Efficient spatial coding for covert selective attention

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ABSTRACT

Selective attention enables the prioritisation of task-relevant visual information, including among internal contents in working memory. Studies targeting the foundational mechanisms of covert selective attention often consider situations where to-be-attended and to-be-ignored visual contents are presented or memorised in distinct directions from fixation – rendering direction sufficient for covert selection. Yet, in everyday life, direction alone is typically insufficient for selection because multiple potential objects of attention compete along any given direction. To gain insight into the mechanisms of covert attention when direction is sufficient versus insufficient for selection, we cued participants to select memorised visual items that were encoded near or far from fixation while manipulating whether direction was sufficient (no competition along direction) or insufficient (competition along direction) for selection. To uncover the nature of spatial coding for covert attention, we tapped into directional biasing of fixational gaze behaviour as a non-invasive read-out of the brain's oculomotor system – a brain system widely recognised for its contribution to covert attention. This unveiled the principle of 'efficient spatial coding' whereby covert internal selective attention considers just direction when sufficient and considers the distance of the attended target only when necessary.

KEYWORDS

Covert attention, Working memory, Spatial coding, Oculomotor system, Internal selection

INTRODUCTION

Attention enables the selection and prioritisation of task-relevant sensory information from the external world [1–5] as well as among internal contents held in working memory [6–11]. In psychology and neuroscience, studies targeting the foundational mechanism of selective covert attention often consider situations where to-be-attended and to-be-ignored visual contents are presented or memorised in distinct directions from fixation. In such situations, covertly selecting the relevant content might be achieved by orienting attention in the appropriate direction. Yet, in crowded environments encountered in everyday life, direction alone is usually insufficient for arriving at to-be-attended visual contents because multiple potential objects of attention may exist – and compete for attention – along any given direction from current fixation. Here we reveal that covert selective attention is deployed differently when direction is sufficient versus when it is insufficient for covertly selecting relevant visual content.

Several prior studies, that considered situations when direction is sufficient for selection, have suggested that attentional deployment can proceed similarly irrespective of whether covertly attended contents are close or far from fixation. For example, invariance to the distance (eccentricity) of visual targets has been reported for various neural signatures of covert selective attention (e.g., [12–14]). In similar vein, a study [15] showed how the spatial biasing of fixational eye-movements – a behavioural oculomotor signature of covert attentional orienting (cf. [15–20]) – depended on target direction, regardless of distance. Such findings directly hint at a mechanism whereby covert attention may arrive at relevant visual targets simply by orienting in the appropriate direction, irrespective of target distance. Yet, as clarified above, direction is often *not* sufficient for selection.

To gain insight into the mechanisms of covert attentional shifting when direction is sufficient versus insufficient for selection, we employed an internal-selective-attention task as a model [6,8,18,21]. In this task-setting, attention is inherently "covert" as it is directed to internal representations held within the spatial lay-out of visual working memory. Across three complementary experiments, we cued participants to select memorised items that were encoded near or far from fixation and, critically, manipulated whether direction was sufficient (no competition along direction) or insufficient (competition along direction) for arriving at cued visual memoranda. To unveil the nature of spatial coding employed by covert attention across our conditions, we tapped into directional biasing of fixational gaze behaviour (cf. [15,17,20,22]) as a non-invasive read-out of attentional coding in the brain's oculomotor system – a brain network widely recognised for its role in covert attention [23–27]. Our findings reveal that biases in fixational gaze behaviour depend on visual target distance, but, crucially, only when direction is insufficient for selection. This uncovers a surprising level of efficiency of covert attentional deployment that flexibly adapts to spatial demands – relying on direction when sufficient and only considering the distance of to-be-attended visual targets when necessary.

RESULTS

Participants performed a task that required selective attention to visual contents held in working memory (**Fig. 1a**). After encoding multiple visual items into working memory, a colour change of the central fixation dot (retro-cue) prompted participants to select the colour-matching item from working memory for an ensuing comparison to a test stimulus (clockwise/counter-clockwise judgment).

Cued memory items were either near (3 degrees) or far (6 degrees) from the central fixation dot. To study spatial coding for covert attention, we investigated spatial biases in fixational gaze behaviour (cf. [15,17,20,22,28,29]) during the attentional selection of near and far items. We did so across two conditions. In the first condition (**Fig. 1a**, labelled "direction sufficient"), the memory items were always at opposite sides from fixation, such that direction (left or right) alone was sufficient to arrive at the cued memory content, regardless of whether the item was near or far at encoding. In the second condition (**Fig. 1a**, labelled "direction insufficient"), there were always two items to each side of fixation, rendering

direction alone insufficient for the selection of the cued memory item – thus making the near/far distinction relevant for attentional selection.

Participants were able to perform this task and showed similar performance regardless of whether we cued the near or the far memory items (**Fig. 1b**). We found a main effect of the number of items on both accuracy ($F(24) = 43.85$, $p < 0.001$, partial $\eta^2 = 0.65$) and reaction times ($F(24) = 9.55$, $p = 0.005$, partial $\eta^2 = 0.29$) with slightly worse performance in the direction-insufficient condition that contained four instead of two memory items. When comparing performance as a function of the cued item's distance (3 versus 6 degrees) we found that participants were slightly faster to respond to the near items, ($F(24) = 5.42$, $p = 0.029$, partial $\eta^2 = 0.184$), but no significant difference in accuracy ((24) = 0.44, $p = 0.51$, partial $\eta^2 = 0.018$). Importantly, in contrast to what we will next be showing for fixational gaze behaviour (i.e. our main findings), we found no significant interaction between direction-sufficiency and target distance, neither on accuracy ($F(24) = 3.08$, $p = 0.09$, partial $\eta^2 = 0.11$) nor on reaction times ($F(24) < 0.001$, $p = 0.98$, partial $\eta^2 < 0.001$).

