Action similarity warps visual feature space in working memory

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Visual working memory (VWM) retains representations of past visual information for future action. Yet to date, most studies have approached VWM as just serving perception beyond the immediate. Whether and how prospective actions shape information in VWM remains largely unknown, in part because typical experimental setups limit behavior to simple button presses. In two experiments (one preregistered), using a novel interactive VWM task, we show that the similarity of the actions that we intend to perform on memory items adaptively distorts their representation. Participants memorized the orientation of two bars, after which they were informed as to which manual actions they should reproduce these orientations with in a memory recall test. We observed that perceptually similar items were remembered as more distinct when paired with different action plans versus the same action plan. A control experiment showed that this action-induced effect reflects a true change in the visual representation rather than a motor bias. These findings demonstrate that VWM representations are flexibly adapted to guide specific overt actions and provide evidence that action plans can retrospectively warp sensory feature space in VWM.

action planning | visual working memory | representations

Visual working memory (VWM) enables us to retain prior information in service of upcoming behavior, connecting past perception to future action. To date, studies have predominantly approached VWM as a mental repository that holds past visual information for retrospective recollection and almost exclusively investigated how VWM representations change as a function of the perceptual attributes of what is stored, such as stimulus quantity (1), visual similarity (2), perceptual noise (3), or perceptual complexity (4). Yet, more recent VWM accounts emphasize that, ultimately, VWM serves to adaptively guide upcoming actions (5, 6), supporting a reconceptualization of VWM from a memory *of* something to a memory *for* something (7). Indeed, we search for our keys because we want to grasp them, and we memorize the outlines of a puzzle piece because we want to combine it with other pieces already laid on the table.

So far, few studies have considered how future action plans affect how information is stored in VWM. This is likely, at least in part, because traditional experimental setups limit the possibility for action to very simple movements, like button presses (whether on a response box, keyboard, or mouse). Moreover, in most earlier studies on the interaction between VWM and motor requirements, actions were not actually planned toward the item held in VWM itself, but toward environmental aspects that happened to coincide with the VWM content (8–11). These studies provide initial, though indirect, support for the notion of "attention for action" in VWM (6, 12). According to this view, planning an action leads to the instantiation of recurrent feedback signals from motor to visual areas, which result in the strengthening or prioritization of action-relevant sensory representations in working memory.

If the primary purpose of VWM is to indeed optimally guide future behavior (5–7, 12), one may expect that VMW sacrifices veridical memory representations for representations that better facilitate efficient interactions with the environment. When the cognitive system is presented with perceptually similar (but not identical) sensory inputs that are to be assigned to different motor outcomes, it is faced with a fundamental problem, namely how to keep the two memorized items apart and thus prevent interference at the motor output level (13). In this case, exaggerating the perceptual difference between two similar memories that are linked to distinct actions would ensure better coupling between the sensory information and the corresponding actions, thereby reducing the probability of executing the wrong motor plan. Recent studies using mouse or keyboard responses have shown that, depending on their visual similarity, VWM representations of stimuli can be biased toward or away from those of other items that are concurrently held in memory (2, 14, 15). Specifically, perceptually similar items are reported as more dissimilar than they actually are (resulting in an observed repulsion bias), while perceptually dissimilar items are reported as more similar than they actually are (resulting in an observed attraction bias) (14, 16, 17).

Significance

Visual working memory (VWM) allows us to store past visual percepts to inform imminent actions. As such, VWM representations should be flexible and easily adaptable to one's current action goals. Yet, we still do not know whether and how future actions influence memory storage. Using a novel interactive VWM task, we found that when one plans to act differently on two perceptually similar objects, these are remembered as more distinct compared to when one plans to perform the same type of action on them. This finding demonstrates that planning the future changes the past: Action intentions can retrospectively distort sensory memories in a way that renders them most suited to serve behavior.

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It has been argued that these biases serve respectively the functional purposes of increasing visual memory distinctiveness and memory stability (17). However, if VWM ultimately serves action, we may expect not just perceptual attributes of stimuli but also—and especially—motor requirements to play a role in tuning memory representations. To date, no study has investigated whether and how the similarity of *actions* that are assigned to different memorized items can influence the way they are represented in VWM.

