Head-direction tracks internally directed selective attention in visual working memory

Jude L. Thom[#1], Anna C. Nobre[1,2], Freek van Ede*[2,3], Dejan Draschkow[#*1,2]

[1] *Department of Experimental Psychology, University of Oxford, Oxford, United Kingdom*
[2] *Oxford Centre for Human Brain Activity, Wellcome Centre for Integrative Neuroimaging, Department of Psychiatry, University of Oxford, Oxford, United Kingdom*
[3] *Institute for Brain and Behavior Amsterdam, Department of Experimental and Applied Psychology, Vrije Universiteit Amsterdam, Netherlands.*
* *These authors contributed equally*
[#] *Corresponding authors: Jude Thom (jude.thom@linacre.ox.ac.uk ; https://orcid.org/0000-0002-6204-2949), Dejan Draschkow (dejan.draschkow@psy.ox.ac.uk ; https://orcid.org/0000-0003-1354-4835)*

Abstract

We shift our gaze even when we orient attention internally to visual representations in working memory. Here, we show the bodily orienting response associated with internal selective attention is widespread as it also includes the head. In three virtual reality (VR) experiments, participants remembered two visual items. After a working memory delay, a central colour cue indicated which item needed to be reproduced from memory. After the cue, head movements became biased in the direction of the memorised location of the cued memory item – despite there being no items to orient towards in the external environment. The head-direction bias had a distinct temporal profile from the gaze bias. Our findings reveal that directing attention within the spatial layout of visual working memory bears a strong relation to the overt head orienting response we engage when directing attention to sensory information in the external environment. The head-direction bias further demonstrates common neural circuitry is engaged during external and internal orienting of attention.

Introduction

We often move our head when orienting attention overtly to sensory information in our environment. We can also orient attention covertly to items in the external world, in the absence of large head movements. For example, you may be watching a film whilst directing your attention towards your phone when you are expecting a phone call. Covertly orienting attention to items in the environment is accompanied by subtle overt manifestations of orienting behaviour, including directional biases in eye-movements [1–4].

We can also orient attention internally to items maintained in the spatial layout of visual working memory [5–10]. Similar to attentional selection in the external world, internal selective attention within visual working memory is associated with small directional eye-movement biases toward the memorised locations of attended items [11–14] (see also: [15,16]). This overt manifestation of internal selective attention occurs despite the external absence of the attended memory items and even when memorised item location is not required for task performance.

Head movements are also affected by covert attentional selection. Covert attention activates neck muscles [17,18] and the lag between head and eye movements is affected by the congruency of covert attentional cues [19], suggesting that the head and eyes may each be modulated or involved when directing covert attention towards items in the external environment. The potential involvement of head and eye movements may be separable, provided differences in the neurophysiological pathways controlling head and eye movements [20]. Therefore, it is important to explore both the head and eyes when asking questions relating to bodily orienting behaviour, since the head and eyes may contribute in distinct ways as part of a broader bodily orienting response [21].

If the overt ocular traces of covert selective attention in memory [11–14] are part of a more widespread bodily orienting response, then directing internal selective attention to items in working memory should also be accompanied by head movement. Therefore, it is conceivable that internally directed selective attention in working memory may not only be associated with small orienting behaviour of the eyes but also of the head.

To test whether such an embodied orienting response of eyes and head occurs during internally directed spatial attention, we analysed head- and eye-tracking data from a VR study investigating selective attention in visual working memory [11]. The head-tracking data, which was not interrogated previously, allowed us to address whether head movements are similarly biased towards the memorised locations of selectively attended items in visual working memory.

Materials and Methods

The data were collected as part of a study which used VR to examine different spatial frames of working memory in immersive environments [11]. To answer the current research question, we focused on head-movement data, which were not analysed in the previous study [11]. In this section, we describe the experimental materials and methods relevant to the focus of our research question. Information on additional manipulations which were not the focus of the current study can be found in [11].

Participants

We analysed data from three experiments (1-3). Each experiment had a sample size of 24 human volunteers. The participants in Experiments 1-2 were the same and were recruited separately from the participants in Experiment 3 (Experiments 1-2: mean age 25.8 years, age range 18-40 years, all right-handed, 20 female; Experiment 3: mean age 25.5 years, age range 19-37 years, 1 left-handed, 13 female). All participants had normal or corrected-to-normal vision. Participants provided written consent prior to the experiments and were compensated £10 per hour. Protocols were approved by the local ethics committee (Central University Research Ethics Committee #R64089/RE001 and #R70562/RE001).

Materials and Apparatus

Participants wore an HTC Vive Tobii Pro VR headset. Participants held the controller in their dominant hand, using their index finger and thumb to press response buttons. The positions of the headset and hand controller were recorded by two Lighthouse base stations, using 60 infrared pulses per second. These pulses interacted with 37 sensors on the headset and 24 sensors on the controller, providing sub-millimetre tracking accuracy. The headset contained a gyroscope and accelerometer, allowing for the precise recording of head rotational positions (accuracy < 0.001°). The headset contained a binocular eye tracker (approximately 0.5° visual angle accuracy, sampling rate 90 Hz). Two OLED screens displayed the environment in the headset (refresh rate 90 Hz, 1080 x 1200 pixels, field-of-view 100° horizontal × 110° vertical). We used Vizard (Version 6) to render and run the VR experimental environment on a Windows desktop computer.

In the VR environment, participants stood in the centre of a virtual room (4.2 m long, 4.2 m wide, 2.5 m tall) with a grey concrete texture applied to the four walls (Fig 1A). The working memory items were two coloured bars (length 0.5 m, diameter 0.05 m), which appeared 2 m in front of the participant. One item appeared 1 m to the left, on the front wall. The other appeared 1 m to the right, on the front wall. The centres of the items were 2 m apart.

Procedure and Tasks

Participants were given time to get used to the headset, controller, lab room, and virtual environment before the experiments began. This included 24 practice trials in which participants learnt how to make responses and became familiar with the trial sequence.

In all experiments, each trial consisted of the same main steps (Fig 1A). At the beginning of each trial, participants stood upright in the centre of the room and fixated a fixation cross with their eyes (size 12 cm x 12 cm). After 500 ms of fixation, two items appeared (as described in Materials and Apparatus). Both items

were slanted at independently drawn random orientations (ranging 0-180°). One item was red, and the other was blue. The colour of each item was allocated randomly on each trial. Participants were instructed to remember the orientations of the items during a delay.

