses with more than two factors we also report the inclusion Bayes Factor across matched models (BF_{incl}) for interaction terms. This compares the models that contain that effect to the equivalent models stripped of this effect by dividing the sum of the $P(M|data)$ of the former by the $P(M|data)$ of the latter. The full results of the Bayes Factor Analyses can be found on the Open Science Framework via the following link:

<https://osf.io/z7b2k/>.

Reaction times

We performed the same set of analyses for median reaction times (RT) on correct trials, as described for accuracy above. However, for the comparison between fixed task blocks and mixed task blocks, the RT measure is confounded by increased stimulus processing demands at probe onset in the conditions without task-foreknowledge. As such, we only report RT results for the task context effect, the retro-cue effect, and for task-switching. See supplementary material for full RT results.

Results

Performance on the two tasks

Figure 2 shows the overall performance on the two tasks. Accuracy was mostly matched across participants with no main effect of task context ($p = .199$, $BF_{10} = .418$). The RTs were significantly faster on the change-detection task ($M = .702$, $SD = .105$ sec.) than on the rotation-discrimination task ($M = .751$, $SD = .145$ sec.): $F_{1,29} = 11.64$, $p = .0329$, $BF_{10} = 4.003$. This effect was driven by three participants with slow median RTs on the rotation-discrimination task (see outliers, Figure 2). Thus, the rotation-discrimination and change detection tasks were mostly matched in terms of task difficulty.

Table 1. Mean and standard deviation of accuracy for all task conditions.

	Task-foreknowledge with retro-cue		Task-foreknowledge without retro-cue		No task-foreknowledge, with retro-cue		No task-foreknowledge, without retro-cue	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Change- detection	0.8387	0.0669	0.7679	0.0625	0.8011	0.0654	0.7440	0.0714
Rotation- discrimination	0.8256	0.0810	0.7519	0.0799	0.8160	0.0811	0.7048	0.0784

Benefit of task-foreknowledge

Figure 3A (left) shows accuracy for trials with or without task foreknowledge. As predicted, accuracy was significantly higher on the fixed task blocks where participants had foreknowledge about the task ($M = .796$, $SD = .0587$) than on the mixed task blocks where participants did not know the task context until the onset of the probe ($M = .7665$, $SD = .0579$): $F_{1,29} = 27.34$, $p < .001$, $BF_{10} = 34.108$. There was no significant interaction between task-foreknowledge and task context and Bayes Factor indicated evidence against this interaction ($p = .8117$, $BF_{incl} = .199$).

In the task-switching literature, trials following a task-switch are associated with slower RTs and more errors than trials following task-repetition¹⁷. As potential switch-costs in the mixed task blocks could also contribute to the main effect of task-foreknowledge, we repeated the previous analysis, but only included task-repeat trials (figure 4A, right). The main effect of task-foreknowledge remained significant ($F_{1,29} = 11.18$, $p < .0023$, $BF_{10} = 4.536$), showing improved performance with task-foreknowledge on task-repeat trials. As above, there was no significant interaction between task-context and task-foreknowledge for the repeat trials and Bayes Factor Analysis indicated evidence against this interaction ($p = .3286$, $BF_{incl} = .322s$).

In summary, we obtained evidence that prospective knowledge of the task-context improved WM accuracy for both the rotation-discrimination task and the change detection task, and this benefit was not accounted for by task-switching.