The current study addressed this outstanding issue in two experiments, the second of which was preregistered, and both of which are illustrated in Fig. 1. On each trial, participants were asked to memorize the orientation of two sequentially presented bars. Only after VWM encoding—so, retrospectively—participants were instructed to plan an action on each bar, as indicated by an action cue. Crucially, the actions linked to the two bars could be either the same (i.e., grip+grip or slide+slide) or different (i.e., grip+slide or
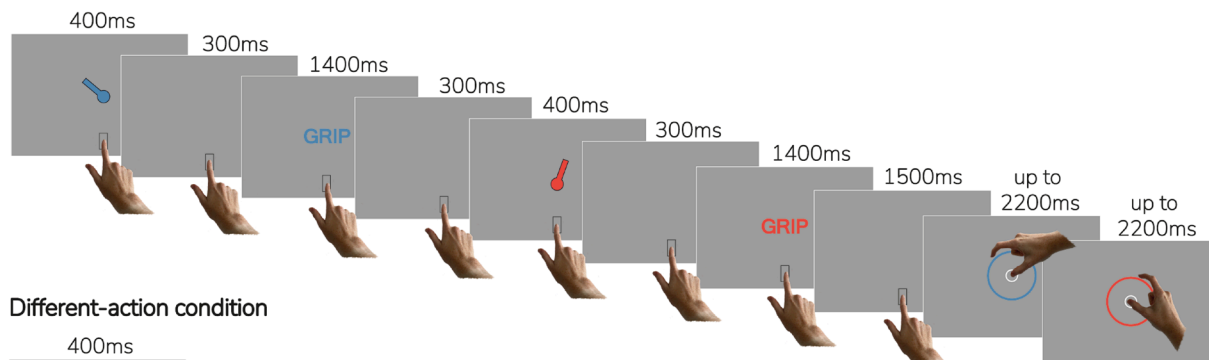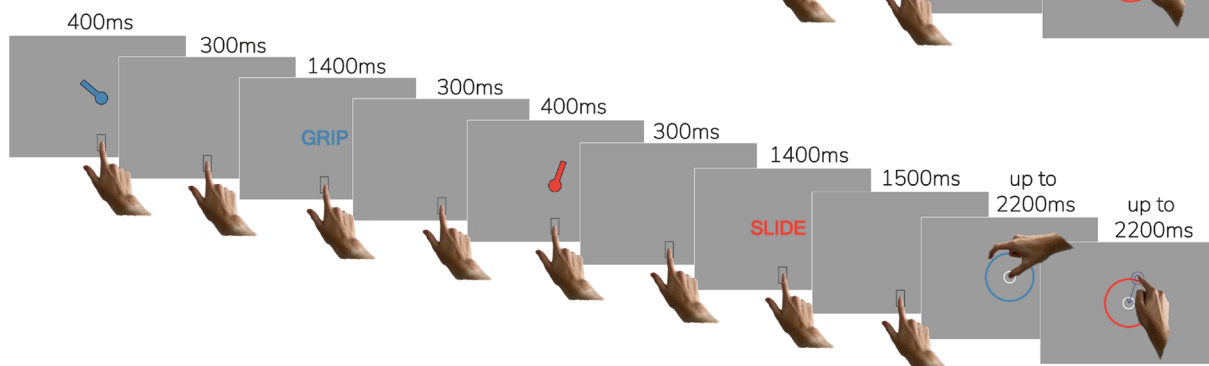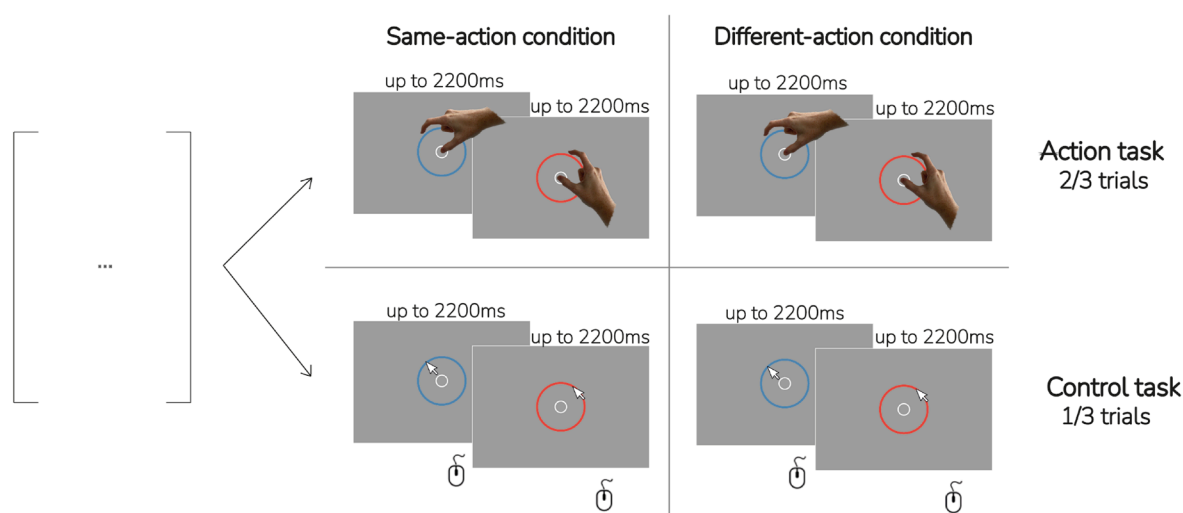
Fig. 1. Experimental design of Experiment 1 (*A*) and Experiment 2 (*B*). *A*) On each trial, participants memorized the orientation of two sequentially presented bars and their associated cued action (i.e., GRIP or SLIDE). At the end of the trial, they were probed to reproduce the memorized orientations by performing the action that was associated with it on the touch screen. In the same-action condition, the two orientations were associated with the same action, while in the different-action condition, the two orientations were coupled with two different actions. The two action conditions were randomly intermixed. *B*) The task in Experiment 2 was identical to the task used in Experiment 1, except that now, unpredictably, on a third of the trials, we inserted a control task in which participants reported the orientations by means of a mouse click instead.

slide+grip). After participants memorized the two orientations and their associated actions, they reported the memorized orientations by performing the prepared actions on a touch screen. This design allowed us to investigate whether action similarity affects feature similarity within VWM. Specifically, we asked whether orientations that are tied to different types of actions are remembered as more different than orientations tied to the same action. If so, then this would provide evidence that newly forged action associations can retrospectively change past sensory traces.

Results

Experiment 1: Memory Items Linked to Different Action Plans Repel Each Other More Than Items Associated With the Same Action Plan. In Experiment 1, we investigated how planning two distinct actions on two objects held in VWM differentially influenced the interaction between their mnemonic representations compared to planning the same action on these objects. To this end, thirty-two participants performed the VWM task illustrated in Fig. 1A. They memorized the orientation of two sequentially presented bars, each followed by an action cue. The two bars as well as the action cues were presented sequentially and not simultaneously, to ensure that observed effects occurred during

memory maintenance rather than perceptual encoding (14). After a delay, participants were asked to reproduce each orientation by executing the corresponding action on a touch screen, which was either a grip or a slide movement. In the *same action* condition, the types of action were identical for both bars (i.e., grip+grip or slide+slide), while in the *different action* condition, each bar was associated with a distinct action type (i.e., grip+slide or slide+grip).