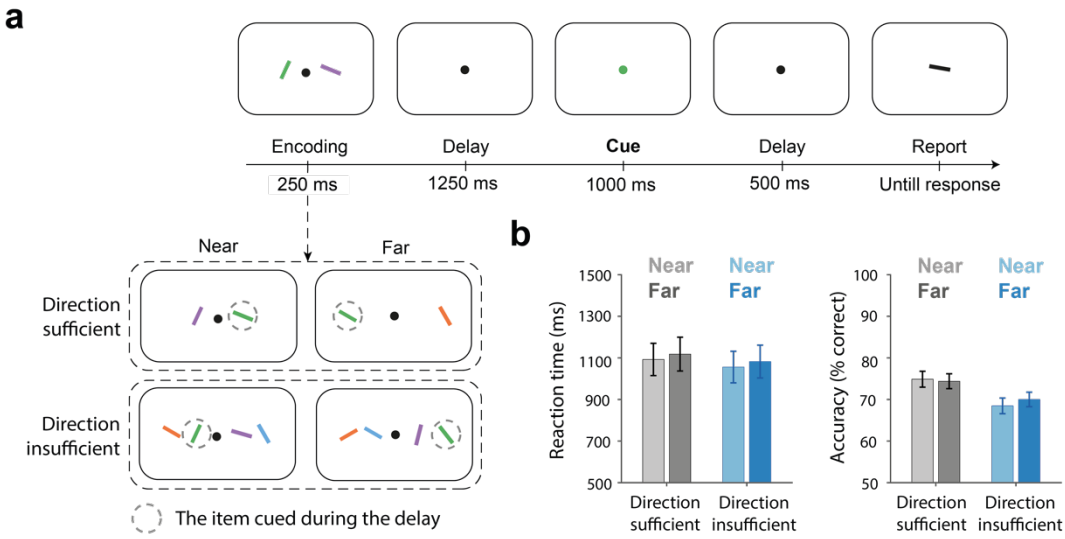

Figure 1. Cued selective-attention task and behavioural performance in Experiment 1. a) Task schematic (Top panel). Participants memorised two or four bars with different colours and orientations that appeared on each side of the central fixation dot. Following a delay, a colour change of the central fixation dot serving as a retro-cue. This retro-cue prompted participants to select the color-matching visual item from working memory in order to compare its orientation to a black bar in the upcoming test display. Upon the test display, participants were asked to report whether the cued memory item should be rotated clockwise or counter-clockwise to match the black bar. The task contained four key conditions (left bottom panel): (1) whether the cued memory item had been presented near (3°) or far (6°) from fixation, and (2) whether direction (left/right) was sufficient of insufficient to select the cued memory content. Dashed circles serve to highlight the cued item in the different conditions, and were never presented in the actual experiment. **b)** Behavioural performance. Mean reaction (left) and mean accuracy (right) in different task conditions. Error bars indicate ±1SEM calculated across participants (n = 25).

Fixational gaze behaviour reveals efficient attentional coding that adapts to spatial demands

Having established largely comparable performance between near and far items, we now turn to our central findings regarding oculomotor signatures of internal attentional selection across our four conditions. To do so, we turned to biases in fixational gaze behaviour that occur during the selection of internal contents, as we have demonstrated recently ([18,20,28,29]; building on [15,17]).

We found reliable biases in horizontal gaze position in each of our four key conditions (**Fig. 2**). When we cued an item in working memory that had been presented on the right of fixation at encoding (purple time courses in **Fig. 2**), gaze became biased toward the right. Likewise, when we cued a left memory item (green time courses in **Fig. 2**), gaze became biased toward the left. These biases occurred following our non-spatial colour retro-cue, in the absence of any stimulus being currently present or expected to the left or right of fixation – thus reflecting internal selection of the cued memory content.

Critically, when direction was sufficient for selection (**Fig. 2a**), the gaze bias looked similar regardless whether we cued the memory item that had been encoded near or far from fixation. However, when direction was insufficient for selection, the gaze bias became substantially larger when selecting the far item (compare left and right panels in **Fig. 2b**). This observation – an effect of distance only when direction is insufficient – is our central finding that we unpack further below.

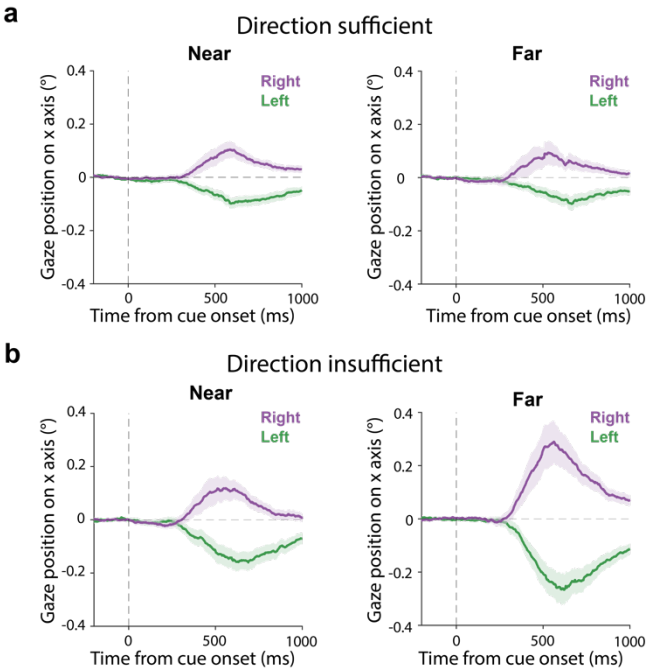

Figure 2. Spatial biases in gaze during internal selection of left and right memory items as a function of item distance and direction sufficiency. Time course of horizontal gaze position following cues directing attention to the right (purple line) and the left (green line) memory item when direction was sufficient (panel a) or insufficient (panel b) for selection. Selecting near or far items are split into left and right panels. Shading indicates ±1SEM calculated across participants (n = 25).