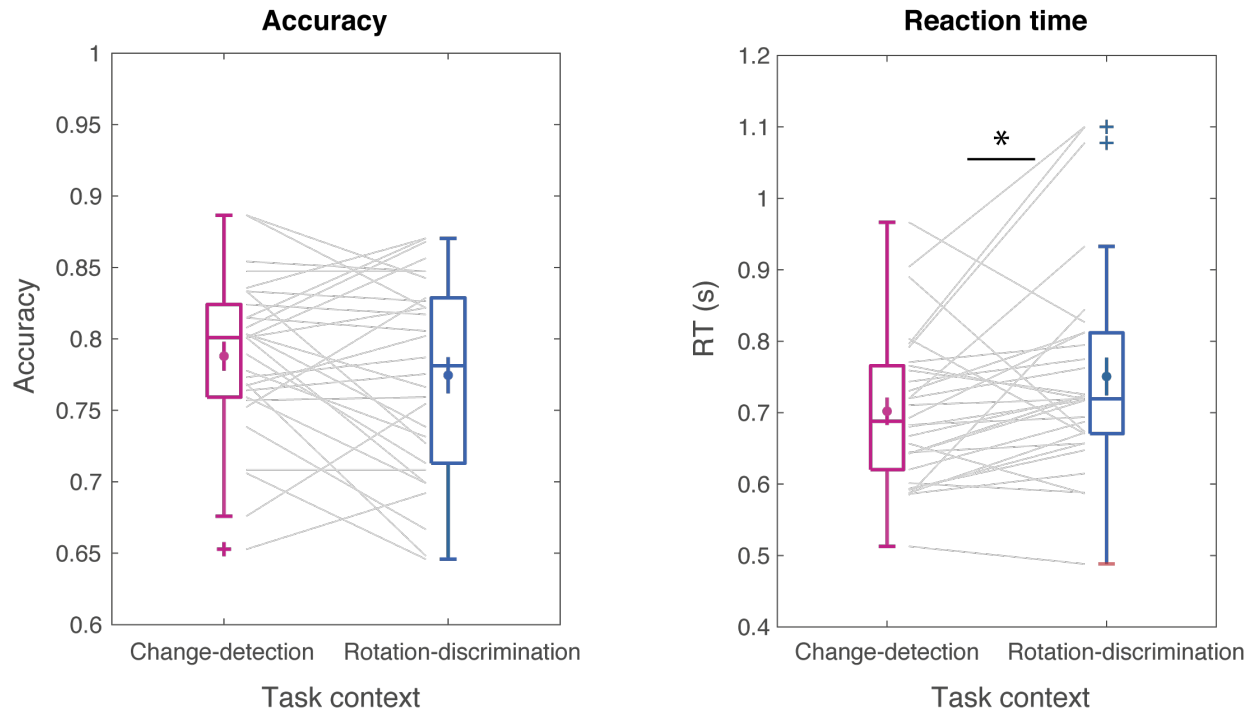
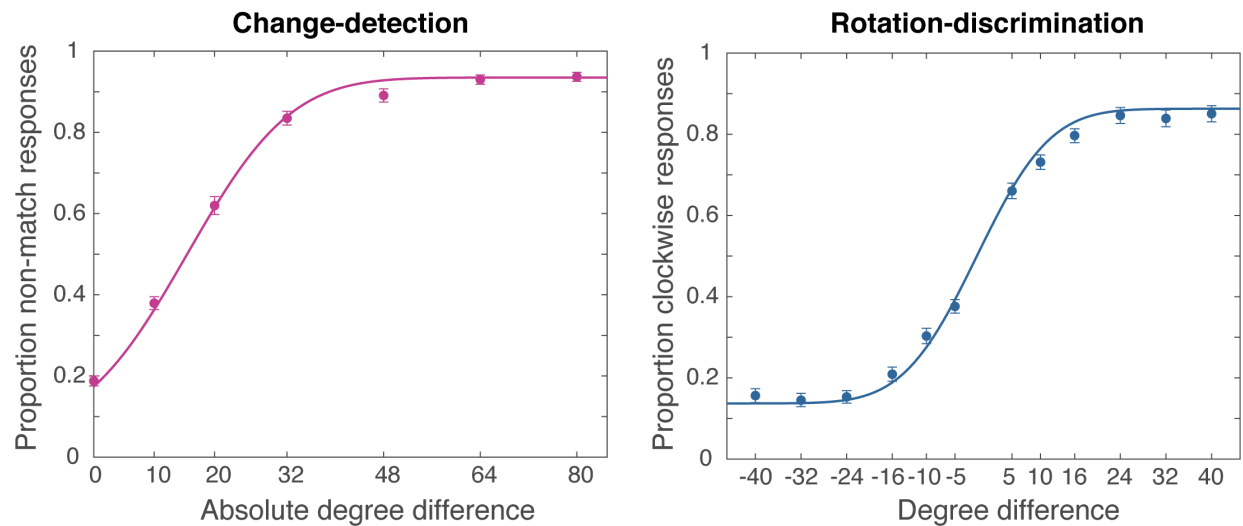
A**B**