We measured the extent to which the reported orientation of each bar was biased by the orientation of the other bar concurrently held in working memory, as a function of action condition. Specifically, separately for each action condition, we computed the absolute error of each report, defined as the difference in degrees between the reproduced and the veridical orientation of each stimulus, and then assigned a positive sign to it if the error represented a bias away from the other bar (i.e., repulsion), while negative errors reflected a bias toward the other bar (i.e., attraction). These are shown in Fig. 2, separately for the first and the second report. We first examined error biases separately for the first report since any observed bias at this stage could not be induced by a preceding action, and therefore more likely reflects a true change in the memorized perceptual similarity of the two orientations. Consistent with previous studies, we found repulsion and attraction biases for perceptually similar and dissimilar items,
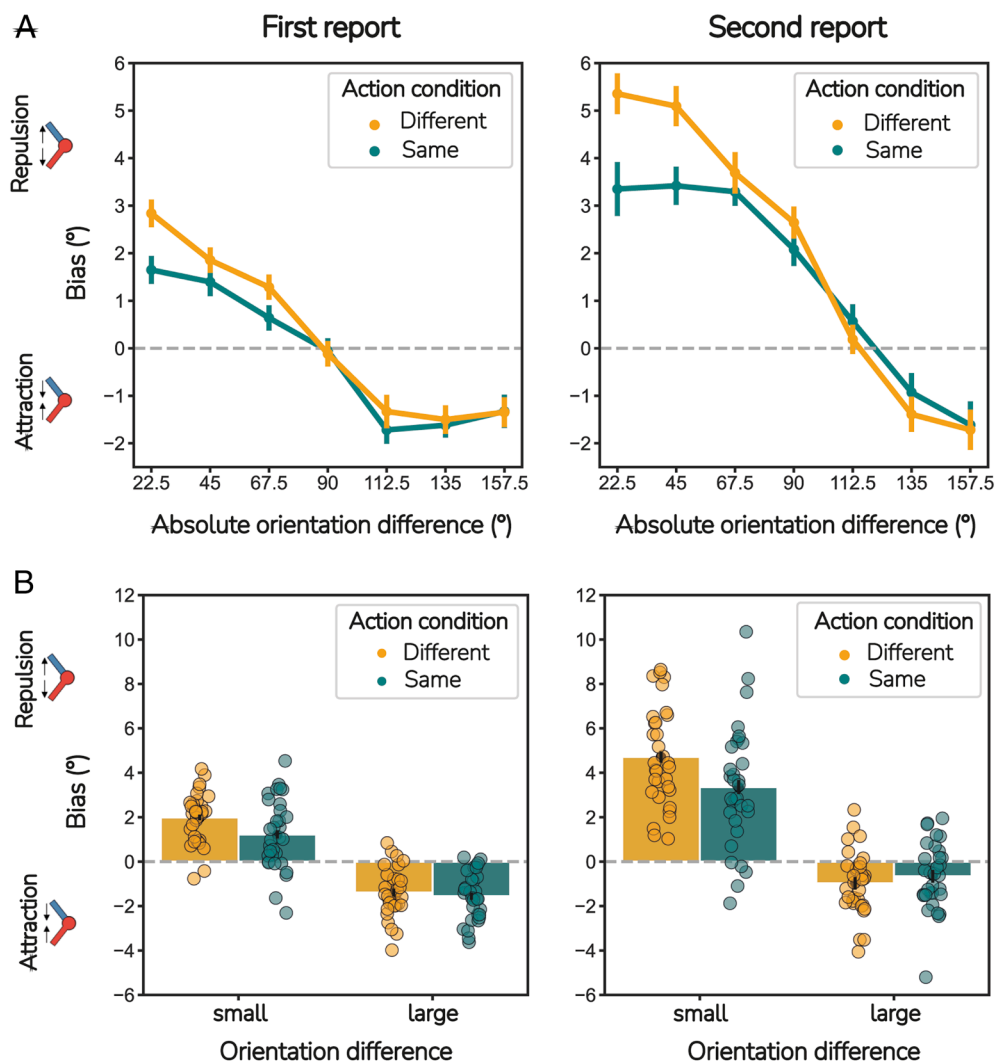
Fig. 2. Planning two different versus two same actions enhanced repulsion between two similarly oriented bars concurrently held in VWM, in Experiment 1. A) Biased error for each absolute orientation difference; B) Biased error grouped across small (22.5 °, 45.0 °, and 67.5 °) and large (112.5 °, 135.0 °, and 157.5 °) absolute orientation differences. Positive errors indicate repulsion between the two items concurrently held in VWM, while negative errors indicate attractive biases.

respectively, as indicated by a main effect of *orientation difference* (μ_{small} =1.60 ± 0.215, μ_{large} = −1.47 ± 0.147, log-ratio=58.895, $P < 0.001$). For small orientation differences, on average, repulsive biases were observed, while reports for large orientation differences revealed attractive biases. Importantly, we observed a main effect of *action condition* (μ_{diff} = 0.308 ± 0.167, μ_{same} = −0.178 ± 0.167, log-ratio=7.611, $P = 0.0058$), reflecting a stronger positive bias in the different action condition than in the same action condition. While there was no significant interaction between the variables *orientation difference* and *action condition* (log-ratio = 2.705, $P = 0.10$), Fig. 2 (*Top Left* panel) suggests that the effect mainly originates at small orientation differences between the two bars. Exploratory Sidak-corrected post hoc comparisons between the two action conditions, for small and large orientation differences separately (Fig. 2) (*Bottom Left* panel), confirmed that at small orientation differences, there was significantly more repulsion between the two memorized orientations in the different action condition (t-ratio = 3.115, $P = 0.0037$, CI = [0.287,1.262]), whereas there was no evidence for a difference in attraction between the two conditions at large orientation differences (t-ratio = 0.786, $P = 0.677$, CI = [−0.293,0.684]).

These results were then replicated for the second report, where we observed main effects of *orientation difference* (μ_{small} = 4.04 ± 0.403, μ_{large} = −0.81 ± 0.204, log-ratio = 47.260, $P < 0.001$) and of *action condition* (μ_{diff} = 1.88 ± 0.242, μ_{same} = 1.35 ± 0.242, log-ratio = 6.378, $P = 0.012$), plus now also an interaction (log-ratio = 16.463, $P < 0.001$). Sidak-corrected post hoc tests again revealed a greater repulsion bias in the different compared to the same action condition, for small orientation differences (t-ratio = 4.642, $P < 0.001$, CI = [0.779,1.917]), but no evidence for condition differences in attractive biases for large orientation differences (t-ratio = 1.153, $P = 0.436$, CI = [−0.933,0.242]).

Consistent with the idea of action-induced alterations of VWM representations, Experiment 1 thus revealed stronger repulsion for two similar items concurrently held in VWM when each item is linked to a different action compared to when they are associated with the same action. We found no difference in attraction at larger orientation differences (beyond 90°), suggesting that the action effect is repulsion-specific.