Following the delay, the fixation cross changed to a blue or red colour – matching the colour of the left or right item in working memory. The colour cue indicated the item for which the orientation response needed to be reproduced (target item) and signalled that participants could initiate the response when ready. The target item was randomly selected in each trial irrespective of orientation, location, and colour. Participants had unlimited time to recall the orientation of the target item and activate a response.

Once a response was initiated, participants had 2000 ms to dial in the orientation of the target item, using the controller. The response activation generated a dial made of two handles (diameter 0.06 m) on a circular torus (diameter 0.5 m, tube diameter 0.02 m), which was centred at the fixation cross. This dial was only present during the response stage. The handles moved along the torus according to the controller's orientation, allowing participants to reproduce the orientation of the target item. Participants confirmed their response by pressing the trigger button of the controller. Immediately after confirming their response, the dial disappeared, and participants received feedback on their performance. Feedback was presented on a 0-100 scale, with 100 being perfect reproduction of the target item's orientation. This number was presented above the fixation cross for 500 ms. Feedback was followed by a 700 ms delay. After this delay there was an inter-trial interval randomly selected between 1500 and 2000 ms.

There were 100 stationary trials in each experiment (50 left target item, 50 right target item). Trials were presented in 5 blocks with 20 trials each. The headset re-calibrated the gaze tracking at the beginning of each block. Participants completing Experiments 1-2 performed both tasks in the same session, in counterbalanced order. Each experiment lasted approximately one hour, and the full session lasted approximately two hours.

Data Analysis

Tracking and behavioural recordings were stored in a comma-separated variable file (CSV), for each participant. We used R Studio (Version 1.3.1093, 2020) to analyse the data. The data files and analysis scripts are available online here: *https://github.com/thomjude/headbias_sharing.git*

The "head-direction" variable was the horizontal distance between the fixation cross and the intersection of a vector projecting from the front of the headset and the virtual wall. The "gaze-direction" variable was the horizontal distance between the fixation cross and the gaze-fixation point on the virtual wall (averaged between both eyes). For an illustration of the head-direction variable, see Fig 1B.

We also recorded yaw, roll, and translation of the headset (Fig 2) to look at the contributions of these individual components of the head-direction vector. Head yaw is the rotational position around the head's vertical axis. Head roll is the rotational position around the head's longitudinal axis. For example, rotating your head whilst reading a large sign left-to-right would be reflected in changing yaw values and tilting your head to read a slate sign would change roll values. Translation refers to the horizontal movement of the entire headset (e.g., if the participant moved their entire head to the left whilst looking straight ahead). Together, yaw, roll, and translation are components which can influence the horizontal head-direction.

We epoched the data from 500 ms before cue to 2000 ms after cue. We smoothed all time-course data over 4 samples (44 ms smoothing window average). The data in each trial was baselined by subtracting the mean value between 200 and 0 ms before the cue from all values in the trial. We excluded trials in which head-direction or gaze direction exceeded 0.5 m (half the distance to the locations of the memoranda) in either direction of the fixation cross during the epoched time window (-500 ms – 2000 ms) to remove the effect of large outliers. We also excluded trials with a yaw or roll of over 20 degrees in either direction (average percentage of excluded trials per participant: M 5.96%, SE 0.01; total percentage of excluded trials: 16.58%).

We compared behaviour between right- and left-item trials in the three experiments separately to check if the side of the target item affected performance. We used within-subject ANOVAs to check for effects of target side on error and response time. To follow-up findings (including null findings), we conducted Bayesian t-tests [65] with the default settings of the 'Bayes Factor' package [66]. Bayes-factor values either indicated evidence in favour of the alternative hypothesis ($B_{01} > 3$), in favour of the null hypothesis ($B_{01} < 0.33$) or suggested inconclusive evidence ($B_{01} > 0.3$ and $B_{01} < 3$)[67].

Next, we plotted the change in the time-course data (head-direction, yaw, roll, translation, gaze direction) from baseline (-200 – 0 ms before cue), separately for left- and right-item trials. To increase sensitivity and interpretability, we constructed a single measure of 'towardness'. Towardness aggregated horizontal movement towards the target item on each trial, combining leftward movement in left-item trials and rightward movement in right-item trials. A positive towardness indicated a horizontal position in the direction of the target item. Towardness for each time step was given by the trial-average horizontal position in right-item trials minus the trial-average horizontal position in left-item trials (where position values left of fixation were negative) divided by two. The same procedure for calculating towardness was used for all time-course head and gaze data. We used this towardness variable to determine the significance of the biased movements (compared to zero), using "cluster-depth" [22] cluster-based permutation tests [68,69]. We ran the cluster-based permutation testing in R with the 'permuco' package [22,23].

Results

Participants performed a visual working memory task in a VR environment while we tracked their head and gaze. In the task, participants remembered the orientations of two coloured bars, one on the left and one on the right, for a short delay (Fig 1A). After the working memory delay, a colour cue indicated the bar for which participants needed to reproduce the orientation on a dial.

Head-direction tracks internal selective attention in visual working memory

After the colour change in the fixation cross (cue onset), horizontal head-direction became biased in the direction of the memorised external location of the cued memory item (Figs 1B-1E). This head-direction bias occurred although there was no information present or expected at the external location corresponding to the memorized item after the colour cue.

The bias in horizontal head movement was leftwards in trials in which the colour cue corresponded with the memory item that had been encoded on the left ("left item"), and rightwards in trials in which the colour cue corresponded with the memory item that had been encoded on the right ("right item"). Fig 1B illustrates the nature of the head-direction bias in left- and right-item trials. The average head-direction after the colour cue for trials with cued memory items on the left and right are plotted separately in Fig 1C. To quantify this head-direction bias and express it as a single measure, we combined the head-direction bias from left and right item trials into a measure of towardness [13]. The towardness of the head-direction became evident starting at approximately 500ms after the onset of the cue (Fig 1D; cluster $p < .05$; largest cluster ranging between 1167-1367 ms).

To explore the scale of the head-direction bias, we calculated density maps of single-trial head-direction values, and subtracted density maps between left-and right-item trials. To focus on the window of interest, we considered all head-direction values when the head-direction bias was most pronounced (500-2000 ms; Fig 1E). This revealed the subtle nature of the head-direction bias. Participants did not move their head-direction all the way to the memorised locations of the items (circles in Fig 1E). Instead, participants subtly moved their head-direction towards the memorised item locations (< 0.5° of rotation), with head-direction biases remaining close to fixation – akin to the type of directional biases we have recently observed in gaze [11–14]. The properties of the head-direction bias were similar across three slightly different versions of the task (Exp 1-3) and are plotted separately in Fig S1. There were no significant effects of target side (left vs right) on behavioural performance (error and response time) in any of the experiments (see Fig S2).