Figure 2. Performance on the change-detection (pink) and rotation-discrimination (blue) tasks. **A.** Accuracy shown in the left panel and reaction times are shown in the right panel. * $p < .05$. **B.** The proportion of 'non-match' (left) and clockwise (right) responses for each degree offset between the memorized item and the probe, with a cumulative Gaussian function fit overlaid for the change-detection task (left) and rotation-discrimination task (right). Error bars show standard error of the mean. Grey lines show individual participants

Retro-cue benefit

Replicating previous results, we found that participants performed better with informative retro-cues than with neutral cues across the two tasks. Accuracy was higher with retro-cues ($M = .82$, $SD = .059$) than without ($M = .742$, $SD = .059$): $F_{1,29} = 140.65$, $p < .001$, $BF_{10} = 8.143 \times 10^{19}$. Similarly, RTs were faster with retro-cues ($M = .687$, $SD = .121$) than without ($M = .768$, $SD = .107$): $F_{1,29} = 227.25$, $p < .001$, $BF_{10} = 1.045 \times 10^6$.

In addition, there was a significant task-type x retro-cue interaction for accuracy: $F_{1,29} = 7.68$, $p < .0096$, $BF_{incl} = 1.603$, indicating that the retro-cue benefit was larger for the rotation-discrimination task than the change-detection task, though the Bayes Factor suggests only weak evidence for this effect. Post-hoc pairwise comparisons showed that the retro-cue benefit was significant for both rotation-discrimination (with retro-cue: $M = .8208$, $SD = .0745$, without retro-cue $M = .7283$, $SD = .0715$, $t_{29} = 4.9076$, $p < .001$) and change-detection (with retro-cue: $M = .8199$, $SD = .0606$, without retro-cue: $M = .7559$, $SD = .0596$, $t_{29} = 3.8301$, $p < .001$). There was no significant difference in accuracy for the two tasks either with ($p = 0.55071$) or without ($p = 0.31685$) an informative retro-cue.

In summary, we found that retro-cues improved performance on both tasks, with some evidence that the retro-cue effect was larger for change-detection than rotation-discrimination judgements.

Retro-cue benefit does not interact with task-foreknowledge

Figure 3B shows the benefit of retro-cuing on trials with and without task-foreknowledge. We found no evidence that the retro-cue effect benefits from knowing the task in advance, as there was no interaction between retro-cueing and task-foreknowledge ($F_{1,29} = 1.18$, $p = .286$, $BF_{incl} = 0.311$) and Bayes Factor indicates evidence for the null hypothesis. There was also no significant three-way task-context x task-foreknowledge x retro-cue interaction. Although there was a small trend for this interaction ($F_{1,29} = 4.05$, $p = .0534$, $BF_{incl} = 1.095$), Bayes Factor did not suggest evidence for or against the interaction. Thus, we found evidence for the null hypothesis that the retro-cue benefit did not interact with prospective task knowledge.