Experiment 2: The Action-Associated Repulsion Occurs at the Level of Sensory Representations Rather than Motor Representations.
The aim of Experiment 2 was twofold: (1) to confirm the findings of Experiment 1 in a preregistered study (*Materials and Methods*) and (2) to control for the possibility that the action-dependent repulsion effect observed in Experiment 1 reflected a motor bias rather than a sensory bias (18). As mentioned, any bias observed at the time of the first report cannot be attributed to a preceding motor response. Nonetheless, given that at the end of the delay period observers held two potential action plans in memory, any repulsion effect might still originate at a motor level, between representations of the planned action rather than between two sensory representations. In Experiment 2, we controlled for this possibility by presenting thirty-six participants with the same overall task as in Experiment 1, where they had to perform either the same or different actions on two memorized orientations (Fig. 1*B*). However, on a minority of trials, and unpredictably so, participants were asked to instead report both orientations by means of a mouse click on the rim of the response circle (rather than by executing any of the planned actions). This *control* task thus consisted of a third, unprepared action, and thus, it served as neutral test of how the actually prepared actions would affect the memory representation. We hypothesized that in these control trials, we would still observe a greater repulsion effect

between memories initially associated with different actions. If so, then the enhanced repulsion effect cannot simply be explained at the motor level but must contain a sensory component. Note that to increase the power to replicate the action similarity-induced repulsion effect, this time we pooled the data from a range of randomly sampled small orientation differences between 15° and 35°. This is the range for which repulsion biases were maximal in Experiment 1. For symmetry, we also pooled the large orientation differences from the range between 145° and 165°.

Fig. 3 shows the results. For the first report in the action task, we replicated the stronger repulsion bias in the different-action compared to the same-action condition for small orientation differences (t ratio = 4.667, $P < 0.0001$, CI = [0.401,1.384]) that we also observed for Experiment 1. Critically, this repulsion effect was also present in the control task, in which, just like in the action task, memory items initially associated with two different motor actions were reported as more distinct compared to when these items were linked to the same action plan, even though the orientations were now reported via an unplanned mouse click (t = 3.971, $P = 0.0001$, CI = [0.356,1.662]). We next explored potential differences in the size of this effect between the action and control task (not preregistered). To this end, our statistical model of the error biases included the variables *task*, *action condition*, and *orientation difference,* and their interactions. This analysis revealed a main effect of task (μ_{action} = 0.478 ± 0.160, $\mu_{control}$ =0.776 ± 0.171, log-ratio = 7.038, $P = 0.008$), reflecting the fact that report biases were overall more positive in the control task, and a main effect of action condition ($\mu_{different}$ = 0.840 ± 0.165, μ_{same} = 0.415 ± 0.164, log-ratio = 15.161, $P = 0.0001$), which reflected more positive biases in the different-action condition. We again observed a significant interaction between the variables *action condition* and *orientation difference* (log-ratio = 22.256, $P < 0.001$), confirming the greater repulsion effect in the different action condition for small orientation differences (t-ratio = 5.979, $P < 0.0001$, CI = [0.639,1.263]), while there was no difference in attraction for large orientation differences (t-ratio = −0.437, $P = 0.662$, CI = [−0.381,0.242]). Importantly, *task* did not interact with *action condition*, nor with *orientation difference* (log-ratio = 0.243, $P = 0.622$; log-ratio < 0.001, $P = 0.982$). Thus, the action-related repulsion effect was comparable for both tasks. Together, these first report data indicate a change in the interaction between the mnemonic representations as a function of differential action planning, and not simply interference at the motor level.

For the second report too, we replicated our previous finding of Experiment 1 of a greater differentiation between perceptually similar memory items when these were linked to different actions. This was true for the action task trials (t-ratio = 11.112, $P < 0.0001$, CI = [2.540,4.063]), and again also for the control task trials (t-ratio = 7.692, $P < 0.0001$, CI = [1.760,3.517]), thus providing further evidence against a simple explanation in terms of a differential motor bias. When including the variables *task*, *action condition*, *orientation difference,* and their interactions in our statistical model, we again found a significant interaction between the variables *action condition* and *orientation difference* (log-ratio = 44.019, $P < 0.0001$), with post hoc comparisons showing a greater repulsion effect for small orientation differences (t-ratio = 10.950, $P < 0.0001$, CI = [2.44,3.500]), but surprisingly, now also greater attractive biases at large orientation differences in the different-action condition (t-ratio = 3.036, $P = 0.0024$, CI = [−1.17, −0.251]) across the two tasks. Here too, there was no interaction between *task* and *action condition* (log-ratio=1.404, $P = 0.236$), nor a triple interaction (log-ratio = 2.217, $P = 0.137$), and thus, there was no evidence that the degree of the action-related biases differed between the action and control tasks. There was an interaction between *task* and
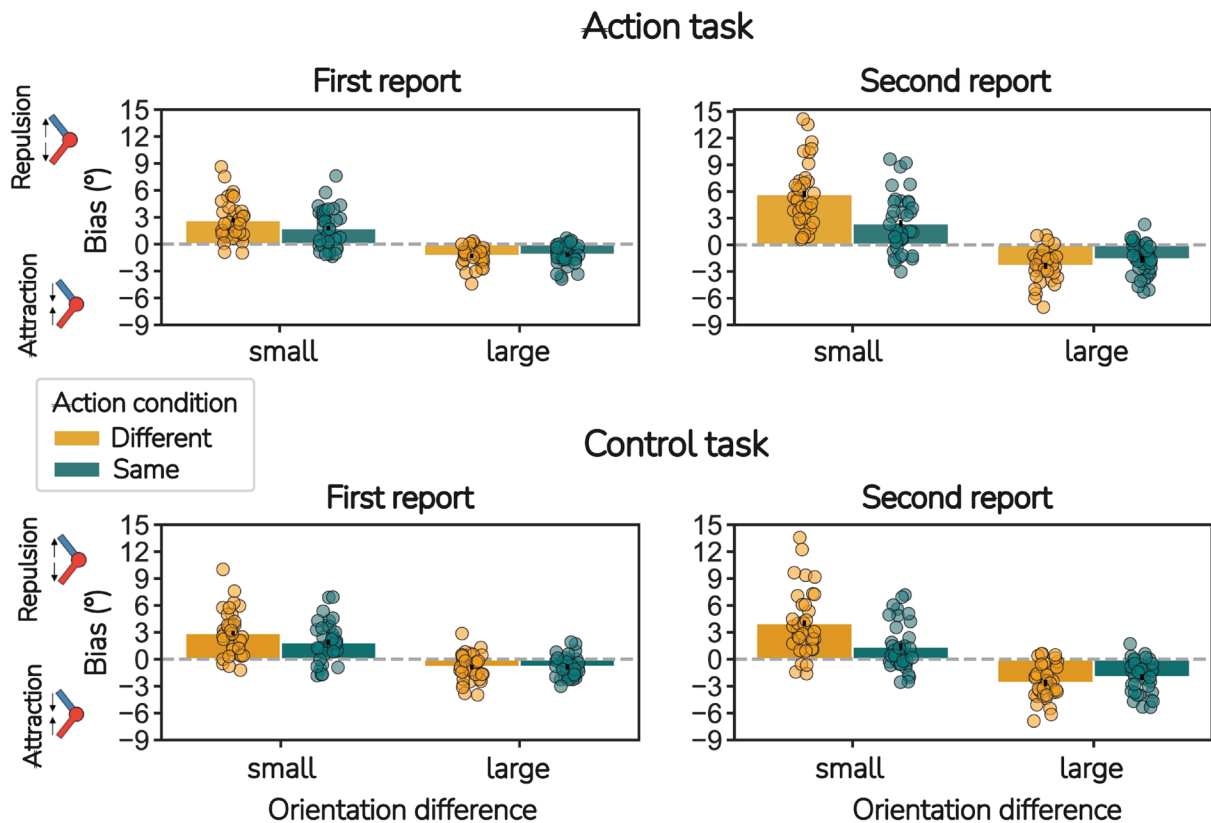
Fig. 3. The action-dependent repulsion effect is present in both the action and the control task in Experiment 2. Biased errors are shown separately for first and second report (*Top* and *Bottom* row, respectively) and the two tasks. The biases are grouped across small (from 15° to 35.0°) and large (from 145° to 165°) absolute orientation differences. Positive errors indicate repulsion between the two items concurrently held in VWM, while negative errors indicate attractive biases.