To quantify these biases and compare them between conditions, we combined trials with cues to left and right memory items to yield a single time course of "towardness" (as in [20,28,29]). Towardness time courses are shown in **Figure 3a-b**. When direction was sufficient for selection (**Fig. 3a**) we found that gaze after the retro-cue became significantly biased in the direction of the cued memory item, both when the cued item was near (cluster $P < 0.001$) or far (cluster $P < 0.001$). Critically, however, as appreciated by the overlay in **Figure 3a**, the bias was virtually identical, no matter whether the selected memory item was near or far at encoding (no clusters found). In contrast, when considering the selection of near and far items in the condition with two items to each side of fixation – rendering direction *insufficient* for selection – the gaze bias was clearly modulated by distance (**Fig. 3b**), with a larger bias when cued to select the further item. This was substantiated statistically: we again observed robust spatial biases in gaze position both when the cued item was near (cluster $P < 0.001$) and far (cluster $P < 0.001$), but this time we also found a robust difference between them (cluster $P < 0.001$; black horizontal line in **Fig. 3b**). These findings were further corroborated by a statistically significant interaction between the factors direction sufficient/insufficient and cued item near/far ($F(24) = 16.5$, $p < 0.001$, partial $\eta^2 = 0.41$), when considering the gaze bias collapsed over the a-priori defined window of 400-1000 ms after cue onset (a window chosen a-priori based on [20]).

Importantly, in all four conditions, the observed gaze biases originated from biases in fixational gaze behaviour. This can be appreciated by the heat maps (two-dimensional density plots) of the difference in gaze position following cues to select the left or right item, as depicted in **Figure 3d-e** (see

Supplementary Fig. 1 for the heatmaps of gaze density following for cues to left and right memory items separately).

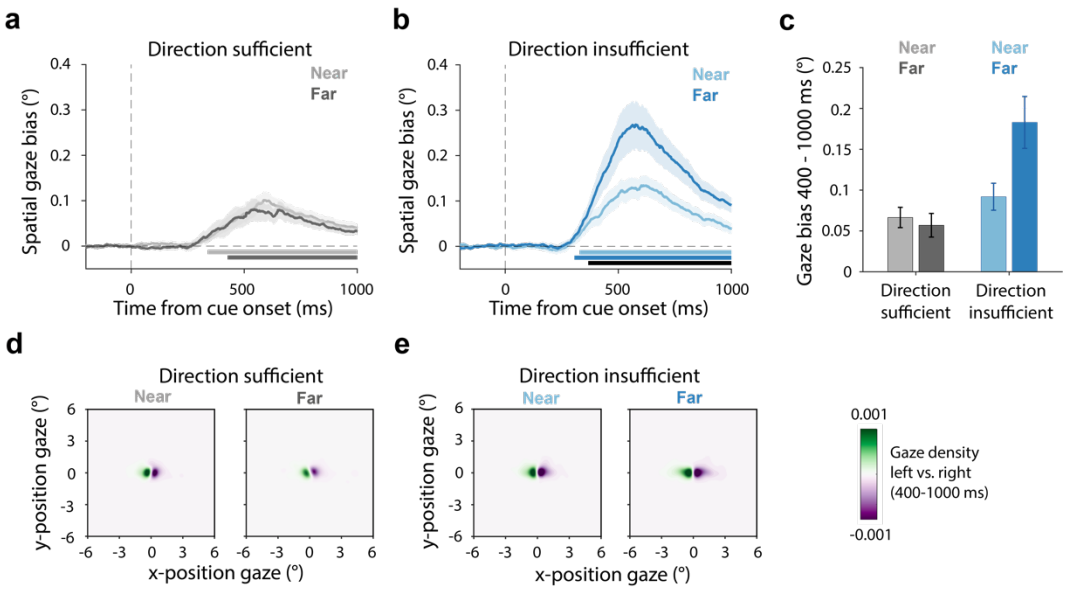

Figure 3. Fixational gaze bias is larger when selecting the far item but only when direction is insufficient for selection. a-b) Time courses of biases in gaze toward the location of the cued memory item when this item was near (light) or far (dark) from fixation as a function of whether direction is sufficient (panel **a**) or insufficient (panel **b**) for selection. See **Supplementary Fig. 1** for complementary gaze time courses in left and right trials separately. **c)** Gaze bias averaged across the a-priori defined window from 400 to1000 ms after the cue (based on [20]). **d-e)** Heatmaps of two-dimensional gaze position following the cue (in the 400-1000 ms post-cue window) when selecting the near (left panel) or far (right panel) items, separately for when direction was sufficient (**d**) or insufficient (**e**). Here we show the difference of this density between selecting left and right items. See **Supplementary Fig. 2** for heatmaps of gaze in left and right trials separately. Shading in panels a-b and error bars in panel c indicate ±1SEM calculated across participants (n = 25).

Replication of larger fixational gaze bias when selecting the further item when direction is insufficient

A central finding in Experiment 1 was the observation of larger fixational gaze biases when selecting the further item, when direction was insufficient for selection. To assess the reliability of this specific finding, we ran a replication experiment (Experiment 2) where we only included the direction-insufficient condition (yielding double the number of trials in this key condition). Importantly, this corroborated this central findings from Experiment 1, replicating a larger gaze bias when selecting the further item (**Fig. 4a**, cluster $P < 0.001$; **Fig. 4b**, $t(24) = 4.23$, $p < 0.001$, Cohen's $d = 0.85$). This was again driven by biases in fixational gaze behaviour (**Fig. 4c**).