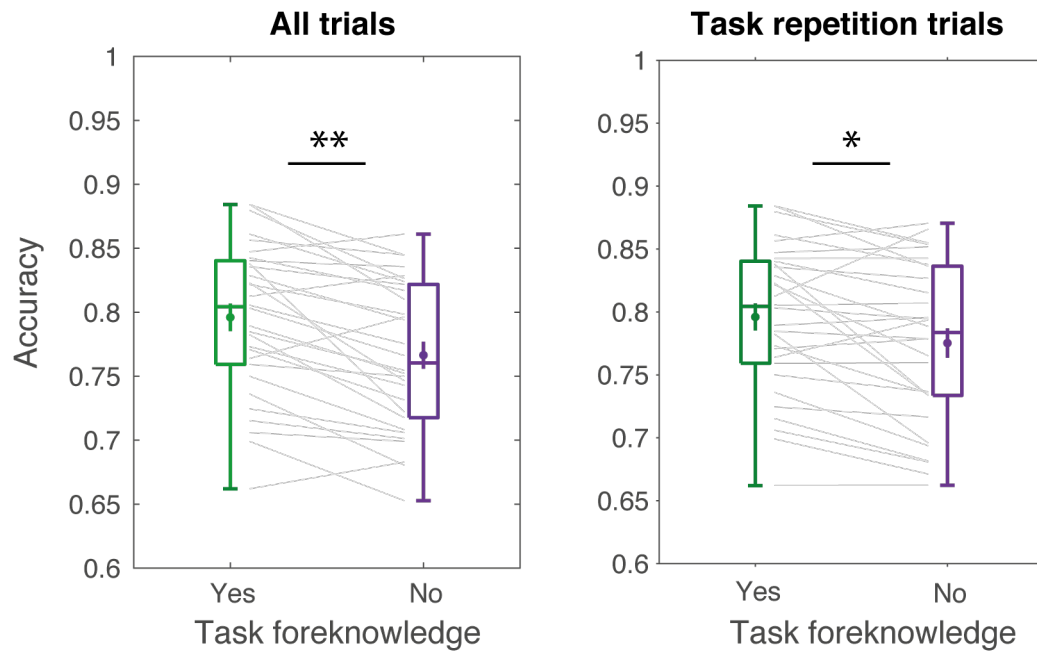
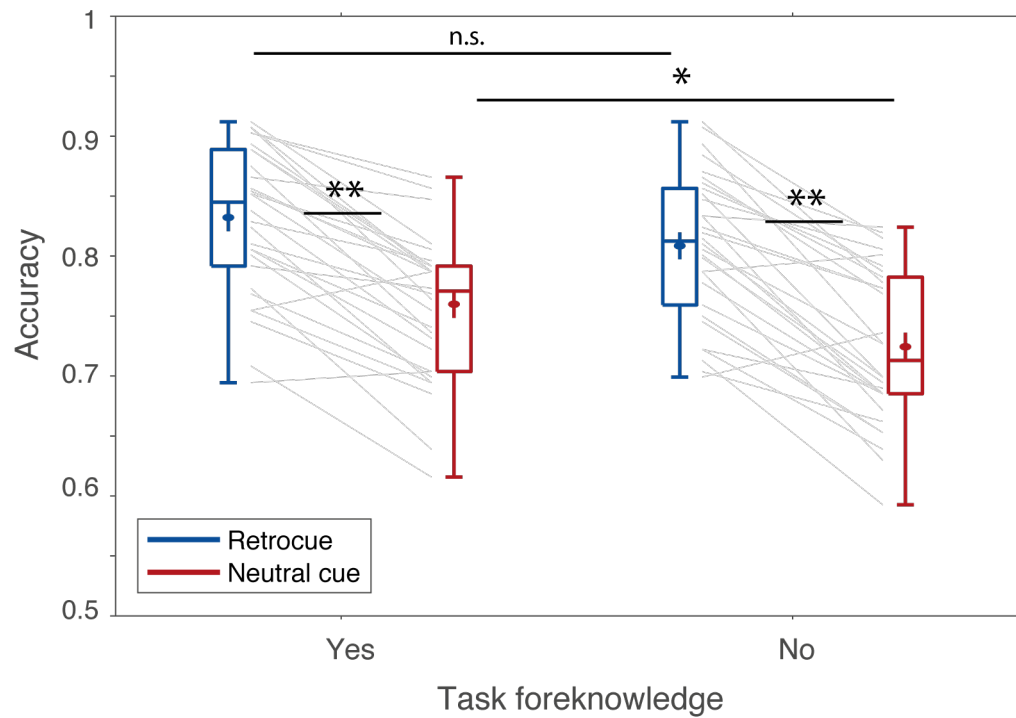
A**B**