orientation differences (log-ratio = 15.897, P = 0.0001), and post hoc comparisons revealed that, in the action task, there was overall significantly more second-report repulsion for small orientation differences than in the control task (t = 7.731, P < 0.0001, CI = [0.989,1.661]), while this did not occur for second-report attractive biases at large orientation differences (t = 1.641, P = 0.192, CI = [–0.060,0.678]). Finally, we observed a main effect of task (μ_{action} = 0.574 ± 0.258, $\mu_{control}$ = -0.290 ± 0.267, log-ratio = 46.381, P < 0.0001), reflecting again overall more positive biases in the action task. We also observed a main effect of condition ($\mu_{different}$ = 0.605 ± 0.280; μ_{same} = -0.321 ± 0.247; log-ratio = 11.336, P = 0.0008) with the different action condition leading to more positive biases, independent of task, and a main effect of orientation differences (μ_{small} = 2.61 ± 0.477; μ_{large} = -2.33 ± 0.247; log-ratio = 12.396, P = 0.0004). Given the absence of these latter effects in Experiment 1 and in the first report data of Experiment 2, we will not draw strong conclusions from this.

Taken together, Experiment 2 thus replicated and extended the findings of Experiment 1: A greater repulsion bias at small orientation differences for different- compared to same-action trials. Moreover, this effect remained present in the control task, where in the end the planned actions were not performed. This excludes an explanation in terms of the repulsion happening purely at the motor planning or execution level. Hence, our analyses on the report biases indicate that the mnemonic trace of the two memorized bars had changed at a perceptual level. This conclusion is further corroborated by additional analyses (reported in Supplementary Information) through which we ruled out alternative explanations of the observed repulsion effect. Specifically, a previous study found that repulsion biases between items concurrently held in VWM tend to increase with longer maintenance delays (19). A possibility was therefore that our finding resulted from a difference in reaction times between the

different and the same action condition, if participants took longer to report the memorized orientations in the different action condition. In *SI Appendix*, SI.1, we show that in the first report, participants were equally fast in responding to the touch screen. In the second report, participants were indeed somewhat slower in the different action condition, but there was no correlation between report biases and reaction times. Moreover, in Experiment 2, participants were overall slower to respond in the control condition, yet biases did not increase for that condition.

Finally, participants may have been more prone to confusing the two memory items in the same action condition, resulting in a larger number of swaps (20). Mistaking one item for another would count as a response toward the other item and thus detract from any repulsion effect. As a result, the greater repulsion biases observed in the different action condition might actually reflect a decrease in repulsion in the same action condition. In *SI Appendix*, SI.2, we assessed swaps using the Mixture-Swap model (20), which allowed us to also rule out this possibility. While participants did indeed make significantly more swap errors in the same action condition, they also still displayed a significantly greater repulsion bias in the different action condition once we accounted for the contribution of swap errors. Overall, our main and supplementary analyses indicate that a change in perceptual representations of the two bars underlies the observed repulsion effect.

Discussion

VWM fundamentally supports imminent or future behavior. Yet, little is known about how action planning may modulate information represented in VWM. In the current study, we addressed this research gap and asked whether action planning can alter how

similar objects look to our mind's eye. Previous work has shown that visual similarity between items in VWM results in repulsive biases, such that visually similar items are perceived as more different from each other than they really are (14, 21). Here, we show that on top of these sensory interactions, the dissimilarity of the actions associated with visual items leads to additional warping of the visual feature space in VWM. Critically, the control manipulation of Experiment 2 showed that this effect cannot be attributed to competition at the level of motor execution. Thus, our findings demonstrate that action planning leads to differential interactions within VWM, resulting in a concomitant warping of visual feature space. As such, they critically extend past work by demonstrating that the instantiation of sensory memory-motor links in VWM may not only induce a mere *strengthening* of action-relevant features (22, 23) but can also qualitatively *distort* these features. This observation has important theoretical implications, as it demonstrates that physical action planning, not just visual task demands, can mold information representation in VWM. It further emphasizes the importance of incorporating action effects in our current computational models of VWM, which so far have solely focused on how physical features of memorized stimuli, like color or orientation, are encoded and represented in VWM (24). Our study also shows the necessity of moving beyond purely passive to more interactive experimental setups, to gain a full understanding of how VWM serves upcoming behavior.