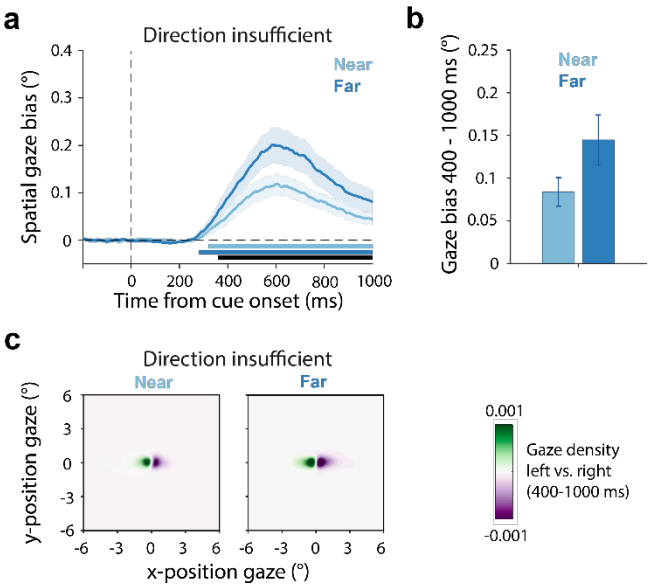

Figure 4. Experiment 2 replicates larger gaze biases when selecting the far item when direction is insufficient for selection. a) Time courses of biases in gaze toward the location of the cued memory item when this item was near (light) or far (dark) from fixation. **b)** Heatmaps of two-dimensional gaze position following the cue (in the 400-1000 ms post-cue window) when selecting the near (left panel) or far (right panel) items Shading and error bars indicate ±1SEM calculated across participants (n = 25).

Larger fixational gaze bias when selecting the further item is driven by spatial competition, not memory load

In Experiment 1, we manipulated spatial demands on internal selective attention while varying the number of items, with direction being sufficient for selection where there were two items (one left, one right), but insufficient when there were four (two left, two right). We designed Experiment 3 to again manipulate spatial demands (direction sufficient/insufficient) while keeping the memory load the same.

In Experiment 3, in the direction-sufficient condition, there were still four items, but these were each placed along separate axis from fixation (up, down, left, and right) such that direction was sufficient to select any one of them (**Fig. 5a**, left). In contrast, the direction-insufficient condition (**Fig. 5a**, right) was like before, with two items competing along each direction (e.g., two up and two down, or two left and two right), rendering direction insufficient for selection. Like in Experiment 1, participants were able to perform this task in all four conditions (**Supplementary Fig. 2**).

By equating memory load between our conditions of interest, we thus eliminated memory load as a potential mediating factor for our findings in Experiment 1. Importantly, our gaze data in Experiment 3 confirmed those from Experiment 1: again showing a larger gaze bias when selecting the further item, but only in condition where direction was insufficient for selection (**Fig. 5c**; cluster $P < 0.005$) and not in the direction-sufficient condition (**Fig. 5b**; no cluster). These findings were again corroborated by a significant interaction (**Fig. 5d**; $F(24) = 5.2$, $p = 0.032$, partial $\eta^2 = 0.18$), while heat maps in trials with horizontal and vertical configurations again revealed the fixational nature of the gaze biases under investigation (**Fig. 5e-f**).