Figure 3. Task-foreknowledge. **A.** The benefit of task foreknowledge for accuracy for all trials (left) and for task-repetition trials only (right). * $p < .01$, ** $p < .001$. **B.** Accuracy for trials with and without an informative retro-cue as a function of task-foreknowledge. * $p < .05$, ** $p < .001$. Error bars show standard error of the mean. Grey lines show individual participants

Task switch-cost

There was a main effect of task switching in the mixed task blocks for accuracy ($F_{1,29} = 6.47, p = .0165, BF_{10} = 0.671$) and RTs ($F_{1,29} = 73.69, p < .001, BF_{10} = 5.702 \times 10^3$), suggesting that task-switching has detrimental effects on WM performance in line with switch-costs previously reported in the task-switching literature. However, it should be noted that the Bayes Factor analysis indicated no evidence for a switching effect for accuracy. There was no switching x task-type interaction, no switching x retro-cue interaction and no three-way task-type x switching x retro-cue interactions for either accuracy or RT ($p > .05$ and $BF_{incl} < 1$).

In summary, switching between tasks in the mixed blocks was associated with higher RTs and, to some extent, lower accuracy relative to repeat trials.

A

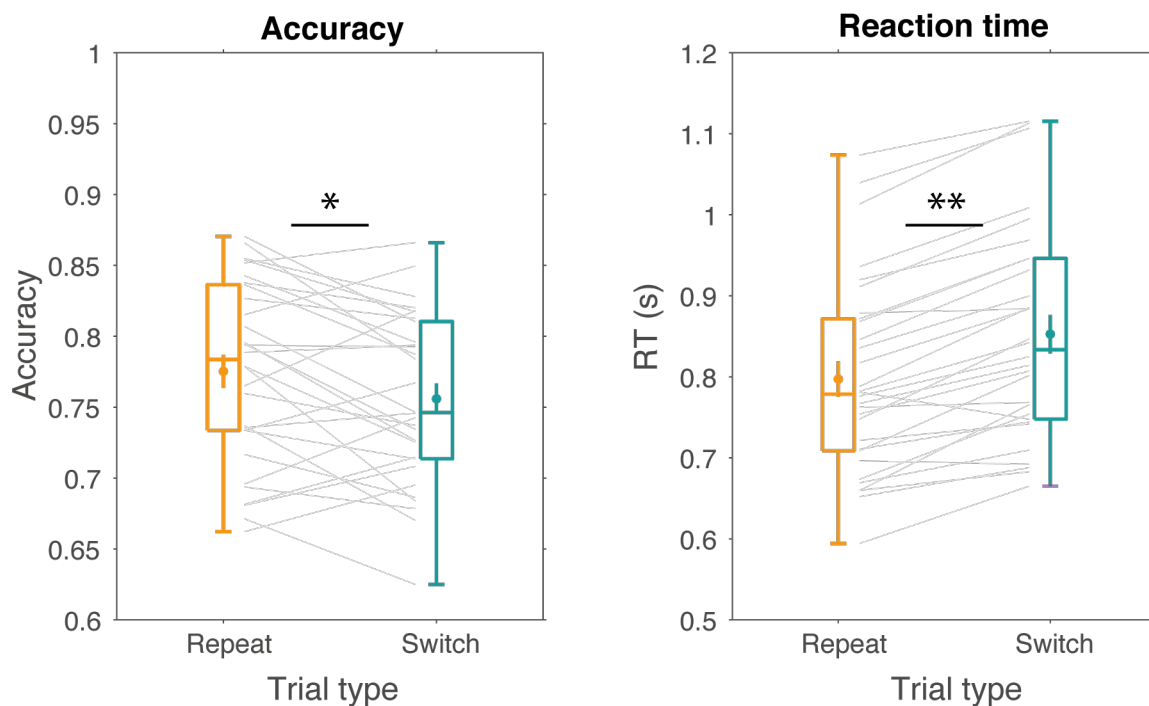


Figure 4. Task switching in mixed task blocks. Accuracy (left) and reaction time (right) for task repeats (orange) and task switch trials (cyan). * $p < .05$, ** $p < .001$. Error bars show standard error of the mean. Grey lines show individual participants

Discussion

In support of our hypothesis that it is adaptive to store WM content in a prospective task-oriented code, we find that WM accuracy improves with advance knowledge of the task context by which WM content is probed. We further show that accuracy is higher for task-repeats than task-switches in the mixed task blocks, but find evidence that task-foreknowledge benefits performance over and above the effects of task repetition. Retro-cues further improve performance, replicating previous results, but retro-cued prioritization does not benefit from having advance task knowledge.

Studies of WM tend to focus on performance within a single task, e.g. continuous report tasks¹⁶ or change detection tasks⁷, where subjects always know how the information held in memory will be used to guide performance. Here, we show that prospective knowledge of task-context benefits WM performance indicating that, when possible, WM content may be configured in a task-specific format in a way that promotes behaviour. We suggest this is analogous to forming a task-set by linking the possible sensory inputs to task-appropriate actions in preparation for the target¹⁸.