Two aspects of our data favor an account in which the observed action-similarity-dependent repulsion effect results from a sensory change in the VWM representations, rather than reflecting a mere motor bias. First, we observed action-related repulsion already during the first report, which was not preceded by any movement yet. This means that the effect was at the very least already caused by action planning, rather than action execution. Second, in Experiment 2, we also observed a greater repulsion bias for the subset of trials in which participants were informed only at test that they should withhold the planned actions and report on both orientations by means of a mouse click. Thus, the effects of action planning on orientation reproduction persisted even when the action plans were canceled and replaced by a neutral third response. These effects again cannot be explained by competition at the level of motor execution. Rather, the results suggest that the original action plans must have affected the perceptual memory traces themselves. These findings corroborate observations in previous studies, which showed that action-induced effects on working memory result primarily from action planning rather than from action execution per se (e.g., refs. 11, 22–25).

Equally importantly, the modulation appears to have occurred entirely retrospectively, within memory, and not at perceptual encoding. Note that the action cues always followed the encoding of the orientations, and thus, participants could not predict whether these orientations would be associated with the same or different actions until after the second of the two bars was encoded. Therefore, our action manipulation could have only influenced the interaction between the two VWM representations during the memory delay phase. This is comparable to what has been found for visual similarity-based biases within VWM, which also appear to occur after encoding (17, 19), and it further indicates how VWM representations can flexibly adapt to future goals.

One possible explanation for the observed repulsion effect is that it stems from differences in memory load between the two action conditions, rather than from variations in action similarity. Specifically, while participants memorized two orientations in both conditions, only in the different action condition did they memorize two distinct action plans. Nevertheless, it is unlikely that the increased memory load in the different action condition caused the results. A recent study (26) found precisely the opposite, that is, that higher memory loads lead to greater attraction biases between items held in VWM, while lower memory loads are linked to more pronounced repulsion biases.

Rendering perceptually similar stimuli more different in memory is the process of pattern separation (27, 28): Differences between ambiguous sensory inputs are enhanced in order to reduce the overlap, and thus the confusability, between them. This becomes especially important when two similar objects are assigned to two different motor outcomes since excessive memory interference between the two items can lead to wrong and potentially detrimental interactions with one's surrounding environment. In support of this notion, as reported in *SI Appendix*, SI.2, we found that the probability of confusing the two items (i.e., swap errors) in the different action condition was significantly reduced compared to that observed for the same action condition. The observed greater repulsion biases in the different action condition may therefore have benefitted behavior by more clearly linking the two objects to the proper motor output.

This still leaves the question of what are the exact mechanisms underlying this effect. One possibility is offered by common coding theory (29, 30), which assumes a shared representation for perception and action, as actions are coded in terms of sensory effects. If neural populations represent combinations of visual features and action information, tying in different actions should lead to greater separation of activity patterns especially when the visual features themselves are similar, as we found. Alternatively, the observed enhanced repulsion effect may be purely sensory in nature, induced through differential attentional weighting of the visual representations within VWM. Studies that manipulated visual similarity within VWM have reported that attended items induce stronger biases than unattended ones (14, 15, 19, 31). As proposed by Olivers and Roelfsema (2020), planning an action on an object in VWM may automatically enhance the representation of that object, which is then expressed as attentional prioritization (see refs. 22, 23) for empirical support). If we were to additionally assume that planning two different action types leads to more attention to each of the items in VWM in our experiments, this could then explain the stronger repulsion effect. Indeed, there is some evidence that concurrently planning two different actions can lead to independent and parallel modulation of attention to items encoded in VWM (32). This idea also aligns with recent proposals that selective attention originates within parallel fronto-parietal circuits, each subserving the planning of a specific type of action (e.g., reaching vs grasping (33, 34). Finally, even if two action types do not cause overall more attention to be available, we can still explain our finding if different action types lead to a different distribution of feedback signaling. Specifically, when similar sensory features cause population activities to overlap, two different action plans may result in stronger weighting of those neurons that do distinguish between the orientations. While similar actions will lead to similar feedback loops and thus similar weighing of associated sensory representations, differential actions would activate more separated feedback loops, and thus lead to more precise weighting of each of the associated sensory activations, allowing for clearer decorrelation of sensory patterns. In any case, future neuroimaging studies are needed to delineate at which levels in the perceptual hierarchy the action-based modulation can penetrate to alter or weigh sensory representations within VWM.

While we found greater repulsion biases for similarly oriented bars in the different action condition in both reports across the two different experiments, we did not find much evidence for differential attraction biases (except for the second report data of the control condition in Experiment 2). We may have lacked the

power to detect a difference in attraction biases between the two conditions in our study because 1) large orientation differences may lead to ambiguity as to whether they concern a clockwise or a counterclockwise rotation difference (e.g., a clockwise orientation of 160° may be interpreted by the participant as a counterclockwise orientation of 200°, even though the way we designed the stimuli was meant to create a 360° orientation space), and this adds noise to the measurements; 2) in Experiment 2, we sampled relatively large orientation differences (from 145° to 165°), for which attraction biases are typically much smaller (14); 3) In general the source of the attraction bias is less clear. It may mainly reflect a decision strategy in that, when uncertain which of the two items is being probed, it pays off to choose an orientation somewhere in between the two stimuli (i.e., toward the average). Unlike the repulsion bias, which appears to have a sensory origin (35), such a decision strategy may not be affected by the associated action plans. Furthermore, the average of two orientations will remain the same, independent of the amount of repulsion between the two (e.g., the average between 10° and 100° is the same as the one between 5° and 105°). Future studies are necessary to determine whether and how action planning may affect interactions between perceptually dissimilar objects in VWM.

In conclusion, we provide important evidence for the separation of information in VWM on the basis of future actions, demonstrating the action-oriented nature of VWM. By warping the representational space, different action plans help distinguish between similar visual memories.

Materials and Methods

Participants. Participants took part in the experiments in exchange for credits or money (10 euros per hour). Both experiments were approved by the Scientific and Ethics Review Board of the Faculty of Behavior and Movement Sciences at the Vrije Universiteit Amsterdam. Prior to each experiment, participants received an Information Letter detailing the task and data handling procedures, along with a paper Informed Consent form. Participants all had normal or corrected-to-normal vision and had to be between 18 to 35 y old. We recruited 32 participants (average age: 21.8 ± 4.06; 24 female) for Experiment 1. This number of participants was based on previous studies which examined intratrial serial dependence between VWM representations (14). We recruited 36 participants (average age 21.6 ± 3.62; 27 female) for Experiment 2. In both experiments, participants with fewer than 70% of trials after data cleaning were excluded from the analysis and replaced before their data were further examined (see the *Data analysis* section below for criteria).