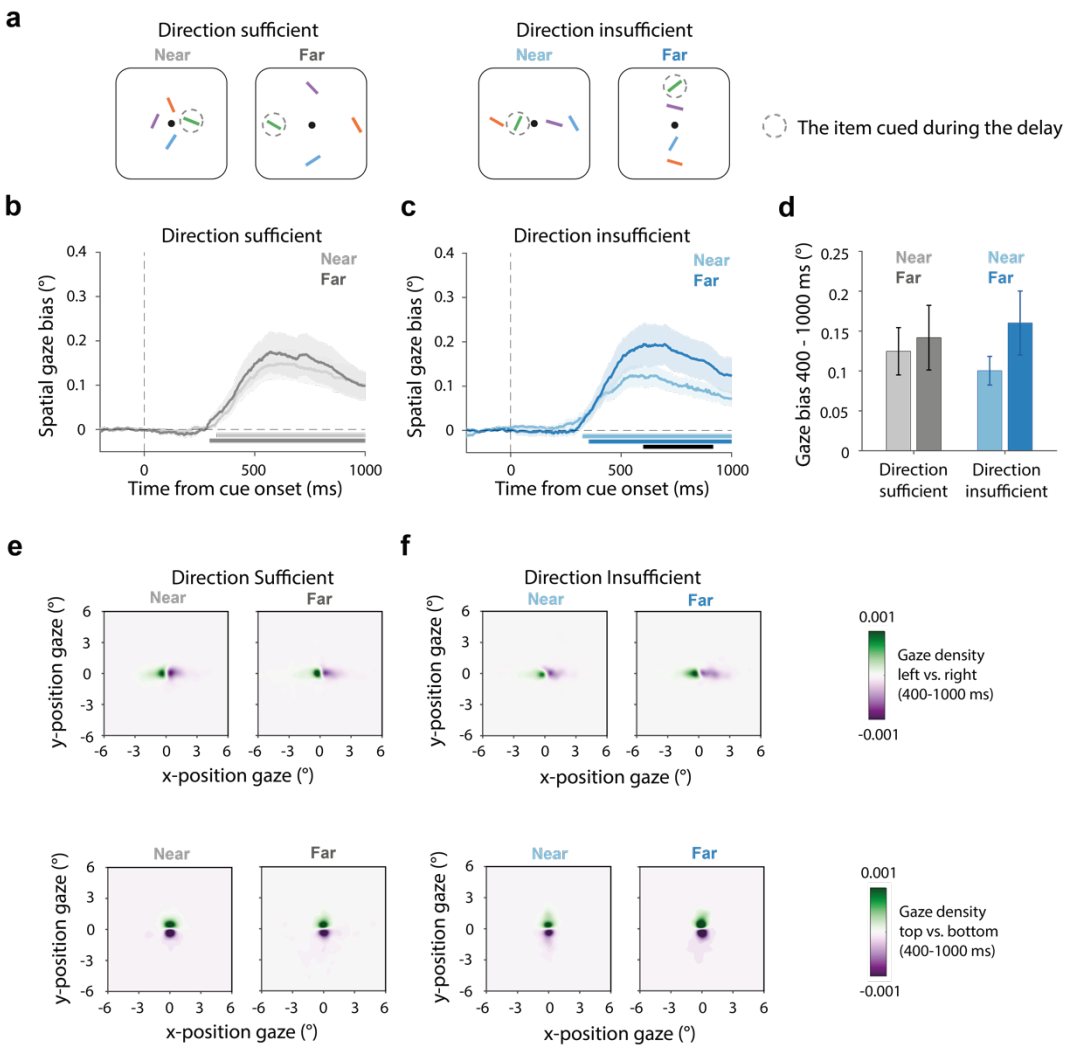

Figure 5. Larger fixational gaze bias when selecting the further item is driven by spatial competition, not memory load. a) Representative encoding displays used in Experiment 3. In Experiment 3 there were always 4 items but these could be placed either on opposite axes (2 items vertical, 2 items horizontal) to make direction sufficient for selection (left panel), or they could be placed on the same axis (4 items vertical or 4 items horizontal) rendering direction insufficient for selection (right panel). **b-c**) Time courses of biases in gaze toward the location of the cued memory item when this item was near (light) or far (dark) from fixation as a function of whether direction is sufficient (panel b) or insufficient (panel **c**) for selection. **d)** Gaze bias averaged across the a-priori defined window from 400 to1000 ms after the cue (based on [20]). **e-f)** Heatmaps of two-dimensional gaze position following the cue (in the 400-1000 ms post-cue window) when selecting the near (left panel) or far (right panel) items, separately for when direction was sufficient (panel e) or insufficient (panel f). Here we separately show the heat maps in trials where the cued item was on the horizontal axis (top panels) or vertical axis (bottom panels). Shading in panels b-c and error bars in panel d indicate ±1SEM calculated across participants (n = 25).

DISCUSSION

By manipulating spatial demands on internally directed selective attention, we uncover a novel principle of covert attention – that of efficient spatial coding. As revealed by spatial biases in fixational gaze behaviour, covert attention in the brain's oculomotor system considers just the attended target's direction when sufficient and additionally considers its distance only when necessary. As such, our data reveal a surprising degree of efficiency in oculomotor coding for covert internal selective attention that flexibly adapts to the spatial demands of the task at hand.

Selective attention is inherently about resolving competition, no matter whether dealing with sensory content or internal memory representations. Sensory inputs compete for processing and, likewise, internal memory representations compete for priority to guide upcoming behaviour. In both cases, selective covert attention serves to bias competition toward the important information to prioritise its

processing (e.g., [3,5,11,30,31]). In the laboratory, attentional competition is often conceptualised and investigated in situations in which few visual objects are presented, each in distinct directions from fixation (e.g., to the left and right). In such cases, objects compete with regard to the *direction* to which to shift attention, but not with regard to distance along any given direction. This is unlike crowded environments faced in everyday life where multiple stimuli often also compete for attention along any given direction from the current fixation. Our findings now reveal how spatial coding for covert attention – as read out from spatial biases in fixational gaze behaviour – is employed differently depending on whether direction is sufficient or insufficient for selection. This highlights how this specific type of competition is a relevant variable to consider in studies of covert selective attention.

By looking at biases in fixational gaze behaviour (cf. [18,20,28,29]), we indirectly gain insights into the role of the brain's oculomotor system in covert internal attention. Our findings build on, and are consistent with, a rich literature demonstrating a central contribution of the oculomotor system in directing covert selective attention [4,23,25,26], including within the spatial layout of working memory [32,33]. Importantly, our results also uniquely reveal how this role is not limited to simple "orienting responses", not even in deep-brain structures that project to the eyes. Indeed, one viable scenario is that the (subcortical) oculomotor system – with its long evolutionary origins – might predominantly serve to engage low-level orienting responses that move the organism in the appropriate direction (c.f. [16,34,35]). Yet, our data imply a more nuanced and more clever contribution of the oculomotor system in covert selective attention. This aligns with an increasing body of work demonstrating high-level cognitive processing within deep-brain structures, such as the superior colliculus [25,36,37], that has been implicated in spatial biases in fixational gaze behaviour that we report here [38].

Considering overt attention, which involves moving the eyes to fixate on a distant target, it is obvious that object distance is relevant, regardless of competition. For covert attention, however, selection could, in theory, be achieved by orienting attention in the appropriate direction, regardless of object distance. Indeed, without competition along direction, this is precisely what we found. We are not the only ones who found this: at least several other studies also reported a relative invariance to the eccentricity of visual targets, when considering neural measurements (e.g., [12–14]) as well as fixational gaze behaviour [15]. At the same, other studies did find neural modulations of covert attention as a function of target distance (e.g., [46–49]). Here, we unveil a key variable that may underpin whether or not this is found: whether direction is sufficient for selection or not. To be clear, our central conclusion does not regard whether mechanisms of covert attention *are* or *are-not* eccentricity dependent, but rather that the utilisation of visual-target eccentricity for covert internal attention is contingent on – and efficiently adapts to – the nature of the attentional demands at hand.