WM theories have primarily focused on mechanisms for storing representations of sensory information³⁻⁶. Our findings highlight the importance of incorporating prospective, task-dependent aspects of WM function into theoretical frameworks. If WM-guided behaviour relied exclusively on precise representations of past sensory input during the delay, we would not expect performance to change as a function of whether the task is known in advance. If a common neural code underlies WM in both tasks, then there should be no particular advantage to maintaining the orientation with or without task-foreknowledge, as the complete visuomotor transformation would have to occur following target onset in both cases. Instead, our results are consistent with a dynamic coding framework of WM function³³⁻³⁵.

According to dynamic coding theories, WM-guided behaviour is achieved by a neural reconfiguration that changes the way the brain processes new input. Monkey neurophysiology studies have discovered neurons in the prefrontal cortex that are tuned to mixtures of task features, e.g. they are selective to a certain stimulus only when presented in a certain context³⁶.

Such mixed selectivity neurons may be well-suited to compute stimulus-response mappings for combinations of task-variables, allowing for efficient implementation of task-sets^{37,38}. In our paradigm, task-foreknowledge may allow for a more efficient computation of the relevant stimulus-response mappings, facilitating context-dependent responses.

The results reported here are closely related to the literature on task switching. We found relative costs of task-switches relative to task-repeats in the mixed task blocks with further benefits to performance when the task was explicitly known in advance in the fixed task blocks, mirroring the phenomena of ‘switching’ and ‘mixing’ costs in the task-switching literature^{17,39,40}. Perhaps new WM content is automatically configured according to the most recent task, resulting in a benefit for task-repetitions. We propose that the task-foreknowledge benefit in our study may be supported by a re-configuration of the items stored in WM into task-sets in preparation for an upcoming target, similar to the configuration of task-sets thought to underlie task cueing benefits in the task-switching literature^{17,20,41} (but c.f.²²). A crucial difference between WM paradigms and task-switching paradigms is that new and perhaps multiple items are stored on every trial imposing additional processing demands for computing task-sets in WM tasks. Nevertheless, our results suggest that task-foreknowledge may promote flexible WM-guided behaviour for at least a limited set of items. Neuroimaging studies employing different WM tasks in the same study may be better able to elucidate whether WM contents are indeed maintained in a task-specific configuration⁴².