Stimuli and Procedure. The experiments were coded in OpenSesame 3.3.8 (36) and were presented on a DELL P2418HT Touch Screen (1080 × 1920 pixels, refresh rate of 100 Hz). Participants performed the tasks standing, facing the 45°-reclined screen at a self-selected distance. In both experiments, participants memorized the orientation of two sequentially presented bars, that each was followed by an action cue informing participants which action they, after a delay, would have to execute to report the given bar orientation (Fig. 1).

In Experiment 1, the orientation of each bar was reported at test by performing a specific action on a dial appearing at the center of the touch screen. Following the encoding of each of the bars, the action to be performed on that bar was indicated by a cue and was either a grip movement (indicated by the word GRIP) or a slide movement (indicated by the word SLIDE). In the *same action condition*, both bars were associated with the same action cue (i.e., GRIP+GRIP or SLIDE+SLIDE), while in the *different action condition*, each bar was associated with a different action cue (i.e., GRIP+SLIDE or SLIDE+GRIP). The two action conditions were randomly intermixed within each block. The order of report (report the first or second stimulus first) was counterbalanced across blocks. To make it easier for participants to remember the order of report, one bar was red (RGB: 231,71,61), the other blue (RGB: 74,134,177), and the dials shown at test matched the color of the bar to be reported (Fig. 1). Following (14), we randomly selected the orientation of one of the two bars from 16 equally spaced angle values between 11.25° and

348.75° (in steps of 22.5°), with all orientations sampled twice within a block. The orientation of the other bar was then established by setting the angular difference in orientation between the two bars to one of the following values: ± 22.5°, ± 45.0°, ± 67.5°, ± 90.0°, ± 112.5°, ± 135.0°, ± 157.5°, or 180°. Each of these angular differences was also sampled twice within the same block, once for the same action and once for the different action condition. Finally, we ensured that the two action cues GRIP and SLIDE were presented an equal number of times within the same block. Each block therefore consisted of 32 trials. At the start of each block, we added 5 "buffer trials" to absorb any task order adjustments between different blocks, and which were discarded from the analysis. After practicing the task for 16 trials, participants performed 16 blocks of 37 trials each, for a total of 592 trials, of which 512 (i.e., 16 × 32) were retained for the analysis.

To start each trial, participants placed the index finger of their dominant hand on a small rectangle shown on the lower part of the screen, at a distance of 400 pixels from central fixation, and kept it there throughout the trial, until the appearance of the memory test. As soon as participants touched the rectangle, a colored bar (max width × max length: 45 × 160 pixels) was centrally displayed on the screen for 400 ms; the bar was then followed by a 300 ms-long blank display and, subsequently, by a cue in the same color of the bar (width × height: 256 × 64 pixels), indicating the action to be performed at test, i.e., either GRIP or SLIDE. This action cue was presented centrally on the screen for 1,400 ms. After another 300 ms-long blank display, a second colored oriented bar was shown at the center of the screen for 400 ms, again followed by a 300 ms-long blank display and the central presentation of the second action cue for 1,400 ms, now drawn in the color of the second bar. Participants were instructed to memorize both orientations and associated action cues. After a memory delay of 1,500 ms, participants saw a dial at the center of the screen. The color of the dial indicated which of the two encoded bar orientations had to be reported by performing its associated action (the order of which was fixed throughout a block). Participants responded by lifting the index of their dominant hand from the rectangle followed by the designated action on the screen. By ensuring that participants could not to move their dominant hand until the memory test appeared, we prevented the "off-loading" of the memory by already preparing the gesture in advance. Upon the execution of the first response or, if no response was registered, after a maximum time interval of 2,200 ms, the first dial was replaced by a second dial of a different color, to which participants again responded with the associated action. Here too, participants had to provide their response within 2,200 ms. The time limit was meant to encourage participants to already plan the actions in advance. We also encouraged high accuracy by providing feedback after each response: A number between 0 and 100 appeared on the screen indicating how close the participant's response was to the original orientation, with the number 100 indicating a perfect score (i.e., less than 1° error).

In Experiment 2, on 2/3 of the trials, participants performed the same task as in Experiment 1 (*action task*). However, in 1/3 of the trials, they were unexpectedly at test, presented with a different task (*control task*). The control task was identical to the action task until report: Participants saw and memorized two serially presented bars and their corresponding action cues, but at test, they were asked to report the two orientations not by performing their associated actions but by means of a mouse click on the circumference of the test dials. Action- and control-task trials were randomly intermixed, hence participants did not know in advance whether, on a given trial, they would be performing the action or the control task, as this became clear only at test, when the control task was cued by the letter M (for mouse) at the center of each test dial. Participants had 3500 ms to provide their answer in the control task, to account for the longer time needed to reach toward the mouse compared to directly reach toward the screen in the action task. In Experiment 2, for both the action and the control tasks, we sampled the orientations and orientation differences between the two bars in a different way compared to Experiment 1. In Experiment 1 we observed the largest effect of action condition when the orientation difference between the bars was ±22.5°. To increase the power of our study in replicating this action similarity-related repulsion effect, we therefore randomly sampled small orientation differences between 15° or 35°. For symmetry, we also only sampled large orientation differences between 145° and 165°. We expected to observe attraction in large orientation difference trials, but did not have any prediction about possible differences between the two action conditions for these trials. Within each block, for each combination of factors (i.e., action condition x task), we had an equal number of trials with small and large orientation differences between

bars. Moreover, within each block, for each combination of factors and for each group of orientation differences (i.e., small and large), we set the orientation of one of the two bars in a way that it could take any value between 0° and 359°, with the constraint that the selected orientation belonged with equal probability to one of the four circle quadrants. In this way, the whole stimulus space was evenly sampled, reducing the possibility of inducing behavioral biases toward a certain part of the circular space. Finally, we made sure that the action cues GRIP and SLIDE were equally often presented for each combination of action condition, task, and orientation difference group.