We investigated covert attention through an internal-selective-attention task in which attention was directed internally within the spatial layout of visual working memory. Though not as prevalent as the study of externally directed covert attention, this approach has advantages as a model system. Unlike when covertly attending to external visual items, when selecting visual items internally there are no visual items on the display to look at, thus taking away any incentive for overt shifts of gaze. Accordingly, any spatial biases in gaze behaviour are a relatively pure reflection of the deployment of covert attention, as mediated by of the brain's oculomotor system. It is also worth noting how, in this set-up, we are able to observe similar signatures reported in previous covert selective attention studies (e.g., [20,21,39,40]), including biases in fixational gaze behaviour that were of special interest here. The observed lack of a distance effect when direction was sufficient was, in fact, fully in line with a prior report during covert externally directed attention [15]. Nonetheless, a relevant question for future research is to extend our findings on internal selective attention to those on covert attention directed to visual objects in the external environment – an endeavour that may replicate current findings but that may also expose interesting differences.

Our results are complementary to a large body of work on the role of eccentricity in vision (e.g., [41–45] that is concerned, for example, with the change in resolution when moving from central to peripheral vision. Our task was not designed to tap into such differences. In fact, when comparing performance, we did not observe lower accuracy for the far item in any of the three experiments. Instead, our question regarded the principles subserving attentional selection of near and far items; specifically, whether distinct spatial-attention operations are employed when direction is sufficient or insufficient for selection. To the best of our knowledge, this question had not directly been addressed before.

By uncovering a novel principle of covert selective attention – that of efficient spatial coding – our work paves the way for future exploration. The use of fixational gaze behaviour as an indicator of covert selective attention, while powerful, has its limitations. Future studies could employ complementary, neural measures across different brain areas to extend our findings. For example, it is conceivable that the observed differentiation between purely-directional versus direction-plus-distance coding might not only vary between different task demands, but also between different brain areas even when the task demands are the same. This represents an exciting frontier for future research. Extending our findings to other types of spatial attention (e.g., spatially divided attention, attention in other modalities, attention to external stimuli, …) presents another direction for future research. The present set of studies thus breaks new ground that opens avenues to further unravel the principles and mechanisms of covert selective attention.

METHODS

Ethics. Experimental procedures were reviewed and approved by the local Ethics Committee of the Vrije Universiteit Amsterdam. Each participant provided written consent before participation and was reimbursed €10/hour.

Participants. We conducted three experiments with independent participant recruitment. Twenty-five healthy human volunteers participated in each experiment (Experiment 1: age range: 18-36; 7 male and 18 female; 22 right-handed and 3 left handed; Experiment 2: age range: 18-31; 6 male and 19 female; 23 right-handed and 2 left-handed; Experiment 3: age range: 18-27; 3 male, 21 female, and 1 non-binary; 24 right-handed and 1 left-handed). Sample size of 25 per experiment was set a-priori based on previous publications from our lab that relied on the same outcome measure [20,28,29]. In Experiment 1, to achieve the intended sample size, two participants were replaced due to chance-level performance. No participants required replacement in Experiments 2 and 3. All participants had normal or corrected-to-normal vision.

Stimuli and procedure. We developed a task in which direction was either sufficient or insufficient to arrive at cued visual objects in working memory. Below, we first explain the basic task, before turning to our two key manipulations.

In all three experiments, participants engaged in an internal covert selective attention task that required selection and prioritization of a visual item from working memory in order to compare the selected memory item to an upcoming test display (**Fig. 1a**). Each trial began with a start fixation (200 ms) followed by a brief (250 ms) encoding display where two or four bars with different colours and orientations appeared on either side of the fixation dot. To balance the display around the central fixation dot (that was 0.07° in radius), items always appeared on both sides of the screen with the same eccentricity (detailed below). After a 750 ms working-memory retention interval, the fixation dot changed colour for 1000 ms serving as a retro-cue. This retro-cue cued with 100% validity which memory item (i.e. the colour-matching item) would have to be compared to the upcoming test stimulus. The retro-cue was followed by another retention delay of 500 ms before the test display appeared. During the test display, a black bar appeared at the center of the screen. The test bar was always rotated between 10 to 20 degrees clockwise or counter-clockwise from the cued bar in memory. Participants reported whether the cued memory item should be turned clockwise or counter-clockwise to match the black bar in the test display. Participants received feedback immediately after response by a number ("0" for wrong, or "1" for correct) appearing for 250 ms slightly above the fixation dot. After the feedback, inter-trial intervals were randomly drawn between 500 and 1000 ms.

We had two key manipulations. We manipulated: (1) whether cued memory items were presented near (3°) or far (6°) from fixation, and (2) whether direction (e.g. toward left or right) was sufficient or insufficient for arriving at the cued memory content. In the "direction-sufficient" condition, items were presented only near or only far on opposite sides of fixation. In contrast, in the "direction-insufficient" condition, items competed, such that items were presented in the same direction at both near and far locations, on both sides of fixation. In Experiment 1 **(Fig. 1a)**, we only used horizontal placement of the items such that in the direction-sufficient condition the display contained two items that were each near *or* each far on either side of fixation. In contrast, the direction-insufficient condition contained four items that occupied both near *and* far on both sides of fixation – thus rendering distance necessary for selection. Experiment 2 replicated the direction-insufficient condition from Experiment 1. In Experiment 3 (**Fig. 5**), we used both horizontal and vertical placements of the memory items to manipulate direction sufficient/insufficient while keeping memory load constant. This time, we always used four items but placed all four items either along the same axis (all four horizontal or all four vertical) such that direction was insufficient, or on opposite axes (two items vertical, two items horizontal), such that direction was sufficient.