Human neuroimaging has shown that ‘output gating’ in WM (i.e. selecting memorised information to guide future behaviour) engages neural areas traditionally associated with motor planning and task-set preparation^{24,28–30}. Recruitment of these areas may contribute to a task-oriented reconfiguration of the neural state in preparation for upcoming behaviour⁴³. However, we did not find evidence that task-foreknowledge improved the retro-cue benefit as expected if the ability to prepare task-specific stimulus-response mappings was necessary for WM prioritization²³. Instead, our results suggest that attentional selection of the stimulus is sufficient to produce the retro-cue benefit, though further research will be necessary to examine this effect across a wider range of tasks and WM loads.

With our behavioural task, we cannot rule out that costs in the mixed task blocks could arise due to interference from additional attentional demands at the time of the probe. Although task-cues were matched on fixed and mixed task blocks, the cue was imperative only in the mixed blocks, incurring additional processing demands. Thus, to obtain a more detailed understanding of the mechanisms that underpin the task-foreknowledge benefit, a more fruitful avenue may be to use multivariate pattern analysis of neuroimaging data to delineate the nature of WM delay representations in different task contexts.

To conclude, we find evidence that advance task knowledge improves WM accuracy, suggesting it may be adaptive to store WM content in a task-oriented code for guiding future behaviour. This highlights the prospective nature of working memory and challenges the classic notion that WM function is exclusively supported by retrospective representations of past sensory inputs.

Acknowledgements

This research was funded by a Biotechnology and Biological Sciences Research Council grant (BB/M010732/1) and James S. McDonnell Foundation Scholar Award (220020405) to Mark G. Stokes and by the NIHR Oxford Health Biomedical Research Centre. Frida A.B. Printzlau is funded by a Biotechnology and Biosciences Research Council studentship. Nicholas E. Myers is funded by the Wellcome Trust (grant 201409Z/16/Z) and University College Oxford. Paul S. Muhle-Karbe is supported by the Wellcome Trust (grant 210849/Z/18/Z), the Research Foundation Flanders (grant 12R8817N) and a Cephalosporin Junior Research Fellowship from Linacre College Oxford. Sanjay G. Manohar is funded by the MRC clinician scientist fellowship (MR/P00878X) and Leverhulme research grant (RPG-2018-310). We would like to thank Ilenia Salaris for assistance with data collection.

References

1. Baddeley, A. D. *Nat. Rev. Neurosci.* **4**, 829–839 (2003).
2. Funahashi, S., Bruce, C. J. & Goldman-Rakic, P. S. *J. Neurophysiol.* **61**, 331–49 (1989).
3. Harrison, S. A. & Tong, F. *Nature* **458**, 632–635 (2009).