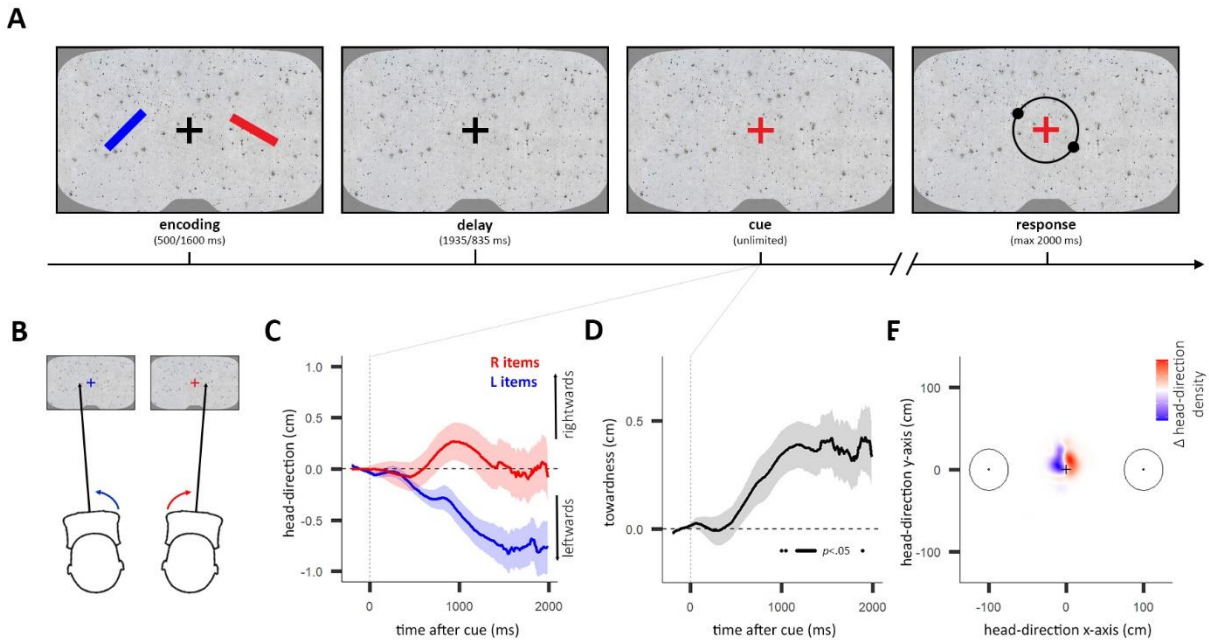

Fig 1. Head-direction tracks attentional selection in visual working memory. A) Participants remembered the orientations of two coloured items in a VR environment. After a delay, the fixation cross retrospectively cued the colour of the target item. Participants then reported the orientation of the target item using the controller. **B)** We recorded the shift in head-direction. **C)** Average head-direction for left (L) and right (R) item trials as a function of time after cue. Shading indicates ± 1 SEM. **D)** Towardness of head-direction as a function of time after cue. Horizontal line indicates a significant difference from zero, using cluster-based permutation testing. Shading indicates ± 1 SEM. **E)** Density map showing the difference in head-direction density between right minus left item trials (500-2000 ms after cue). Circles indicate the locations of the items during encoding. **C-E)** Data aggregated from Exp 1-3. See Fig S1 for separate plots of head-direction and head-direction towardness as functions of time after cue for Exp 1-3.

The head-direction bias is driven by movement along the head's yaw axis

To determine which head-movement components contributed to the head-direction bias, we separately analysed yaw, roll, and translation. Like the head-direction vector, yaw followed the movement pattern of head-direction in left- and right-item trials, which was also confirmed by a significantly positive towardness cluster (Fig 2A; $p < .05$, cluster-corrected). Roll showed a non-significant towardness trend (Fig 2B; $p > 0.999$ for all clusters of the full time window) and translation did not move towards the memorised locations of the cued memory items (Fig 2C; $p > 0.257$ for all clusters of the full time window). Thus, the leftwards-rightwards rotation along the head's yaw axis was the primary factor contributing to the directional head-direction bias when selectively attending items in our visual working memory task.