In the encoding display, bars were randomly assigned two or four distinct colours from the colours pool: green (RGB: 133, 194, 18), purple (RGB: 197, 21, 234), orange (RGB: 234, 74, 21), and blue (RGB: 21, 165, 234]). Bars were also drawn at distinct orientations ranging from 0° to 180° with a minimum difference of 20° between each other. During the test display, the gratings were always dark grey (RGB: 64, 64, 64) and were always oriented clockwise or counter-clockwise from the cued memory target, with a change in orientation randomly drawn between 10 to 20 degrees.

Experiment 1 consisted of 4 sessions, that each contained 10 blocks of 16 trials. Two key manipulations (with each two levels) were included in this experiment: eccentricity of the cued item (near versus far) and direction-sufficiency (direction-sufficient versus direction-insufficient). All these conditions were randomly mixed within each block. resulting in a total of 640 trials, with each of our four key conditions containing 160 trials. In Experiment 1, we initially aimed to collect 800 trials per participant. However, after two participants, we recognized that the experiment took too long, and we therefore reduced this to 640 trials per participant from participant 3 onward. Experiment 2 mirrored the structure of Experiment 1, retaining 4 sessions that each contained 10 blocks of 16 trials. Because Experiment 2 served to verify the findings from the direction-insufficient condition in Experiment 1, we only included this condition. Because the total number of trials remained 640, we were able to replicate the difference between selecting an item that was near or far (in the direction-insufficient condition) with double the number of trials as in Experiment 1. Finally, Experiment 3 expanded to include 5 sessions, with each session consisting of 5 blocks of 32 trials. The eccentricity and direction-sufficiency manipulations from the previous experiments were retained, but a new variable was introduced: the axis on which the target could appear (horizontal versus vertical). Due to this added variable, the total number of trials was increased from 640 to 800, such that each key condition contained 100 trials per participant.

Before the start of each experiment, participants practiced the task for approximately five minutes. Experiments 1 and 2 each required approximately 80 minutes to complete while Experiment 3 required approximately 100 minutes per participant.

Eye tracking. We used an EyeLink 1000 (SR Research, with 1000 Hz sampling rate) to track gaze from a single eye (right eye in all participants except 1 for which the left eye provided a better signal). The eye-tracker camara was positioned on the table approximately 5 cm in front of the monitor and approximately 65 cm in front of the eyes.

Gaze data were read intoMatlab using the Fieldtrip toolbox [50]. In line with previously established protocols [18,20,29], we first identified blinks and replaced identified blink clusters (extending 100 ms before and after detected blinks) with Not-a-Number (NaN) to effectively mitigate any artifacts from the blinks. Then, data were epoched from -1000 to +2000 ms relative to the onset of the retro-cue.

We focused our analysis on biases in gaze position over time. To investigate directional biasing of gaze by covert internal selective attention, we first baseline corrected the eye data by subtracting the mean data in the [-200 to 0 ms] baseline window. Then, we examined eye data on the x-axis when the cued item was on the left or the right side. In Experiment 3 we additionally analysed gaze position on the y-axis when the cued item was below or above fixation. Following our prior studies [20,28,29], we condensed the relevant data from the left/right and top/bottom trials into a single gaze time course of "towardness" that captured the bias of gaze towards the memorized location of the cued memory item. We could then compare this measure of towardness across our experimental conditions.

To complement the towardness time courses that we used for statistical evaluation, we aimed to visualize the fixational nature of the gaze bias (as in [20,28,29]). To this end, we created 2-dimensional (2D)

heat maps of gaze density. For this, we collated gaze-position values across time and trials (without averaging) using the data from the 400 to 1000 ms window after the retro-cue (a time window set a-priori based on [20]). We then counted the number of gaze samples within 0.1° x 0.1° bins, ranging from -6° to 6° and sampling the full 2D space in steps of 0.05°× 0.05°. To obtain a density map, we divided 2D gaze-position counts by the total number of gaze-position samples. For visualization purpose, density maps were smoothed using a 2D Gaussian kernel with an SD of 0.25° × 0.25° (using the built-in function "imgaussfilt" in MATLAB).

To represent the heat map associated with the directional gaze biases of interest, we first obtained the maps separately following cues to left, right, top, and bottom items and subtracted maps between conditions in which cues were associated with items in the opposite direction: left versus right and top versus bottom (see also **Supplementary Fig. 1**). We did this separately for each or our core experimental conditions (i.e., select near/far, and direction-sufficient/insufficient).

Statistical analysis. To evaluate and compare towardness time courses, we employed a cluster-based permutation approach [51], which is well-suited for evaluating multiple neighbouring time points while avoiding multiple comparisons. In this approach, we generated a permutation distribution by randomly permuting trial-average time courses at the participant level 10,000 times and identifying the largest clusters after each permutation. P-values were computed as the proportion of permutations where the largest post-permutation cluster exceeded the size of the observed cluster(s) in the original (non-permuted) data. Using Fieldtrip, we performed this permutation analysis with default cluster settings: grouping similarly-signed significant data points from a univariate t-test at a two-sided 0.05 alpha level, and defining cluster size as the sum of all t-values within the cluster.

Behavioral-performance data (accuracy and reaction times) were statistically evaluated using a two-way repeated-measures ANOVA with distance (near/far) and direction-sufficiency (sufficient/insufficient) as factors. ANOVA results were supplemented with post-hoc t-tests. As measures of effect size, we used partial eta squared for ANOVA and Cohen's d for follow-up t-tests. P-values of follow-up t-tests were Bonferroni corrected for multiple comparisons.

Data availability. All data will be made publicly available before publication.