In Experiment 2, participants came to the lab on two consecutive days and performed 12 blocks on each day. Each block consisted of 48 trials: 32 trials for the action task and 16 for the control task. Of the 32 action task trials, 16 were same-action-condition trials and 16 were different-action-condition trials. Of the 16 control-task trials, eight were same-action-condition trials, while eight were different-action-condition trials. In the first session, the 12 blocks were preceded by three practice blocks of eight trials each: One block for the action task, one for the control task, and one in which action task and control task were randomly intermixed. This helped participants to learn the task more easily. At the start of the second session, participants practiced eight trials with the action and control task intermixed. In Experiment 2, we added three buffer trials at the beginning of each block, as here too, there were two types of blocks: *see-first-report-first* and *see-second-report-first* blocks. Across the two sessions, participants performed 1,224 trials, of which 1,152 were retained for the analysis.

Data Analysis. In Experiment 1, our main aim was to examine whether associating two oriented bars in VWM with a different action would lead to differential repulsion or attraction memory biases compared to when the two orientations were associated with the same action. In Experiment 2, we asked whether the greater repulsion biases observed in Experiment 1 when coupling different actions to the two bars in VWM were attributable to a mere motor bias or to a bias which was more perceptual in nature. In both experiments, we therefore focused our analysis on the error bias, which we computed by first calculating the absolute error in terms of degree angles between the reported orientation and the encoded one, and by then attributing a sign to such error while considering the orientation difference between the two memory items [cf. (14)]. We assigned a positive value to errors which indicated a repulsion between the two bars concurrently held in memory, that is, when participants reported the two orientations as being more different than they actually were. We then assigned a negative value to errors indicating attraction, hence when participants reported the two orientations as being more similar than they actually were.

In both Experiment 1 and Experiment 2, we excluded those trials in which participants did not accurately remember the to-be-performed actions and those trials in which participants lifted the index finger of their dominant hand from the screen during the memory delay stage (in Experiment 1, 3.70% of all trials; in Experiment 2, 5.85%). In Experiment 1, we also excluded those trials in which the difference between orientations was 180° (32 trials per participant). Moreover, for both experiments, we excluded all those trials in which participants reported the orientations with an error which deviated more than 2.5std from the participant's mean error of each combination of action condition and orientation difference (i.e., in Experiment 1: 8.55% of trials) or each combination of action condition, orientation difference, and task (i.e., in Experiment 2: 3.55% of trials) (see later in the text for a description of such variables). If after data cleaning fewer than 358 (Experiment 1) or 806 (Experiment 2) trials (~70% of the total number of trials) remained for the analyses, we replaced the participant. In total, we replaced no participants in Experiment 1 and three in Experiment 2.

Error Biases. All data analyses were conducted in RStudio 2022.07.2. Experiment 1 was an exploratory study, as we did not have a clear hypothesis regarding the direction of the investigated effect. Our statistical analysis for Experiment 1 hence reflects its exploratory nature. First, we ran a linear mixed-model analysis on the report biases by grouping together the responses to any angle below 90°, which we called small orientation differences, and the responses to angles greater than 90°, which we called large orientation differences. We did not consider responses to 90° in this analysis, as in previous studies this orientation difference presented on average virtually null biases in the first report (e.g., ref. 14). We were mainly interested in analyzing data coming

from the first report, as here responses could not be biased by the execution of a previous motor response, as could be the case for the second report. We therefore ran a separate model for each report. We followed the protocol delineated in (37). First, we considered the most complex model in terms of fixed effects, therefore considering both the variables orientation difference (small/large) and action condition (same/different), and their interaction. We then identified the random part of the model and the best variance structure for its fixed effects. Only once the random part and the variance structure were defined, we determined the best combination of fixed effects by dropping one fixed effect at the time. For the first report, we found that the winning model was one with 1) the fixed-effects *action condition* and *orientation difference*, but not their interaction, 2) a random intercept per participant and random slope for the variable *orientation difference*, 3) a specified variance structure for the variable *orientation difference* [error bias = action condition + orientation difference, ~ (1 + orientation difference | participant), weights = varComb(varIdent(form = ~1| orientation difference))]. Although the interaction between *action condition* and *orientation difference* was not significant, given the exploratory nature of the experiment, we also ran Sidak-corrected post hoc tests between the different and the same action conditions for each level of the orientation difference variable, with the purpose of better characterizing our results. For the second report, we found that the best model was identical to that identified for the first report, except that this time the interaction between *orientation difference* and *action condition* was also included (error bias = action condition * orientation difference, ~ [1 + orientation difference | participant], weights = varComb(varIdent(form = ~1| orientation difference))]. For the second report as well, we ran Sidak-corrected post hoc tests to better characterize the interaction.

Based on Experiment 1, in Experiment 2, we expected to find a significant difference between the two action conditions for small orientation differences. Specifically, as stated in our preregistration (https://doi.org/10.17605/OSF.IO/M2YFB), we expected more repulsion in the different action compared to the same action condition for small orientation differences, while we did not have a clear hypothesis for the direction of the effect at large orientation differences. We predicted that if the difference in repulsion bias observed in Experiment 1 reflects a sensory change in the mnemonic representations for items that are associated with a different vs same action plan, then we would find that not only in the action task but also in the control task, participants would display greater repulsive biases in the different action condition than in the same action condition. Given the specificity of our hypotheses and as preregistered, after selecting the best model fitting the data, we first looked at planned comparisons between the different and same action condition for small orientation differences in both the action and the control task. For the first report, we found that the winning model was one with the fixed-effects *action condition*, *orientation difference*, *task* (action/control), and the interaction between the variables *action condition* and *orientation difference*. Moreover, the model included the random intercept per *participant*, the random slope *orientation difference*, and the variance structure for the variables *action condition*, *task*, and their interaction [error bias = action condition + orientation difference + task + action condition: orientation difference, ~ (1 + orientation difference | participant), weights = varComb(varIdent(form = ~1| action condition * task))]. For the second report, we found that the winning model counted the variables *task*, *orientation difference*, *action condition* and the interactions between *orientation difference* and *action condition*, and between *task* and *orientation difference*. The random part included the intercept for the variable *participant* and the random slopes of *orientation difference*, *action condition*, and their interaction; moreover, we modeled the variance of the variables *task*, *orientation difference* and their interaction [error bias = action condition + orientation difference + task + action condition: orientation difference + task: orientation difference, ~ (1 + orientation difference * action condition| participant), weights = varComb(varIdent(form = ~1| orientation difference * task))].

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