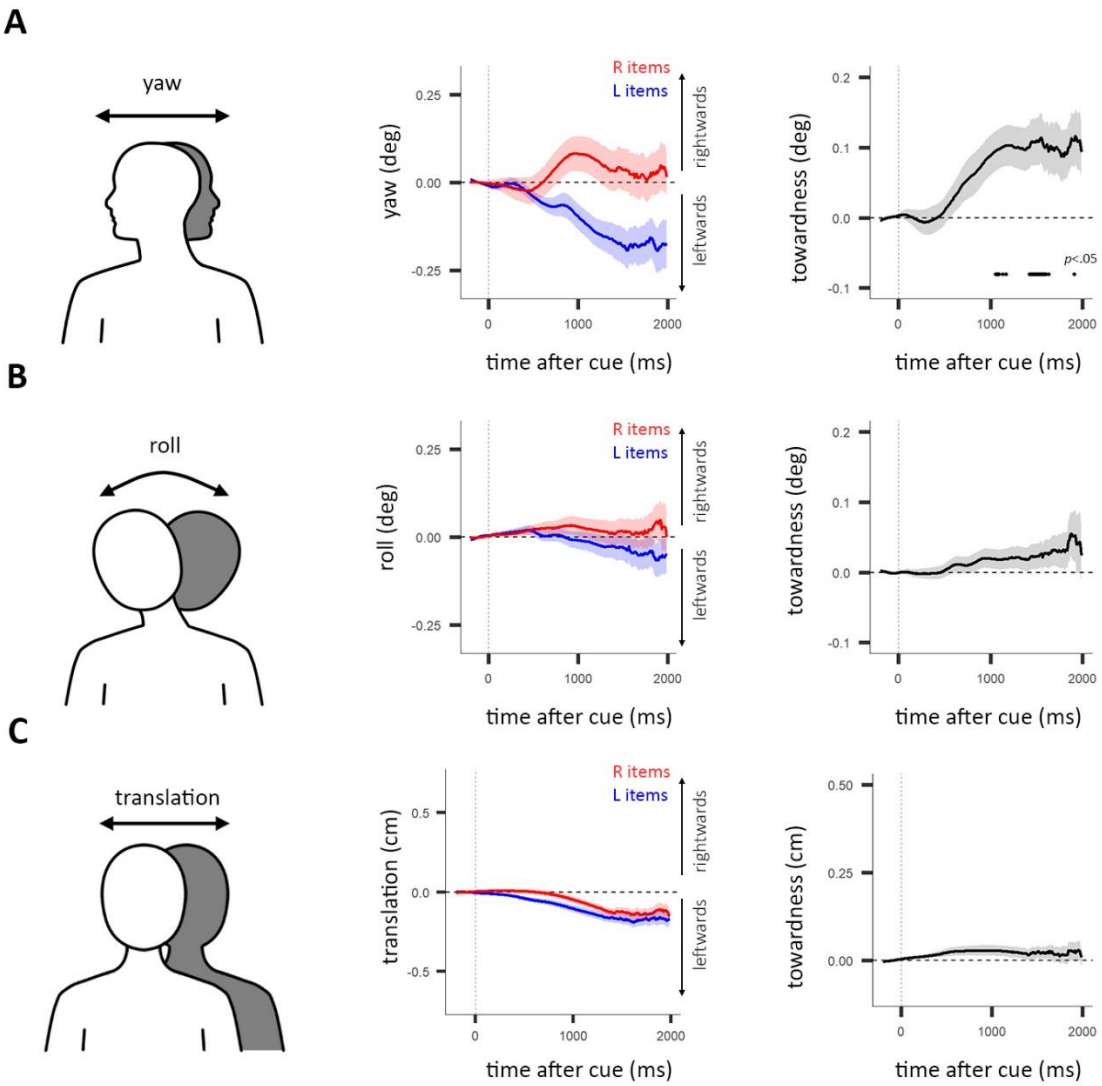

Fig 2. Biased movement in yaw, roll, and translation. A) Left panel) Yaw as a component of head-direction. Centre panel) Average yaw for left (L) and right (R) item trials as a function of time after cue. Shading indicates ± 1 SEM. Right panel) Towardness of yaw as a function of time after cue. Horizontal line indicates a significant difference from zero, using cluster-based permutation testing. Shading indicates ± 1 SEM. **B)** Same as A, using roll instead of yaw. **C)** Same as A, using translation instead of yaw. **B-C)** Lack of horizontal lines in towardness plots in the right panels indicates no significant difference from zero was found, using cluster-based permutation testing with a threshold of $p<.05$.

The head-direction bias is accompanied by a gaze bias in the same direction

Like the head-direction, gaze direction moved towards the location of the cued item during internal selective attention (as we have previously reported in this dataset [11] as well as in prior datasets [7,12–14]). Fig 3A shows the leftwards and rightwards movement of gaze direction in left and right item trials. The gaze towardness was significantly different from zero after the cue ($p < .05$ between 400-1244 ms, cluster-corrected; Fig 3B). We focused our statistical analyses on the data aggregated across the individual experiments to improve sensitivity, noting that the gaze direction for left and right trials and towardness over time were similar between all three experiments (Exp 1-3; S1),

In Fig 3B, we also overlay the head-direction bias for a descriptive comparison. While the head-direction bias and gaze bias both acted toward the memorised location of the cued item, Fig 3B shows the bias lags behind the gaze bias. The largest significant cluster [22,23] for the gaze bias was significant at ~400ms, whereas the significant time window for the head-direction bias started more than a full second after the cue ($p < .05$; head: 1167-1367 ms, gaze: 400-1244 ms).

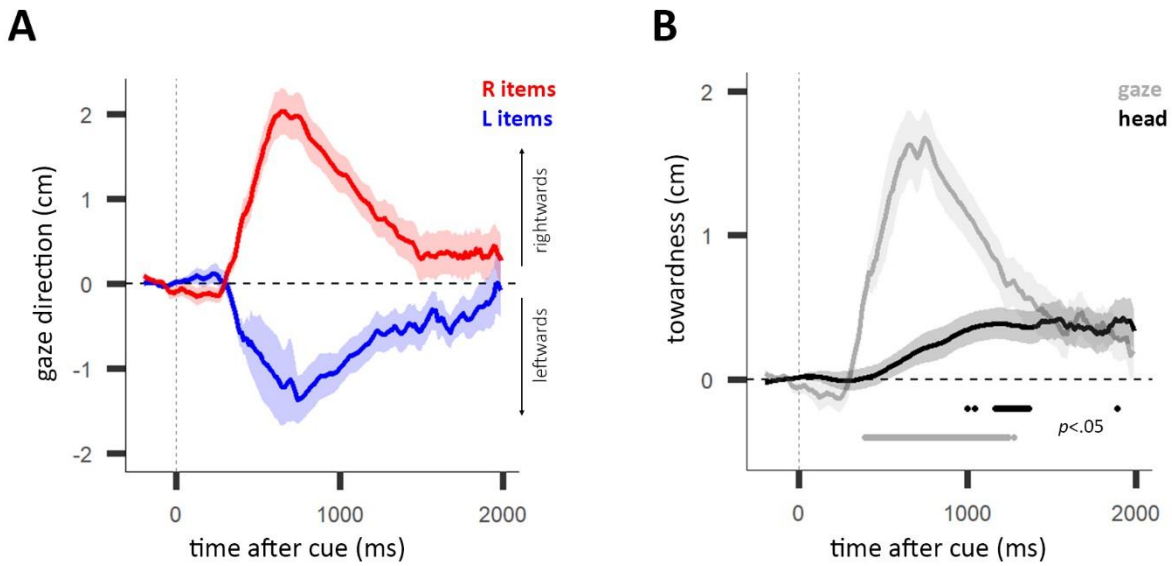

Fig 3. The gaze bias and the head-direction bias. A) Average gaze direction for left (L) and right (R) item trials as a function of time after cue. Shading indicates ± 1 SEM. **B)** Towardness of gaze direction (gaze) and head-direction (head) as a function of time after cue. Horizontal line indicates a significant difference from zero, using cluster-based permutation testing. Shading indicates ± 1 SEM.

Discussion

Our results reveal that, like eyes, the head-direction tracks internally directed selective attention inside visual working memory. This manifests in directionally biased head movements towards the memorised location of attended memory items. The head-direction bias in our task was predominantly driven by the head's rotation around its yaw-axis and accompanies a gaze bias in the same direction. The observed head-direction bias suggests there is a general bodily orienting response during internal selective attention – suggesting brain structures involved in orienting of the eye and head are also engaged when orienting within the internal space of working memory.