4. Pasternak, T. & Greenlee, M. W. *Nat. Rev. Neurosci.* **6**, 97–107 (2005).
5. Serences, J. T. *Vision Res.* **128**, 53–67 (2016).
6. D’Esposito, M. & Postle, B. R. *Annu. Rev. Psychol.* **66**, 115–142 (2015).
7. Luck, S. J. & Vogel, E. *Nature* **390**, 279–281 (1997).
8. Griffin, I. & Nobre, A. C. *J. Cogn. Neurosci.* **15**, 1176–1194 (2003).
9. Pertzov, Y., Bays, P. M., Joseph, S. & Husain, M. *J. Exp. Psychol. Hum. Percept. Perform.* **39**, 1224–1231 (2013).
10. Souza, A. S., Rerko, L. & Oberauer, K. *J. Exp. Psychol. Hum. Percept. Perform.* **42**, 890–910 (2016).
11. Colombo, M. & Graziano, M. *Behav. Neurosci.* **108**, 636–9 (1994).
12. Rainer, G., Rao, S. C. & Miller, E. K. *J Neurosci* **19**, 5493–5505 (1999).
13. van Ede, F., Chekroud, S. R., Stokes, M. G. & Nobre, A. C. *Nat. Neurosci.* (2019).
doi:10.1038/s41593-018-0335-6
14. Gallivan, J. P., Logan, L., Wolpert, D. M. & Flanagan, J. R. *Nat. Neurosci.* **19**, 320–326 (2016).
15. Gallivan, J. P., Bowman, N. A. R., Chapman, C. S., Wolpert, D. M. & Flanagan, J. R. *J. Neurophysiol.* **115**, 3113–22 (2016).
16. Bays, P. M., Catalao, R. F. G. & Husain, M. *J. Vis.* **9**, 7.1-11 (2009).
17. Monsell, S. *Trends in Cognitive Sciences* **7**, 134–140 (2003).
18. Sakai, K. *Annu. Rev. Neurosci.* **31**, 219–245 (2008).
19. Monsell, S., Sumner, P. & Waters, H. *Mem. Cognit.* **31**, 327–342 (2003).
20. Meiran, N. *J. Exp. Psychol. Learn. Mem. Cogn.* **22**, 1423–1442 (1996).
21. Rogers, R. D. & Monsell, S. *J. Exp. Psychol. Gen.* **124**, 207–231 (1995).
22. Allport, A., Styles, E. A. & Hsieh, S. (1994).
23. Myers, N. E., Stokes, M. G. & Nobre, A. C. *Trends in Cognitive Sciences* **21**, 449–461 (2017).
24. Schneider, D., Barth, A. & Wascher, E. *Neuroimage* **162**, 73–85 (2017).
25. Olivers, C. N. L., Peters, J., Houtkamp, R. & Roelfsema, P. R. *Trends Cogn. Sci.* **15**, 327–334 (2011).
26. Sprague, T. C., Ester, E. F. & Serences, J. T. *Neuron* **91**, 694–707 (2016).
27. Myers, N. E., Walther, L., Wallis, G., Stokes, M. G. & Nobre, A. C. *J. Cogn. Neurosci.* **27**, 492–508 (2015).

28. Chatham, C. H., Frank, M. J. & Badre, D. *Neuron* **81**, 930–942 (2014).
29. Tamber-Rosenau, B. J., Esterman, M., Chiu, Y. C. & Yantis, S. J. *Cogn. Neurosci.* **23**, 2905–2919 (2011).
30. Wallis, G., Stokes, M., Cousijn, H., Woolrich, M. & Nobre, A. C. *J. Cogn. Neurosci.* **27**, 2019–2034 (2015).
31. Brainard, D. H. *Spat. Vis.* **10**, 433–436 (1997).
32. JASPTeam. (2018).
33. Stokes, M. G. *Trends Cogn. Sci.* **19**, 394–405 (2015).
34. Stokes, M. G. *et al. Neuron* **78**, 364–375 (2013).
35. Duncan, J. *Nat. Rev. Neurosci.* **2**, 820–829 (2001).
36. Rigotti, M. *et al. Nature* **497**, 1–6 (2013).
37. Fusi, S., Miller, E. K. & Rigotti, M. *Current Opinion in Neurobiology* **37**, 66–74 (2016).
38. Passingham, D. & Sakai, K. *Curr. Opin. Neurobiol.* **14**, 163–168 (2004).
39. Meiran, N., Chorev, Z. & Sapir, A. *Cogn. Psychol.* **41**, 211–253 (2000).
40. Los, S. A. *Acta Psychol. (Amst)*. **94**, 145–188 (1996).
41. Yeung, N. & Monsell, S. *J. Exp. Psychol. Hum. Percept. Perform.* **29**, 455–469 (2003).
42. Muhle-Karbe, P. S., Duncan, J., De Baene, W., Mitchell, D. J. & Brass, M. *Cereb. Cortex* **27**, 1891–1905 (2017).
43. Rushworth, M. F. S., Hadland, K. A., Paus, T. & Sipila, P. K. *J. Neurophysiol.* **87**, 2577–92 (2002).