Code availability. Relevant code associated with the here-presented analyses will be made available through GitHub before publication.

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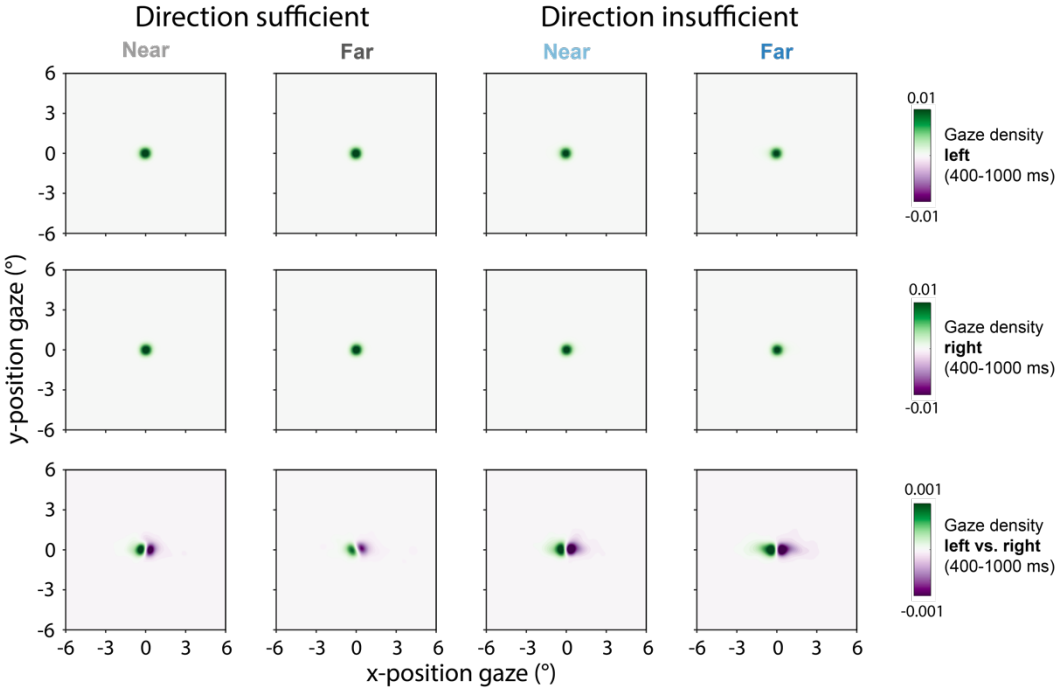
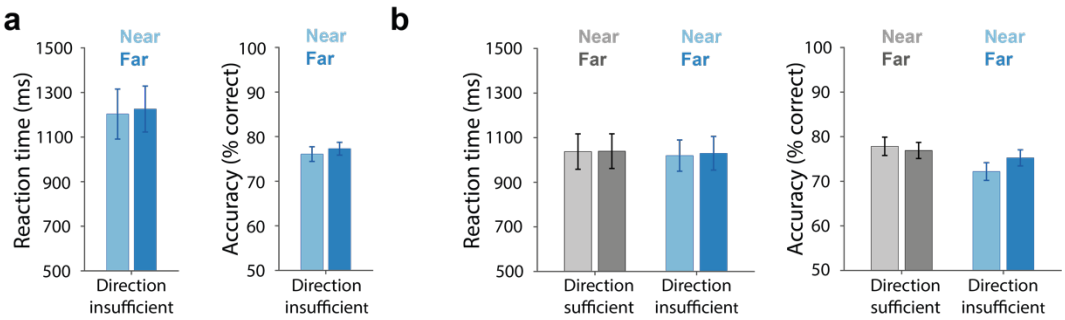
Supplementary Information – Figures S1-S2



Supplementary Figure 1. Complementary visualisation to the heat-maps of gaze density in main Figure 3d-e. Here we plot gaze density also separately following cues that direct attention to left (top row) and right (middle row) memory items, in addition to their difference (bottom row). In each row, the separate four panels shown the data for selecting the item near or far from fixation when direction is sufficient or insufficient.



Supplementary Figure 2. Behavioural performance in Experiments 2 and 3. a) In Experiment 2, participants showed similar performance regardless of whether we cued the near or the far memory items (Reaction time: $t(24) = -1.1$, $p = 0.28$, Cohen's $d = -0.219$; Accuracy: $t(24) = -1.23$, $p = 0.23$, Cohen's $d = -0.246$). **b)** In Experiment 3, for reaction time, there is no significant main effect of direction-sufficiency ($F(24) = 0.86$, $p = 0.36$, partial $\eta 2 = 0.035$) nor on item distance ($F(24) = 0.33$, $p = 0.57$, partial $\eta 2 = 0.013$). We also did not observe an interaction ($F(24) = 0.08$, $p = 0.78$, partial $\eta 2 = 0.003$). For accuracy, we found a significant main effect of direction-sufficiency ($F(24) = 29.02$, $p < 0.001$, partial $\eta 2 = 0.547$), but no main effect of item distance ($F(24) = 3.16$, $p = 0.09$, partial $\eta 2 = 0.116$). Here, we did find a significant interaction ($F(24) = 9.13$, $p = 0.006$, partial $\eta 2 = 0.276$). Post hoc analysis suggests that when direction was insufficient for selection, participants had higher accuracy when selecting the far item compared to the near item ($t(24) = -3.4$, $p_{Bonferroni} = 0.014$, Cohen's $d = -0.68$). However, when direction was sufficient for selection, participants showed similar performance regardless of whether we cued the near or the far memory item ($t(24) = 1.05$, $p_{Bonferroni} = 1$, Cohen's $d = 0.21$). This is possibly a result of more visual crowding for near items in the direction-insufficient condition in Experiment 3.