The head-direction and gaze biases may reflect bodily signatures which are part of a widespread orienting response activating brain areas that are involved in both overt and covert attentional selection. Indeed, there is good evidence that the brain's oculomotor system is also involved in covert orienting of spatial attention [1–4,24–27]. Moreover, from an evolutionary perspective, it is conceivable that our ability to orient internally evolved gradually from external orienting behaviours of the head and eyes – maybe relying on overlapping neural circuitry [28]. From this perspective, the observed subtle bias in head- and eye-movements may reflect an inevitable 'spill over' from activating neural circuitry that has evolved to orient both internally and externally [29].

It is maybe surprising to find this head-direction bias, even when attention is directed internally and without any items in the environment toward which to orient. However, in natural settings, there can be a behavioural benefit of orienting the head and eyes towards the locations of selected memory items. In our task, no subsequent behavioural goal benefited from orienting towards the memorised location of the attended memory item. However, in daily life, items rarely disappear from their location in the external environment. Thus, orienting the eyes and head towards the memorised locations of selected items may serve to guide future behaviour, such as resampling items. In fact, people often resample items in a naturalistic working memory task, when it is easy to do so [30,31]. In this way, the small head-direction and gaze biases towards selected items in working memory may reflect a natural tendency to engage in action in relation to selected memoranda [32–36], even if there was no incentive for this in our task.

In natural behaviour, head and eye movements are intrinsically functionally linked [37–39] and head movements can even compensate for eye movements when people cannot make saccades [40,41]. This coordinated

relationship between head- and eye-movements motivated us to look at both the head and eyes when exploring bodily orienting responses. The head-direction bias revealed here implicates that neural circuitry which controls head movements – at least along the yaw axis – is recruited by, and potentially overlaps with, circuitry that directs internal selective attention. In fact, previous research has found overlap between brain areas thought to process spatial attention and eye and head movements. For example, the frontal eye fields (FEF) play a role in directing attention and controlling eye movements [25,42–45]. Alongside attentional selection and eye movements, the FEF also contributes to head movements. The hemodynamic activity of the FEF responds to head movement [46] and microstimulation to the FEF in primates results in head movement [47,48]. Additionally, modulation of activity in the superior colliculus – an area shown to process not only eye [49–51] but also head movements [52,53] – also affects the deployment of covert attention [54–56]. Our results complement these findings, with the head-direction and gaze biases suggesting overlap between neural circuitry and activity governing attentional selection inside working memory, eye movements, and head movements.

However, control of the head and eye is not entirely linked, as shown by differences in the neurophysiological pathways controlling eye and head movements [52,57,58]. This is demonstrated in the distinct temporal profiles of the head-direction and gaze biases presented here which highlight the value of looking at multiple components of what might be a widespread bodily orienting response involving the head and eyes.

Finally, by using VR, we were able to measure the head-direction bias alongside the gaze bias as participants' head, eye, and body were unconstrained. To date, the benefits of VR have been appreciated most prominently by researchers studying naturalistic human navigation, ethology, and long-term memory [59–64]. Our present findings further highlight the benefits of using VR (combined with eye- and head-tracking) to study bodily orienting behaviour [11,31] related to internal cognitive processes, as showcased here for internal attentional focusing in working memory.

Acknowledgements

This research was funded by a Wellcome Trust Senior Investigator Award (104571/Z/14/Z) and a James S. McDonnell Foundation Understanding Human Cognition Collaborative Award (220020448) to A.C.N, an ERC Starting Grant from the European Research Council (MEMTICIPATION, 850636) to F.v.E., and by the NIHR Oxford Health Biomedical Research Centre. The Wellcome Centre for Integrative Neuroimaging is supported by core funding from the Wellcome Trust (203139/Z/16/Z). The funders had no role in study design, data collection and analysis, decision to publish or preparation of the manuscript. This research was funded in part by the Wellcome Trust [Grant numbers 104571/Z/14/Z, 203139/Z/16/Z]. For the purpose of open access, the author has applied a CC BY public copyright license to any Author Accepted Manuscript version arising from this submission.

References

1. Engbert, R. & Kliegl, R. Microsaccades uncover the orientation of covert attention. *Vision Research* **43**, 1035–1045 (2003).
2. Hafed, Z. M. & Clark, J. J. Microsaccades as an overt measure of covert attention shifts. *Vision Research* **42**, 2533–2545 (2002).
3. Hafed, Z. M., Lovejoy, L. P. & Krauzlis, R. J. Modulation of Microsaccades in Monkey during a Covert Visual Attention Task. *Journal of Neuroscience* **31**, 15219–15230 (2011).
4. Yuval-Greenberg, S., Merriam, E. P. & Heeger, D. J. Spontaneous Microsaccades Reflect Shifts in Covert Attention. *Journal of Neuroscience* **34**, 13693–13700 (2014).
5. Griffin, I. C. & Nobre, A. C. Orienting Attention to Locations in Internal Representations. *Journal of Cognitive Neuroscience* **15**, 1176–1194 (2003).
6. Murray, A. M., Nobre, A. C., Clark, I. A., Cravo, A. M. & Stokes, M. G. Attention Restores Discrete Items to Visual Short-Term Memory: *https://doi.org/10.1177/0956797612457782* **24**, 550–556 (2013).
7. van Ede, F. & Nobre, A. C. Toward a neurobiology of internal selective attention. *Trends in Neurosciences* **44**, 513–515 (2021).
8. Manohar, S. G., Zokaei, N., Fallon, S. J., Vogels, T. P. & Husain, M. Neural mechanisms of attending to items in working memory. *Neuroscience & Biobehavioral Reviews* **101**, 1–12 (2019).

9. Souza, A. S. & Oberauer, K. In search of the focus of attention in working memory: 13 years of the retro-cue effect. *Attention, Perception, & Psychophysics 2016 78:7* **78**, 1839–1860 (2016).
10. Olivers, C. N. L., Peters, J., Houtkamp, R. & Roelfsema, P. R. Different states in visual working memory: when it guides attention and when it does not. *Trends in Cognitive Sciences* **15**, 327–334 (2011).
11. Draschkow, D., Nobre, A. C. & van Ede, F. Multiple spatial frames for immersive working memory. *Nature Human Behaviour 2022* 1–9 (2022) doi:10.1038/s41562-021-01245-y.
12. van Ede, F., Deden, J. & Nobre, A. C. Looking ahead in working memory to guide sequential behaviour. *Current Biology* **31**, R779–R780 (2021).
13. van Ede, F., Chekroud, S. R. & Nobre, A. C. Human gaze tracks attentional focusing in memorized visual space. *Nature Human Behaviour 2019 3:5* **3**, 462–470 (2019).
14. van Ede, F., Board, A. G. & Nobre, A. C. Goal-directed and stimulus-driven selection of internal representations. *Proceedings of the National Academy of Sciences* **117**, 24590–24598 (2020).
15. Ferreira, F., Apel, J. & Henderson, J. M. Taking a new look at looking at nothing. *Trends in Cognitive Sciences* **12**, 405–410 (2008).
16. Spivey, M. J. & Geng, J. J. Oculomotor mechanisms activated by imagery and memory: eye movements to absent objects. *Psychological Research 2001 65:4* **65**, 235–241 (2001).
17. Corneil, B. D., Munoz, D. P., Chapman, B. B., Admans, T. & Cushing, S. L. Neuromuscular consequences of reflexive covert orienting. *Nature Neuroscience 2008 11:1* **11**, 13–15 (2007).
18. Corneil, B. D. & Munoz, D. P. Overt Responses during Covert Orienting. *Neuron* **82**, 1230–1243 (2014).
19. Khan, A. Z., Blohm, G., McPeek, R. M. & Lefèvre, P. Differential influence of attention on gaze and head movements. *Journal of Neurophysiology* **101**, 198–206 (2009).
20. Gandhi, N. J. & Sparks, D. L. Dissociation of Eye and Head Components of Gaze Shifts by Stimulation of the Omnipause Neuron Region. *https://doi.org/10.1152/jn.00252.2007* **98**, 360–373 (2007).
21. Corneil, B. D. & Munoz, D. P. Overt Responses during Covert Orienting. *Neuron* **82**, 1230–1243 (2014).
22. Frossard, J. & Renaud, O. The cluster depth tests: Toward point-wise strong control of the family-wise error rate in massively univariate tests with application to M/EEG. *NeuroImage* **247**, 118824 (2022).
23. Frossard, J. & Reneud, O. Package "permuco." (2021) doi:10.1016/j.csda.2010.02.015.
24. Deubel, H. & Schneider, W. X. Saccade target selection and object recognition: Evidence for a common attentional mechanism. *Vision Research* **36**, 1827–1837 (1996).
25. Moore, T. & Fallah, M. Microstimulation of the Frontal Eye Field and Its Effects on Covert Spatial Attention. *https://doi.org/10.1152/jn.00741.2002* **91**, 152–162 (2004).
26. Moore, T. & Armstrong, K. Selective gating of visual signals by microstimulation of frontal cortex. *Nature* **421**, 370–373 (2003).
27. Nobre, A. *et al.* Functional localization of the system for visuospatial attention using positron emission tomography. *Brain : a journal of neurology* **120 (Pt 3)**, 515–533 (1997).
28. Cisek, P. Resynthesizing behavior through phylogenetic refinement. *Attention, Perception, & Psychophysics 2019 81:7* **81**, 2265–2287 (2019).
29. Strauss, D. J. *et al.* Vestigial auriculomotor activity indicates the direction of auditory attention in humans. *eLife* **9**, 1–18 (2020).
30. Ballard, D. H., Hayhoe, M. M. & Pelz, J. B. Memory Representations in Natural Tasks. *Journal of Cognitive Neuroscience* **7**, 66–80 (1995).
31. Draschkow, D., Kallmayer, M. & Nobre, A. C. When Natural Behavior Engages Working Memory. *Current Biology* **31**, 869-874.e5 (2021).
32. Boettcher, S. E. P., Gresch, D., Nobre, A. C. & Ede, F. van. Output planning at the input stage in visual working memory. *Science Advances* **7**, 8212–8236 (2021).
33. Heuer, A., Ohl, S. & Rolfs, M. Memory for action: a functional view of selection in visual working memory. *Visual Cognition* **28**, 388–400 (2020).
34. Olivers, C. N. L. & Roelfsema, P. R. Attention for action in visual working memory. *Cortex* **131**, 179–194 (2020).
35. van Ede, F. Visual working memory and action: Functional links and bi-directional influences. *https://doi.org/10.1080/13506285.2020.1759744* **28**, 401–413 (2020).
36. van Ede, F., Chekroud, S. R., Stokes, M. G. & Nobre, A. C. Concurrent visual and motor selection during visual working memory guided action. *Nature Neuroscience 2019 22:3* **22**, 477–483 (2019).
37. Foulsham, T., Walker, E. & Kingstone, A. The where, what and when of gaze allocation in the lab and the natural environment. *Vision Research* **51**, 1920–1931 (2011).
38. Land, M. F. Vision, eye movements, and natural behavior. *Visual Neuroscience* **26**, 51–62 (2009).
39. Solman, G. J. F., Foulsham, T. & Kingstone, A. Eye and head movements are complementary in visual selection. *Royal Society Open Science* **4**, (2016).
40. Ceylan, M., Henriques, D. Y. P., Tweed, D. B. & Crawford, J. D. Task-Dependent Constraints in Motor Control: Pinhole Goggles Make the Head Move Like an Eye. *Journal of Neuroscience* **20**, 2719–2730 (2000).

41. Gilchrist, I. D., Brown, V. & Findlay, J. M. Saccades without eye movements. *Nature 1997 390:6656* **390**, 130–131 (1997).
42. Bruce, C. J. & Goldberg, M. E. Physiology of the frontal eye fields. *Trends in Neurosciences* **7**, 436–441 (1984).
43. Robinson, D. A. & Fuchs, A. F. Eye movements evoked by stimulation of frontal eye fields. *https://doi.org/10.1152/jn.1969.32.5.637* **32**, 637–648 (1969).
44. Taylor, P. C. J., Nobre, A. C. & Rushworth, M. F. S. FEF TMS Affects Visual Cortical Activity. *Cerebral Cortex* **17**, 391–399 (2007).
45. Grosbras, M. H. & Paus, T. Transcranial magnetic stimulation of the human frontal eye field: Effects on visual perception and attention. *Journal of Cognitive Neuroscience* **14**, 1109–1120 (2002).
46. Petit, L. & Beauchamp, M. S. Neural Basis of Visually Guided Head Movements Studied With fMRI. *https://doi.org/10.1152/jn.00988.2002* **89**, 2516–2527 (2003).
47. Elsley, J. K., Nagy, B., Cushing, S. L. & Corneil, B. D. Widespread Presaccadic Recruitment of Neck Muscles by Stimulation of the Primate Frontal Eye Fields. *https://doi.org/10.1152/jn.00386.2007* **98**, 1333–1354 (2007).
48. Chen, L. L. & Walton, M. M. G. Head Movement Evoked By Electrical Stimulation in the Supplementary Eye Field of the Rhesus Monkey. *https://doi.org/10.1152/jn.00510.2005* **94**, 4502–4519 (2005).
49. Schiller, P. H. & Stryker, M. Single-unit recording and stimulation in superior colliculus of the alert rhesus monkey. *https://doi.org/10.1152/jn.1972.35.6.915* **35**, 915–924 (1972).
50. Wurtz, R. & Albano, J. Visual-Motor Function of the Primate Superior Colliculus. *http://dx.doi.org/10.1146/annurev.ne.03.030180.001201* **3**, 189–226 (2003).
51. Wurtz, R. H. & Goldberg, M. E. Superior Colliculus Cell Responses Related to Eye Movements in Awake Monkeys. *Science* **171**, 82–84 (1971).
52. Bizzi, E., Kalil, R. E. & Morasso, P. Two modes of active eye-head coordination in monkeys. *Brain Research* **40**, 45–48 (1972).
53. Corneil, B. D., Olivier, E. & Munoz, D. P. Neck Muscle Responses to Stimulation of Monkey Superior Colliculus. I. Topography and Manipulation of Stimulation Parameters. *https://doi.org/10.1152/jn.2002.88.4.1980* **88**, 1980–1999 (2002).
54. Krauzlis, R. J., Lovejoy, L. P. & Zénon, A. Superior Colliculus and Visual Spatial Attention. *http://dx.doi.org/10.1146/annurev-neuro-062012-170249* **36**, 165–182 (2013).
55. Lovejoy, L. P. & Krauzlis, R. J. Inactivation of primate superior colliculus impairs covert selection of signals for perceptual judgments. *Nature Neuroscience 2009 13:2* **13**, 261–266 (2009).
56. Müller JR, Philiastides MG & Newsome WT. Microstimulation of the superior colliculus focuses attention without moving the eyes. *Proceedings of the National Academy of Sciences of the United States of America* **102**, 524–529 (2005).
57. Horn, M. R. van *et al.* Eye-head gaze shifts. in *The Oxford Handbook of Eye Movements* vol. 1 (Oxford University Press).
58. Oommen, B. S. & Stahl, J. S. Amplitudes of head movements during putative eye-only saccades. *Brain Research* **1065**, 68–78 (2005).
59. Stangl, M. *et al.* Boundary-anchored neural mechanisms of location-encoding for self and others. *Nature 2020 589:7842* **589**, 420–425 (2020).
60. Topalovic, U. *et al.* Wireless Programmable Recording and Stimulation of Deep Brain Activity in Freely Moving Humans. *Neuron* **108**, 322-334.e9 (2020).
61. Mobbs, D. *et al.* Promises and challenges of human computational ethology. *Neuron* **109**, 2224–2238 (2021).
62. Helbing, J., Draschkow, D. & Võ, M. L. H. Search superiority: Goal-directed attentional allocation creates more reliable incidental identity and location memory than explicit encoding in naturalistic virtual environments. *Cognition* **196**, 104147 (2020).
63. Li, C.-L., Aivar, M. P., Kit, D. M., Tong, M. H. & Hayhoe, M. M. Memory and visual search in naturalistic 2D and 3D environments. *Journal of Vision* **16**, 9–9 (2016).
64. Draschkow, D. & Võ, M. L.-H. Scene grammar shapes the way we interact with objects, strengthens memories, and speeds search. *Scientific Reports 2017 7:1* **7**, 1–12 (2017).
65. Rouder, J. N., Speckman, P. L., Sun, D., Morey, R. D. & Iverson, G. Bayesian t tests for accepting and rejecting the null hypothesis. *Psychonomic Bulletin & Review 2009 16:2* **16**, 225–237 (2009).
66. Richard D. Morey *et al.* Package "BayesFactor." *[Internet] https://CRAN.R-project.org/package=BayesFactor* (2021).
67. Kass, R. E. & Raftery, A. E. Bayes factors. *Journal of the American Statistical Association* **90**, 773–795 (1995).
68. Maris, E. & Oostenveld, R. Nonparametric statistical testing of EEG- and MEG-data. *Journal of Neuroscience Methods* **164**, 177–190 (2007).
69. Sassenhagen, J. & Draschkow, D. Cluster-based permutation tests of MEG/EEG data do not establish significance of effect latency or location. *Psychophysiology* **56**, (2019).

Supplementary information

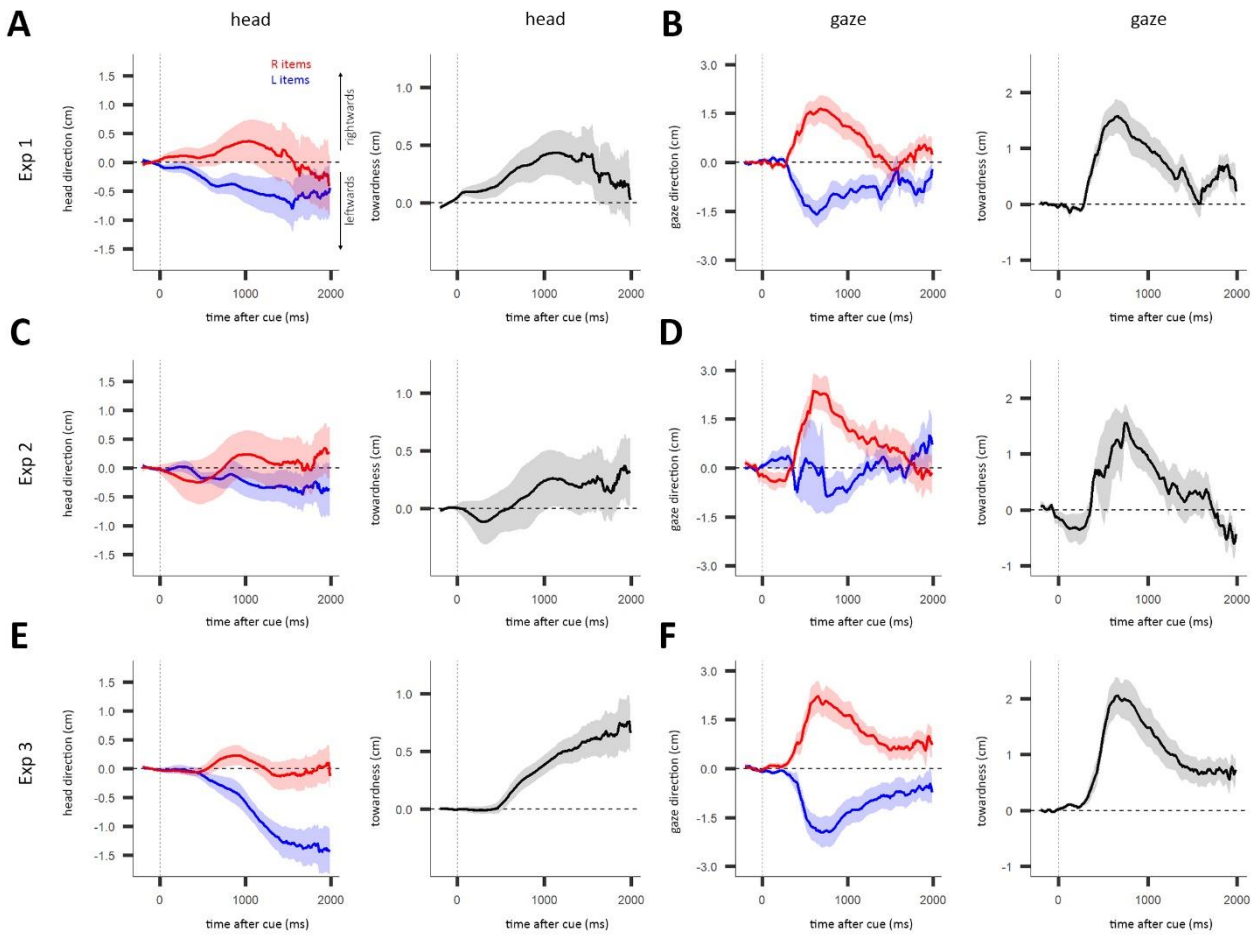

Fig S1. The head and gaze biases for Experiments 1-3. A) Left panel) Average head-direction for left (L) and right (R) item trials as a function of time after cue, using data from Exp 1. Right panel) Towardness of head-direction as a function of time after cue, using data from Exp 1. **B)** Same as A, using gaze direction instead of head-direction. **C)** Same as A, using data from Exp 2. **D)** Same as B, using data from Exp 2. **E)** Same as A, using data from Exp 3. **F)** Same as B, using data from Exp 3. **A-F)** Shading indicates ± 1 SEM.

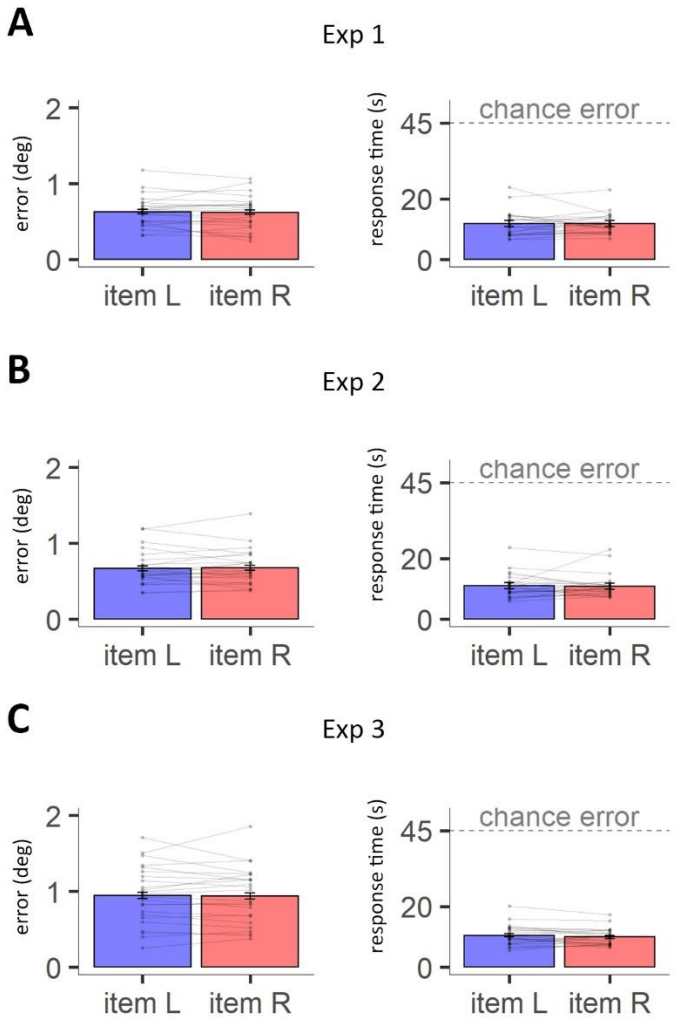

Fig S2. Similar performance in left and right item trials. A) Left panel) Plot comparing the mean error between left item (item L) and right item (item R) trials, for each participant in Exp 1. Connected pairs of points are the means of the same participant. Error bars represent a 95% confidence interval. Right panel) Same as Left panel, for response time instead of error. **B)** Same as A, using data from Exp 2. **C)** Same as A, using data from Exp 3. There was no significant effect of target side on mean error in any of the experiments, Exp 1: (F (1,23) = 0.01, p = .934), Exp 2: (F (1,23) = 0.02, p = .881), Exp 3: (F (1,23) = 2.04, p = .166). For Exp 1-2, the follow-up Bayes t-test supported the null-hypothesis, suggesting the errors are similar between left and right item trials, Exp 1: (B_{01} = 0.22), Exp 2: (B_{01} = 0.22). Similarly, there was no significant effect of target side on mean response time in any of the experiments, Exp. 1: (F (1,23) = 0.19, p = .671), Exp 2: (F (1,23) = 0.23, p = .633), Exp 3: (F (1,23) = 0.07, p = .793). For Exp 1-3, the follow-up Bayes t-tests supported the null-hypothesis, suggesting the response times are similar between left and right item trials, Exp 1: (B_{01} = 0.23), Exp 2: (B_{01} = 0.24), Exp 3: (B_{01} = 0.22).